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SMALL-MAMMAL REGULATION OF VEGETATION STRUCTURE IN A TEMPERATE SAVANNA

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Abstract. Explanations for documented increases in woody plant dominance in grasslands and savannas of North America include atmospheric CO₂ enrichment and changes in climate, livestock grazing, and fire regimes. However, tree/shrub encroachment has also coincided with the eradication of a once widespread native herbivore, the black-tailed prairie dog (*Cynomys ludovicianus*). We used field experiments and repeat aerial photography to demonstrate that prairie dogs, and the herbivores and granivores associated with their colonies, probably maintained grassland and savanna by preventing woody species such as *Prosopis glandulosa* (honey mesquite) from establishing or attaining dominance.

Prosopis seed and pod disappearance was 3–99 times greater within prairie dog colonies. Ants were the primary agent of seed removal, whereas prairie dogs and associated vertebrates were the primary agents of pod removal. Survival of *Prosopis* seedlings protected from vertebrate herbivory was similar on and off prairie dog colonies (≈60%), whereas survival of unprotected seedlings was 3 times greater off- than on-colony. On-colony, prairie dogs and associated herbivores girdled and destroyed all *Prosopis* saplings within 2 d of planting; survival of 1-yr-old seedlings was reduced by 50% after 3 mo of exposure to on-colony herbivores. Despite high levels of woody plant seed disappearance and seedling herbivory, on-colony “seedling” reserves were substantial (950 plants/ha). Thus, prairie dogs and the fauna that occur on their colonies suppressed rather than eliminated *Prosopis* from the colony site. Removal of prairie dogs led to rapid development of *Prosopis* stands. Repeat aerial photography showed that *Prosopis* canopy cover on a colony eradicated in 1950 (27%) increased to a level (61%) comparable to that of off-colony *Prosopis* stands (65%) within 23 yr.

These data illustrate how transitions from grassland to woodland vegetation can be mediated by a rodent herbivore. They further demonstrate how purposeful or inadvertent removal of native herbivores can have unforeseen effects on plant species composition and landscape physiognomy. Investigations of environmental constraints on vegetation distribution and abundance should take into account the historical role of herbivores in shaping the present system. Inconsistencies among historic accounts of woody plant distribution and abundance in semiarid western North America may be resolved by considering population dynamics of prairie dogs. Widespread eradication of this formerly abundant rodent has eliminated a significant constraint to woody plant establishment on many semiarid grassland and savanna landscapes and has thereby facilitated transitions to shrubland and woodland states. Past land management designed to remove one perceived impediment to livestock production appears to have contributed significantly to development of another management problem that is now a major detriment to sustainable livestock production.

Key words: *competition; Cynomys ludovicianus; herbivory; mesquite; prairie dogs; Prosopis glandulosa; seed disappearance; seedling establishment; succession; tree–grass dynamics.*

INTRODUCTION

Historic increases in woody plant stature and density in savannas and grasslands have been documented worldwide (Archer 1995). These changes in vegetation are of considerable socioeconomic concern, as they often contribute to reductions in livestock carrying capacity and thus impact commercial enterprises, pastoral

societies, and subsistence cultures in arid and semiarid environments (Heady 1975, Scifres 1980, Schofield and Bücher 1986, Skarpe 1991, MacLeod 1993, Walker 1993, Young and Solbrig 1993, Bastian et al. 1995). Woody plant encroachment into grasslands and savannas also has potentially important ramifications for desertification, biodiversity, wildlife habitat conservation, nutrient cycling, and soil erosion (Grover and Muck 1990, Schlesinger et al. 1990, Hibbard 1995). To date, our understanding of the proximate causes for these changes in vegetation and the factors influencing their rates, dynamics, and patterns across landscapes are poorly understood. Mesquite (*Prosopis glandulosa*

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[honey mesquite] and *P. velutina* [velvet mesquite]) exemplifies this phenomenon in southwestern North America. Although the geographic range of these unpalatable, arborescent legumes has changed little in southwestern North America in the past 300–500 yr (Johnston 1963), their stature and density have increased markedly in grasslands and savannas since Euroamerican settlement (Inglis 1964, Buffington and Herbel 1965, Hennessy et al. 1983, Archer 1989, Turner 1990, Bahre and Shelton 1993).

Considerable speculation exists regarding what factors might have changed over the past century to enable encroachment of *Prosopis* and other woody species into grasslands. Traditional explanations center around the interactive effects of livestock grazing and reductions in fire frequency or intensity that occurred against a backdrop of periodic drought and directional climate change (Hastings and Turner 1965, Herbel et al. 1972, Neilson 1986, Archer 1994). More recently, it was proposed that increases in atmospheric CO₂ concentrations since the industrial revolution have favored woody plants over grasses (Idso 1992, Johnson et al. 1993). Herbivores are known to exert a significant influence on woody plant distribution and abundance in grasslands and savannas of Africa (e.g., Sinclair 1979, Belsky 1984, Yeaton 1988, Dublin et al. 1990, Stuart-Hill 1992), but their potential role in regulating vegetation dynamics has received less consideration in North America. In this paper, we test the hypothesis that the black-tailed prairie dog (*Cynomys ludovicianus* Ord. [Sciuridae]) is a keystone herbivore (sensu Paine 1966, Brown and Heske 1990, Mills et al. 1993) and ecosystem engineer (Jones et al. 1994) that can maintain grasslands by preventing woody species such as *Prosopis* from establishing or attaining dominance. We propose that widespread anthropogenic extermination of extensive prairie dog colonies in the early 1900s removed a significant constraint to woody plant establishment, thereby increasing the likelihood of transitions from grassland and savanna to shrubland or woodland.

The geographic range of black-tailed prairie dogs extends from north-central Mexico to southern Canada and from eastern Nebraska to western Montana (Hall 1981). Colonies are selectively located on portions of the landscape with gentle slopes and deep soils that are not flood prone (Dahlsted et al. 1981). The number and extent of prairie dog colonies in western North America prior to Euroamerican settlement is unknown. However, in 1919, colonies were estimated to occupy 40×10^6 ha of the Great Plains and Texas (Nelson 1919), with individual colonies encompassing up to 64 750 km² (Bailey 1905). Prairie dog densities on modern colonies range from 18 to 83 animals/ha and vary with site, season, year, and colony age (Garrett et al. 1982). Vegetation on landscapes inhabited by prairie dogs receives frequent and intense defoliation, and plants not consumed are indiscriminately felled and kept low in

stature, presumably to facilitate predator detection (King 1955). In addition, prairie dogs' burrowing activities probably have important indirect effects on vegetation by altering hydrology and nutrient cycling. Prairie dog activities also create habitat for other animals. As a result, the abundance of reptiles, lagomorphs, cricetine rodents, insects, and ants is often higher on prairie dog colonies relative to off-colony (i.e., uncolonized) portions of the landscape (Agnew et al. 1986). Activities of these animals, coupled with those of ungulates (bison, antelope, livestock) that preferentially utilize colonies (Coppock et al. 1983b), may intensify grazing (Cid et al. 1991) and seed predation to further influence plant composition, production, and nutrient cycling (Whicker and Detling 1988).

Prairie dogs have been widely regarded by livestock producers as rangeland pests. Despite evidence to the contrary (e.g., Coppock et al. 1983a, b) they are generally assumed to compete with domestic livestock for forage, and to create health hazards. Extensive eradication programs in the early 1900s reduced the area of prairie dog colonies in the United States by an estimated 98% (U.S. Department of Interior 1963). The removal of this widespread, abundant herbivore undoubtedly influenced vegetation patterns, secondary succession, and plant life-form interactions (cf. Chew 1976, Louda 1989, Brown and Heske 1990) and may have contributed to increases in tree and shrub recruitment on southwestern landscapes.

Our goal was to determine the influence of prairie dogs and the fauna associated with their colonies on the relative abundance and dominance of herbaceous and woody vegetation. We targeted mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) because of the widespread ecological and socioeconomic significance of this genus in southwestern North America, South America, Africa, and Australia (Simpson 1977, McArthur 1984, McKell 1989). Specifically, we (1) experimentally quantified *P. glandulosa* seed and pod removal, and seedling emergence and persistence, on prairie dog colonies relative to portions of the landscape not occupied by prairie dogs; (2) inventoried the "seedling" reserve of *Prosopis* on prairie dog colonies; and (3) quantified temporal changes in *Prosopis* abundance on a landscape where prairie dogs were eradicated in 1950.

METHODS

Study sites

The study was conducted in 1988 and 1989 near the eastern edge of the Rolling Plains resource area (Gould 1975) in north-central Texas. The climate of the region is characterized by hot summers, mild winters, and a 220-d frost-free period that extends from March to November. Average annual precipitation (682 mm) is bimodally distributed, with peaks in May (96 mm) and September (118 mm). Annual rainfall was 489 mm in

1988 and 564 mm in 1989. Regional physiognomy varies from grassland to *Prosopis*-dominated savanna and woodland with an herbaceous understory of short- and mid-height grasses. See Heitschmidt et al. (1985) for additional details on soils, climate, and vegetation of the study area. Small mammals in the region include cricetine rodents (e.g., *Neotoma micropus*, *Reithrodontomys* spp., *Baiomys taylori*, *Peromyscus* spp.) and lagomorphs (e.g., *Lepus californicus*, *Sylvilagus* spp.) (Davis and Schmidly 1994).

We studied two colonies of black-tailed prairie dogs on the W. T. Waggoner Estate Ranch in Throckmorton County near Vernon, Texas. Both colonies were at least 50 yr old, and both were situated on clay loam soils (Soil Conservation Service 1959). The Santa Rosa (SR) colony (33°48' N, 99°29' W; elevation 369 m) occupied 15 ha of nearly level terrain within a 2000-ha *Stipa leucotricha*-*Buchloe dactyloides* grassland. The area had been grazed at moderate stocking density by cattle from October to May. The North Fork (NF) colony (33°57' N, 99°19' W; elevation 405 m), occupied ≈6 ha. The colony was situated within a *S. leucotricha*-*B. dactyloides*-*P. glandulosa*-*Ziziphus obtusifolia* savanna. The pasture that contained the NF colony had been grazed continuously by cattle at a moderate stocking density since the mid-1900s.

Prairie dog colonies are often characterized by distinct concentric zones of vegetation, the composition of which varies as a function of habitation history (Archer et al. 1987, Whicker and Detling 1988). Three vegetation zones were apparent at each colony. The interior zone had abundant burrow mounds interspersed in a matrix of short-statured (2–15 cm) graminoids and scattered herbs. The off-colony zone lacked burrows and was dominated by mid-statured (>25 cm) graminoids. Transitions between the on-colony and off-colony zones were characterized by occasional burrows and a mixture of short- and mid-statured graminoids. *Prosopis* plants of seed-producing stature were absent on both colonies.

Cattle were excluded from a 2-ha portion of the SR site with a permanent three-strand barbed-wire fence that extended into the off-colony vegetation. All seedling establishment trials were conducted within this enclosure. No livestock enclosure was constructed at the NF site.

Prosopis seed and pod disappearance

Prosopis seed production typically occurs in July and August. Seeds are typically 5 mm wide, 7 mm long, and ≈0.05 g in mass. Ripened seeds are long lived (≥40 yr; Tschirley and Martin 1960) and have hard coats that require scarification before germination will occur. Seeds are borne in a fleshy carpel (pod) that is widely consumed by wildlife and domestic livestock; many of the ingested seeds escape mastication and are germinable after excretion (see Brown and Archer 1987). Seeds produced off-colony may therefore be

readily dispersed onto colonies by wildlife or livestock. Previous research suggests that utilization of *Prosopis* pods and seeds by birds is minimal (El Youssoufi 1992). We quantified daily removal of seeds and pods from 7–10 plots randomly located in on- and off-colony zones at SR in August 1988 and at both colonies in July and August 1989. Within each plot, we established three cafeteria-style feeding stations, each with two petri dishes. One petri dish was made inaccessible to ants (*Pogonomyrmex* spp.) (AI) by elevating it 6 cm on an inverted glass jar that allowed vertebrate access. The second petri dish was placed at ground level and was accessible to ants (AA) and vertebrates. Each pair of dishes was randomly assigned to one of three vertebrate enclosure treatments: all (A), partial (P), or none (N). Enclosures constructed of 1-cm mesh hardware cloth (23 cm long × 23 cm wide × 25 cm high with closed tops) excluded all (“A”) vertebrates (e.g., prairie dogs, lagomorphs, and small rodents). Semi-permeable or partial (“P”) vertebrate enclosures were constructed from 2.5-cm hexagonal wire netting (25 cm diameter, 36 cm tall, with closed tops) that allowed cricetine rodents access to stations but excluded larger prairie dogs and lagomorphs. *Prosopis* seeds and pods at the third station were not enclosed (“N”), and were fully accessible to all vertebrates.

We conducted field trials with either all seeds or all pods. For each trial, we placed five pod segments (8–12 mm long; ≈0.25 g air dry mass) or five seeds (≈0.05 g each) into each of the petri dishes, and recorded the number removed from each dish after 24 h. Dishes were then replenished with fresh seeds or pods as necessary; seeds were replaced with pods, or vice versa, for the next trial. Trials were 1–5 d in duration, depending upon weather constraints on site accessibility, and were conducted on different dates at the two colonies. Seed and pod removal were quantified for a total of 8 trials at SR in 1988, and a total of 16 trials at SR and 11 trials at NF in 1989.

Herbaceous standing crop

Herbaceous standing crop was quantified in July 1988 and August 1989 at SR to document differences in grass and forb composition resulting from prairie dog habitation. Aboveground biomass was harvested by species from circular 0.25-m² plots randomly located within on-colony, transition, and off-colony zones ($n = 20$ plots/zone in 1988; $n = 10$ plots/zone in 1989). Biomass was oven-dried at 60°C to constant mass, and weighed to the nearest 0.1 g.

Seedling establishment

Prosopis seedling establishment was quantified at the SR colony. In 1988 and 1989, 60 plots (2 × 2 m) were randomly located within each of three vegetation zones (on-colony, transition, off-colony). Each plot was randomly assigned to one of three vegetation interference treatments: no interference (NI), simulated grazing of

herbaceous plants (SG), and full interference (FI). The NI treatment was designed to minimize herbaceous interference (e.g., shading, competition for water or nutrients) with *Prosopis* establishment and growth and to increase *Prosopis* seedling apparency to herbivores. This was achieved through application of a nonspecific contact herbicide (Roundup) followed by post-treatment removal of standing crop 1 wk prior to initiation of the experiment. The NI treatment was maintained by hand weeding. The SG treatment was designed to simulate grazing of herbaceous vegetation and was achieved by clipping vegetation within plots to a 3-cm height at monthly intervals. The third treatment was an indigenous control with full interference.

Our primary objective in this phase of the study was to quantify the seedling establishment phase of the *Prosopis* life cycle. We therefore used scarified seed (laboratory germination = 90%) collected from populations near College Station, Texas. *Prosopis* seeds readily germinate when placed on the soil surface (Brown and Archer 1989) or when planted at depths of up to 2–4 cm (Haas et al. 1973, Simpson 1977). To minimize predation losses and variability associated with soil-seed contact effects on germination, we planted seeds at a depth of 0.5 cm on 27 June 1988 and 30 May 1989. Within each plot, three groups of 20 seeds each were randomly assigned to the A, P, and N enclosure treatments. To facilitate germination and emergence, plots were watered at 2-d intervals until the first true leaves emerged (≈ 1 wk after planting). The proportion of seeds germinating was recorded 7 d after planting (1988 only). Seedlings were then thinned to three per enclosure treatment. Seedling survival was recorded monthly through August, and again in November.

Fate of established and transplanted Prosopis plants

To assess the impact of prairie dogs and associated herbivores on established *Prosopis* seedlings, we randomly removed A and P enclosures protecting 48 seedlings that had emerged in 1988. Enclosures were removed on 17 May 1989; 15 on-colony seedlings under A and P enclosures were maintained as controls. Plant survival and height were monitored through August 1989.

To assess the impact of prairie dogs on larger *Prosopis* plants, we transplanted foliated branches of *Prosopis* into on-colony, transition, and off-colony zones at SR and NF to simulate *Prosopis* "saplings." Transplanting consisted of inserting basal ends of foliated *Prosopis* branches 5–10 cm into the soil. In July 1988, four transects with 20 "saplings" each (stem diameter = 5–6 mm; mean height [± 1 SE] = 27 ± 1 cm) were established in each zone at NF. Saplings were monitored daily for 38 d and replaced as they withered. Length of shoot (cm) protruding from the soil, linear length (cm) of bark removed, and girdling or severing of stems were noted on daily visits. In 1989, the experiment was repeated and included the SR colony and

larger saplings (stem diameter = 12–20 mm; height = 76 ± 3 cm). The 1989 transplant experiment was conducted for three trials of three consecutive days in June, and one trial in August ($n = 480$ and 240 small and large saplings, respectively).

Occurrence of Prosopis on prairie dog colonies

We determined density, cover, and height of *Prosopis* in 10 belt transects (2×50 m) on and off each colony in 1989. Individual plants were classified as seedlings when cotyledons were present or saplings when cotyledons had dehisced and stems were lignified.

Stand development after prairie dog removal

Throckmorton County records indicated that a colony of prairie dogs in Rock Canyon ($33^{\circ}25' N$, $99^{\circ}11' W$; 406 m elevation) was eradicated in December 1950. Aerial photographs that portrayed the colony site were obtained for 1950, 1963, and 1973. Positive transparencies of these photographs were spatially registered to a common scale (1:2500) with a Kronz reflecting projector. Changes in canopy cover (as a percentage) of *Prosopis* on the area occupied by prairie dogs were quantified by tracing canopies onto frosted acetate and digitizing the resulting polygons into a geographic information system. Off-colony canopy cover was similarly estimated within two spatially registered circular plots (2.41 ha each).

In 1990, we quantified the structure of *Prosopis* stands on and off the former Rock Canyon colony. Belt transects (2×60 m) were randomly located within stands with similar soils on ($n = 10$) and off ($n = 5$) the former colony site. Plant density, plant basal area, total basal area, and relative canopy cover was determined. *Prosopis* size/age relationships were determined from basal stem cross-sections obtained from six trees on and off the former Rock Canyon colony site. The cross sections, which ranged from 7 to 34 cm in diameter, were sanded, stained, and aged by ring counts as described by Flinn et al. (1994).

Statistical analysis

First- and second-order interactions were included in ANOVA models. General linear model procedures were used for unbalanced designs (SAS Institute 1988). Results were considered significant at $P < 0.05$. To simplify interpretation, second-order interactions with Type III sums of squares that contributed $< 2\%$ to the model sum of squares were combined with the error term, and the model reanalyzed. Tukey's hsd multiple-means comparison test was used to compare levels within factors for all significant ($P < 0.05$) main effects and first-order interactions. We performed arcsine transformations (Steel and Torrie 1980) on proportional data, and square-root transformations on all other data. Mean separation tests were conducted on transformed data when necessary. Nontransformed, least-squares means are presented in the tables and figures. When

TABLE 1. Mean (± 1 SE) peak herbaceous standing crop (kg/ha), by functional group, at the Santa Rosa colony for on-colony, transition, and off-colony zones in 1988 and 1989.

Functional group	Year	Zone		
		On-colony	Transition	Off-colony
Mid-grasses	1988	123 \pm 31	894 \pm 207	745 \pm 137
	1989	29 \pm 29	...	2059 \pm 350
Short grasses	1988	616 \pm 67	731 \pm 143	778 \pm 162
	1989	839 \pm 178	...	568 \pm 247
Annual grasses	1988	0 \pm 0	35 \pm 20	430 \pm 73
	1989	0 \pm 0	...	431 \pm 185
Forbs	1988	33 \pm 12	38 \pm 18	70 \pm 42
	1989	133 \pm 75	...	337 \pm 143
Total	1988	771 \pm 71	1698 \pm 130	2022 \pm 144
	1989	1001 \pm 215	...	3394 \pm 265

means from A and P enclosure treatments were not different, data were pooled and the model reanalyzed.

Seed and pod removal data for 1988 and 1989 were analyzed separately. Data from ant-inaccessible (AI) stations in 1988 were excluded from consideration because of design problems with the seed trays. This problem was rectified for the 1989 trials. We used a nested-factorial ANOVA design (Hicks 1973, Smith and Beverly 1981) to analyze proportional seed and pod removal data. Colony, zone, enclosure, and ant access represented crossed factors; trial was nested within colony because trials were conducted on different dates at each colony. For the seedling establishment experiment, mean end-of-season seedling survival for 1988 and 1989 was analyzed in a crossed (year, zone, vegetation treatment, enclosure) ANOVA model. Effects of prairie dogs on the survival and height of established *Prosopis* seedlings were analyzed with Studentized *t* tests. Manipulation of simulated *Prosopis* saplings was analyzed with separate crossed (month, colony, zone) and nested (trial within month) ANOVA models for differences in stem cutting height, number of secondary branches clipped, length of stem bark stripped, and proportion of stems girdled. Density, cover, and height of *Prosopis* on and off each colony were analyzed with a crossed (colony, zone) ANOVA model. Plant density, plant basal area, total basal area, and relative canopy cover on and off the former Rock Canyon colony were analyzed with a nested (transect within zone) ANOVA model for differences between zones. Plant densities within a basal area class on and off the former colony were rank-transformed prior to analysis of variance (Conover and Iman 1981). Simple linear regression was used to assess basal diameter-age relationships of *Prosopis* stems on and off the former Rock Canyon colony site.

RESULTS

Herbaceous standing crop

Total herbaceous standing crop within the livestock enclosure at SR was ≈ 3 times greater off-colony than on-colony (Table 1; J. F. Weltzin, S. L. Dowhower, and R. K. Heitschmidt, *unpublished manuscript*). No an-

nual grasses occurred on-colony in either year, and short-grass biomass was comparable between zones and years. Mid-grass biomass (primarily *Stipa leucotricha*) was at least 6 times greater off-colony than on-colony; this difference was most pronounced in 1989.

Seed and pod removal

Patterns of *Prosopis* seed and pod disappearance differed between on- and off-colony zones (Tables 2 and 3). In both years and on both colonies, seed and pod removal rates were comparable for A and P enclosures (which were pooled for all subsequent analyses). The cause of removal of a small proportion of seeds and pods from AI stations within rodent-excluded plots was unknown.

Ant access explained the majority of the variation in the seed removal model (Table 2). Ant access substantially increased seed removal rates at both colonies (Table 3), with the magnitude of ant effects being significantly ($P < 0.05$) influenced by vertebrate accessibility and zone. For example, when vertebrates had access to seeds, ant access increased removal rates by 60% ($P < 0.05$); when vertebrates were excluded, ant access increased seed removal sevenfold. Seed removal rates were significantly greater on- than off-colony, with differences between zones being greater for ant-accessible (AA) trays (fourfold) than for AI trays (threefold). Seed removal differed significantly between vertebrate enclosure treatments, but was dependent upon zone and colony. On-colony seed removal rates nearly doubled with vertebrate access, whereas off-colony removal rates were not significantly affected by vertebrates ($P > 0.05$). Seed removal from vertebrate-inaccessible trays did not differ significantly between the SR and NF colonies, but was greater at SR than NF when vertebrates had access. Consistent with this pattern, seed removal did not differ significantly for off-colony locations at SR and NF; however, seed removal on the SR colony significantly exceeded that observed at the NF colony. Patterns of seed removal were similar between the two years for the SR colony.

Pod removal attributed to prairie dogs and associated

TABLE 2. ANOVA summary of *Prosopis* pod and seed removal for effects of colony (Santa Rosa or North Fork), zone (on-colony, off-colony), rodent exclosure type (pooled A [all] and P [partial] exclosures and N [no exclosure]), and ant accessibility.

Source	Pod removal					Seed removal				
	df	MS	F	P	r ²	df	MS	F	P	r ²
Colony	1	2.189	34.44	0.0001	5.2	1	0.185	1.17	0.2905	0.6
Trial (Colony)	25	0.063	6.36	0.0001	3.8	25	0.159	7.21	0.0001	12.6
Zone	1	5.207	243.25	0.0001	12.4	1	4.36	51.37	0.0001	13.8
Colony × Zone	1	0.257	12.00	0.0019	0.6	1	0.593	6.99	0.0139	1.9
Trial × Zone (Colony)	25	0.021	2.14	0.0026	1.3	25	0.085	3.86	0.0001	6.7
Exclosure	2	7.951	434.64	0.0001	37.9	2	0.875	42.25	0.0001	5.6
Colony × Exclosure	2	0.10	0.54	0.5816	<0.1	2	0.083	3.99	0.0215	0.5
Zone × Exclosure	2	4.479	244.84	0.0001	21.3	2	0.411	19.87	0.0001	2.6
Colony × Trial × Zone × Exclosure	101	0.018	1.83	0.0003	4.4	102	0.021	0.94	0.6275	6.7
Ant access	1	1.674	167.60	0.0001	4.0	1	9.115	414.13	0.0001	28.9
Colony × Ant Access	1	0.774	77.51	0.0001	1.8	1	0.008	0.36	0.5481	<0.1
Zone × Ant access	1	0.0001	0.01	0.9071	<0.1	1	0.966	43.86	0.0001	3.1
Exclosure × Ant access	2	0.166	16.64	0.0001	0.7	2	0.248	11.28	0.0001	1.6
Error	156	0.01				156	0.022			

Note: Three-way interactions between colony, zone, exclosure, and access terms each contributed <2% to model sums of squares, and are included with the error term. Means are presented in Table 3. Model R²s for pod and seed removal were 0.96 and 0.89, respectively.

vertebrates too large to access both P and A exclosures (e.g., lagomorphs) typically exceeded the level of seed removal. Several times we observed prairie dogs remove pods, consume the fleshy carpel, and then discard the seed intact. Exclosure and the zone x exclosure interaction explained the most variation in the pod removal model (Table 2). Most pods (96–99%) were removed from on-colony stations accessible to vertebrates (Table 3). Pod removal from vertebrate-accessible stations was on average 4 times greater on than off-colony, but did not differ between zones when vertebrates could not access pods ($P > 0.05$). Differences in pod removal by vertebrates were also colony-dependent: pod removal was 11 times greater on- than off-colony at NF, and ≈2 times greater at SR ($P < 0.05$).

Pod removal was greater from AA than AI trays, which suggests that ants removed some pods. However, differences were dependent on colony and vertebrate access. Pod removal from AI and AA trays was 50 and 100% greater at SR than at NF ($P < 0.05$). Ant access

increased pod removal sevenfold when vertebrates were excluded, but only ≈10% ($P < 0.05$) when vertebrates had access. Vertebrate access increased pod removal 3–19-fold for AI and AA trays, respectively, but pod removal did not differ between the two tray types ($P > 0.05$). Differences in pod removal were also year dependent: pod removal rates at the SR site in 1988 were approximately half those observed in 1989.

Seedling establishment

Prosopis seedling emergence was statistically comparable between vegetation treatments and for A and P exclosures (data not shown). Seedling emergence was greater ($P < 0.05$) inside than outside exclosures on-colony, but not in the transition and off-colony zones (Table 4). Overall emergence was greatest ($P < 0.05$) in the transition zone. End-of-season survival of *Prosopis* seedlings did not differ between main effects of year, zone, or vegetation treatment, or between A and P exclosures (Table 5). Establishment of *Prosopis* seedlings protected from vertebrates was uniformly high

TABLE 3. Mean (± 1 SE) seed and pod removal (%) for 1988 and 1989, from ant-accessible and ant-inaccessible stations with and without vertebrate exclosures on and off the Santa Rosa (SR) and North Fork (NF) prairie dog colonies.

Year	Colony	Ant-accessible				Ant-inaccessible			
		Exclosed		No exclosure		Exclosed		No exclosure	
		On	Off	On	Off	On	Off	On	Off
Seeds									
1988	SR	88 ± 6	31 ± 6	86 ± 6	36 ± 6
1989	SR	67 ± 5	27 ± 5	85 ± 5	32 ± 5	9 ± 5	2 ± 5	59 ± 5	13 ± 5
	NF	54 ± 6	33 ± 6	63 ± 6	34 ± 6	6 ± 6	7 ± 6	40 ± 6	13 ± 6
Pods									
1988	SR	20 ± 7	17 ± 7	50 ± 7	26 ± 7
1989	SR	39 ± 3	31 ± 3	98 ± 3	51 ± 3	2 ± 3	5 ± 3	96 ± 3	31 ± 3
	NF	6 ± 4	7 ± 4	99 ± 4	4 ± 4	0 ± 4	0 ± 4	99 ± 4	1 ± 4

TABLE 4. Mean emergence (%) in 1988 of excluded and nonexcluded *Prosopis* seedlings on the Santa Rosa prairie dog colony, in the transition zone, and off the colony.

Exclosure	Zone		
	On	Transition	Off
Yes	52 ^{Aa}	64 ^{Ba}	48 ^{Aa}
No	38 ^{Ab}	62 ^{Ba}	54 ^{Ca}

Note: Means within a column with the same lowercase superscript letter and means within a row with the same uppercase superscript letter were not significantly different ($P > 0.05$).

(>75%) and did not differ between zones (Fig. 1). In contrast, survival of nonprotected seedlings was uniformly low on and at the edge of the colony, but was ≈ 3 times greater off-colony. While seedling survival within a particular zone was not affected by herbaceous interference (e.g., shading, competition for water or nutrients), experimental reductions in herbaceous interference increased the survival of seedlings protected from rodents, but decreased the survival of unprotected seedlings (Fig. 2).

Fate of established Prosopis seedlings

Mean height (± 1 SE) of 1-yr-old *Prosopis* plants was 8.4 ± 0.9 cm when vertebrate exclosures were removed from on-colony plots on 17 May. Within 10 d of exclosure removal, plant survival was 95%, and surviving plants were 6.9 ± 1.0 cm tall. On 15 August, plant survival was 51%, and live seedlings were 3.6 ± 1.0 cm tall. Over the same time period, survival of control plants under rodent exclosures was 100%, and mean height increased from 8.4 ± 0.9 cm to 16.2 ± 1.5 cm.

Fate of Prosopis "saplings"

In 1988, *Prosopis* branches were used to simulate "saplings." The experimental saplings placed off-colony at NF were not damaged. In contrast, 80% of the saplings placed on-colony were severed at ground level

TABLE 5. ANOVA summary of *Prosopis* seedling survival (Figs. 1 and 2) for zone (on-colony, transition, off-colony), vegetation treatment (full interference, simulated grazing, no interference), and rodent exclosure type (pooled A [all] and P [partial] exclosures, and N [no exclosure]).

Source	df	MS	F	Pr > F
Zone	2	0.034	1.04	0.43
Vegetation treatment	2	0.007	0.21	0.82
Zone \times Vegetation treatment	4	0.033	3.02	0.04
Exclosure	1	2.887	263.97	0.0001
Zone \times Exclosure	2	0.082	7.49	0.0035
Vegetation treatment \times Exclosure	2	0.14	12.75	0.0002
Error	21	0.001		

Note: The main effect of year and its interactions and the interaction among zone, vegetation treatment, and exclosure contributed <2% to model sums of squares, so were included with the error term.

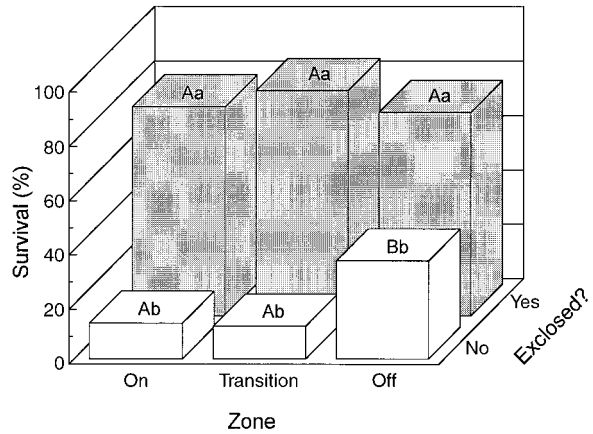


FIG. 1. Mean survival of excluded *Prosopis* seedlings and seedlings that were not excluded, within on-colony, off-colony, and transition zones of the SR prairie dog colony. Means within exclosure with the same uppercase letter and means within zone with the same lowercase letter were not significantly different ($P > 0.05$).

within 1 d; all saplings were felled within 2 d. Among saplings situated at the colony edge, 55% were felled within 1 d, and 91% were felled within 38 d.

Main and interactive effects of colony and season were not significant in 1989 ($P > 0.05$). More small and large saplings were damaged (cut or girdled stems and branches) in the on-colony zone than in transition or off-colony zones (Table 6). Stems were typically severed 10–13 cm above ground level. Prairie dogs and associated fauna did not cut main stems of larger saplings (12–20 cm diameter), but they severed lower secondary stems, and often stripped enough bark from the lower 30–40 cm of the primary stem to effectively girdle it.

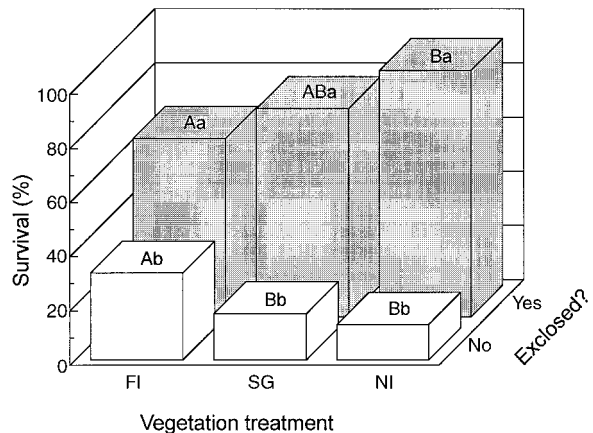


FIG. 2. Mean survival of excluded *Prosopis* seedlings and seedlings that were not excluded in plots with full herbaceous interference (FI), simulated grazing (SG), and no herbaceous interference (NI). Means within exclosure with the same uppercase letter and means within vegetation treatment with the same lowercase letter were not significantly different ($P > 0.05$).

TABLE 6. Fate of transplanted *Prosopis* "saplings" by zone (on-colony, transition, off-colony) in 1989.

Sapling size class	Parameter	Zone		
		On	Trans.	Off
Small	Manipulated	91 ^a	67 ^b	0 ^c
	Height	10 ^a	13 ^b	27 ^c
Large	Manipulated	98 ^a	58 ^b	0 ^c
	Height	76 ^a	76 ^a	76 ^a
	Branches severed	6 ^a	3 ^b	0 ^c
	Stripped	36 ^a	10 ^b	0 ^c
	Girdled	31 ^a	1 ^b	0 ^b

Note: Effects of colony (Santa Rosa or North Fork) and trial within month (July, August) were not significant ($P > 0.05$), so data were pooled. Data for small saplings are mean percentage manipulated (i.e., bark stripped, branches severed, stem girdled) and residual height (cm). Data for large saplings are mean percentage manipulated, residual height (cm), number of secondary branches severed, linear length (cm) of bark stripped, and percentage of stems girdled. Within rows, means with the same superscript letter were not significantly different ($P > 0.05$).

Occurrence of *Prosopis* on prairie dog colonies

Interactive effects of colony and zone were significant ($P < 0.05$) for density, cover, and height of naturally occurring *Prosopis* seedlings and saplings on and off the SR and NF colonies (Table 7). At NF, seedling and sapling densities were significantly greater on- than off-colony, but saplings off the colony were taller and had greater canopy cover. At SR, sapling density, cover, and height values were comparable between on- and off-colony zones. We encountered no seedlings off-colony at either site.

Stand development after prairie dog removal

Prosopis canopy cover on and off the Rock Canyon prairie dog colony was 27 and 46%, respectively, when the prairie dogs were eradicated in 1950 (Table 8). By 1973, canopy cover on the former colony site had increased to a level (61%) comparable to that of off-colony zones (65%). In 1990, canopy cover was greater on than off the former colony site (Table 9). Although the total basal area was comparable on and off the former colony, *Prosopis* plants on the former colony site were smaller and occurred at a higher density than those off-colony (Tables 9 and 10). Slope and intercept

of regressions for basal diameter vs. stem age for on- and off-colony zones did not differ ($P > 0.05$) and yielded the following composite relationship:

$$SA = 19.7 + 1.256(BD) \quad (1)$$

where SA is main stem age (in years) and BD is basal diameter (in centimeters) at 20 cm above ground level ($n = 12$; $P < 0.0001$; $R^2 = 0.88$). Based on Eq. 1, the median age of *Prosopis* stems was 27 yr (maximum = 81 yr) and 42 yr (maximum = 76 yr) on and off the former colony, respectively (Table 9). Eighty-eight percent of the plant stems on the former colony became established after prairie dogs were eradicated in 1950. Among off-colony stands, only 45% of the *Prosopis* stems present in the 1990 survey had become established since 1950.

DISCUSSION

Prairie dogs are known to alter the composition of herbaceous vegetation across landscapes, their influence changing as a function of habitation history (Archer et al. 1987; Whicker and Detling 1988). Our data indicate that prairie dogs and the herbivores associated with their colonies would have been important in creating (e.g., Osborn 1942) or maintaining grasslands or savannas and preventing transitions to alternate shrubland or woodland steady states (cf. Archer 1989, Westoby et al. 1989, Dublin et al. 1990). Their control over ecosystem structure was achieved through a combination of woody plant seed removal and seedling predation and growth suppression.

Prosopis seed removal and seedling establishment

Defoliation of *Prosopis* seedlings and removal of seeds and pods attributable to cricetine rodents was minimal on and off prairie dog colonies. In contrast, prairie dogs and associated populations of lagomorphs and ants significantly influenced *Prosopis* population dynamics by utilizing seeds and pods (Table 3) and by cutting or girdling stems of seedling (Figs. 1, 2) and juvenile (Table 6) plants.

Ants were the most important agents of *Prosopis* seed disappearance, and their activities increased by a factor of four on the prairie dog colony. Prairie dogs and/or lagomorphs associated with prairie dog colonies

TABLE 7. Mean density, relative canopy cover, and height of *Prosopis* saplings (cotyledons dehiscent and bark lignified) and seedlings (cotyledons present) on and off the Santa Rosa (SR) and North Fork (NF) colonies in 1989.

Colony	Zone	Saplings			Seedlings		
		Density (no./ha)	Cover (%)	Height (m)	Density (no./ha)	Cover (%)	Height (m)
SR	On	40 ^a	<1 ^a	0.06 ^a	0 ^a	0 ^a	0 ^a
	Off	60 ^{ac}	<1 ^a	0.13 ^a	0 ^a	0 ^a	0 ^a
NF	On	580 ^b	<1 ^a	0.06 ^a	370 ^b	<1 ^b	0.02 ^b
	Off	250 ^c	6 ^b	1.26 ^b	0 ^a	0 ^a	0 ^a

Note: Within a column, means with the same superscript letter were not significantly different ($P > 0.05$).

TABLE 8. Total *Prosopis* canopy cover (%) on and off the former Rock Canyon prairie dog colony, as determined from aerial photographs. Prairie dogs were eradicated from the colony in 1950.

Zone	Year		
	1950	1963	1973
Former colony	27	35	61
Off-colony	46	42	65

were the primary agents of *Prosopis* pod disappearance, and prairie dogs were observed utilizing the fleshy carpel and leaving the intact seed on the soil surface. The fate of seeds and pods removed from experimental trays was not determined, but high seedling densities on the North Fork colony (Table 7) suggest that consumption or deep burial (emergence of scarified seeds placed at depths >5 cm has been reported at 0% [Haas et al. 1973]) was either low or exceeded by dispersal of *Prosopis* seed onto prairie dog colonies. *Prosopis* large enough to detect on aerial photographs occurred on the Rock Canyon colony prior to prairie dog eradication (Table 8). These plants may have served as the seed source for plants establishing after prairie dog removal (Tables 8–10). However, neither the Santa Rosa nor the North Fork colonies contained plants of seed-producing stature. Where seed-producing *Prosopis* plants are absent, periodic seed input from off-colony populations would be required if on-colony populations (Table 7) were to persist. Many native herbivores (Coppock et al. 1983b, Whicker and Detling 1988) and livestock (Koford 1958) that preferentially utilize prairie dog colonies may also consume *Prosopis* pods (Brown and Archer 1987) from trees in off-colony populations and disseminate viable seed onto the colony. Differences in *Prosopis* seedling and sapling densities between the NF and SR colonies (Table 7) may reflect differences in proximity to off-colony seed sources. Alternatively, maintenance of observed seedling reserves in the absence of seed-producing plants may reflect a residual soil seedbank established during former occupation by *Prosopis*. *P. glandulosa* exhibits strong seed-coat dormancy, and seeds can remain viable in soil up to 40–60 yr (Tschirley and Martin 1960). Thus, seeds may persist long after parental plants are gone.

Persistence and development of *Prosopis* seedlings depends upon abiotic conditions, herbaceous interference, and herbivory. In our study, herbivory was the most important factor influencing survival of *Prosopis* seedlings during their first year (Fig. 1). Together, prairie dogs and associated fauna reduced on-colony seedling survival by a factor of four. However, a strong interaction between herbaceous interference and susceptibility to herbivory was evident (Fig. 2). Among protected seedlings, survival decreased as herbaceous interference increased. In contrast, survival of nonprotected seedlings increased with increasing herbaceous

TABLE 9. Mean plant density, basal area, total basal area, and relative canopy cover of *Prosopis* on and off the former Rock Canyon prairie dog colony in 1990.

Parameter	Zone	
	Former colony	Off-colony
Plant density (no./ha)	2050 ^a	483 ^b
Basal area (cm ² /plant)	102 ^a	342 ^b
Basal area (m ² /ha)	21 ^a	17 ^a
Canopy cover (%)	64 ^a	42 ^b
Median stem age (yr)	27	42
Largest plant age (yr)	81	76
Stems <40 yr old (%)	88	45

Note: Within a row, means with the same superscript letter were not significantly different ($P > 0.05$). Median stem age, age of largest plant sampled, and proportion of stems initiated since eradication of the prairie dog colony in 1950 were determined using Eq. 1.

interference. Benefits to woody plant seedlings that might otherwise accrue from decreased herbaceous interference caused by defoliation or removal of grasses on the colony appear to have been negated, perhaps by increased apparency or susceptibility to discovery (e.g., Feeny 1976).

When *Prosopis* seedlings were protected from herbivory, levels of establishment were comparably high (>75%) on- and off-colony (Fig. 1), despite substantial differences in herbaceous biomass in these areas (Table 1). This suggests that alterations of vegetation, soils, hydrology, and microclimate by prairie dogs and associated herbivores would not necessarily increase the likelihood of woody plant establishment after prairie dogs vacate a site. Other studies have shown that competition with grasses can significantly reduce woody plant growth rates (Polley et al. 1994, Bush and Van Auken 1995), but this does not necessarily translate into significant reductions in seedling survival (Brown and Archer 1989, O'Connor 1995, Archer 1996). In this study, experimental reductions in herbaceous interference did increase seedling survival, but only slightly (Fig. 2); recruitment was quite high (66%), even with full interference. The ability of *Prosopis* to successfully establish and persist in competition with grasses in this northern Texas system has also been demonstrated in grasslands of central and southern Texas (Archer 1996). Thus, in the absence of seedling predation or fire, the probability of *Prosopis* establishment would be high both on and off prairie dog colonies.

Prosopis persistence on colony sites

Our field observations of 1-yr-old seedlings and simulated saplings indicated that the majority of stems and leaves on manipulated plants were not consumed. This was consistent with other observations of indiscriminate clipping and felling of vegetation near ground level by prairie dogs (King 1955), an activity thought to facilitate predator detection. The behavior of indiscriminately felling vegetation suggests that our obser-

TABLE 10. Mean density (no./ha) of *Prosopis* within basal area size classes on and off the former Rock Canyon prairie dog colony in 1990.

Zone	Plant basal area size class (cm ²)					
	0–100	100–200	200–300	300–400	400–500	>500
On-colony	1502 ^{Aa}	291 ^{Aa}	100 ^{Ab}	50 ^{Ac}	33 ^{Ac}	66 ^{Abc}
Off-colony	133 ^{Ba}	83 ^{Ba}	75 ^{Aab}	50 ^{Aab}	17 ^{Ab}	125 ^{Aa}

Note: Means within a row with the same lowercase superscript letter and means within a column with the same uppercase superscript letter were not significantly different ($P > 0.05$).

vations of prairie dog “control” of *Prosopis* may be generally applicable to woody plants. If prairie dogs and associated herbivores do not selectively forage on *Prosopis*, but rather gnaw stems or defoliate plants after they attain a certain height, seedlings may develop root systems and accumulate enough of a bud bank and nutrient reserve to tolerate intense and repeated defoliation later in their life cycle. *Prosopis* seedlings are capable of vegetative regeneration within 2 wk of germination (Scifres and Hahn 1971), and 2- and 4-wk-old seedlings can withstand repeated shoot removal under controlled environment conditions (Weltzin 1990). This resistance to herbivory may enable *Prosopis* seedlings to establish and persist on a prairie dog colony for a period of years. The high density of short (≈ 6 cm tall) plants on the North Fork Colony (Table 7) may thus represent a vegetative reserve or “seedling bank” (Silvertown 1982, O’Connor 1995). The presence of “seedling” reserves on the Rock Canyon colony site may explain the rapid development of *Prosopis* stands after the extermination of prairie dogs in 1950 (Tables 8–10). In addition, the removal of prairie dogs may lead to reductions in populations of other herbivores associated with the colony (Fagerstone and Ramey 1996) that are potentially important to *Prosopis* population regulation (e.g., ants and granivorous deer mice, *Peromyscus maniculatus* [Uresk 1985]). The dynamics of woody plant stand development following prairie dog removal in other ecosystems may depend on mode of seed dispersal, palatability, forage value, and capacity for vegetative regeneration of the shrub or tree species involved.

Prairie dogs and Prosopis stand development

The distribution of woody plants across arid and semiarid landscapes is spatially variable, reflecting the effects of topography, geomorphology, and management practices (Tongway and Ludwig 1990, Knight et al. 1994, McAuliffe 1994, Archer 1995). Our results, along with qualitative observations by Osborn (1942) for shinnery oak (*Quercus* sp.) and sand sagebrush (*Artemisia filifolia*) scrub savanna in Oklahoma, suggest that historic changes in the distribution and abundance of prairie dogs would have affected spatial and temporal patterns of woody plant development in some

landscapes. After prairie dogs were eradicated from the Rock Canyon colony in 1950, *Prosopis* cover on the former colony site increased rapidly (1.5%/yr) relative to other portions of the landscape (0.8%/yr) (Table 8). Observed changes in woody plant canopy cover of *Prosopis* stands in temperate northern Texas are similar to those reported for subtropical southern Texas (1.0%/yr between 1941 and 1983) (Archer et al. 1988) and within the range observed for gallery forest expansion into North American tallgrass prairie (0–3%/yr; Knight et al. 1994). By 1973, woody plant cover on and off the former Rock Canyon colony was similar. However, differences in *Prosopis* stand structure reflecting different prairie dog habitation histories were still evident after 40 yr (Tables 9 and 10). *Prosopis* stands that developed on the former colony were characterized by a high density of small, young plants, whereas the *Prosopis* stands on non-occupied portions of the landscape were characterized by a lower density of larger, older plants.

Implications for interpreting vegetation patterns

Numerous examples indicate the importance of herbivory on seedling density and recruitment (McAuliffe 1986, Boyd 1988, Borchert et al. 1989) and plant population, community, and ecosystem dynamics (McNaughton 1983, Naiman 1988, Pastor et al. 1988, Yeaton 1988, Cantor and Whitham 1989, Dublin et al. 1990, Kerbes et al. 1990, Ruess and Halter 1990, Huntly 1991, Stuart-Hill 1992). Removal or exclusion of native herbivores may also produce significant changes in plant communities and ecosystem processes (Sinclair 1979, Watt 1981, Brown and Heske 1990). In some instances, the structure of modern plant assemblages may reflect prehistoric herbivory (Cox 1984, Janzen 1986, Owen-Smith 1987, Blackmore et al. 1990, Noble 1993).

In arid and semiarid regions of western North America, assumptions about the composition and geographic distribution of pre-settlement vegetation are often used, either explicitly or implicitly, as a baseline to assess impacts of land use. Unfortunately, the dearth of information about pre-settlement vegetation constrains our ability to reconstruct effects of land-use activities on vegetation structure. This lack of historical perspective can place short-term studies in the “invisible present” (Magnuson 1990), and can produce misleading conclusions about the causes of present-day patterns and processes. In this study, for example, explanations for differences in stand structure of *Prosopis* at the Rock Canyon site (Tables 9 and 10) would probably be erroneous without historical knowledge of prairie dog distribution.

Our results suggest that in regions where shrubs or trees such as *Prosopis* might have been competitive dominants, prairie dogs, when present, would have acted as a keystone species (Paine 1966, Mills et al. 1993) to limit the establishment and dominance of woody vegetation and to maintain a grassland physiognomy.

The historic physiognomy of communities in arid and semiarid regions may thus have been highly dependent on the former distribution of prairie dogs. Inconsistencies in historical reports of woody plant distribution and abundance in western North America (e.g., abundant by some accounts; absent by others [Malin 1953, Humphrey 1987]) may reflect the fact that (a) prairie dogs occupy selected topoeudaphic portions of landscapes; (b) prairie dog colonies may expand rapidly with time (mean annual increases in areal extent up to 200%); and (c) disease may periodically reduce prairie dog population density or eliminate entire colonies (Koford 1958, Dahlsted et al. 1981).

Prairie dog colonies occupied some 40×10^6 ha of the Great Plains and Texas in 1919 (Nelson 1919), with individual colonies encompassing up to 64 750 km² (Bailey 1905). Extensive eradication programs initiated in the early 20th century reduced the acreage of prairie dog colonies in the United States by an estimated 98% (U.S. Department of Interior 1963). Our results suggest that eradication of prairie dogs, in conjunction with reductions in fire frequency (e.g., Madany and West 1983, Savage and Swetnam 1990), released suppressed populations of woody plants such as *Prosopis* and made large areas available for their colonization. Although changes in climate (Neilson 1986) and atmospheric CO₂ concentrations (Idso 1992, Polley et al. 1994) favoring woody plants may have occurred in arid and semiarid regions since settlement, their abundance or stature probably would not increase on landscapes where prairie dogs were present. In contrast, widespread eradication of prairie dogs may have been both necessary and sufficient to enable post-settlement increases in shrublands and woodlands throughout much of western North America. Historical land management designed to remove one perceived impediment to livestock production may therefore have contributed significantly to development of another problem that is now a major impediment to sustainable livestock production.

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