VEGETATION OF AN ABANDONED PRAIRIE-DOG TOWN IN TALL GRASS PRAIRIE

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One of the native animals being preserved on the Wichita Mountains Wildlife Refuge in Oklahoma is the blacktailed prairie-dog (*Cynomys ludovicianus*). On private lands this species has been reduced to a mere remnant of its former population, and has been completely eradicated from much of its territory.

Despite complete protection since 1935, one colony on the refuge had declined to only a few individuals in 1946 when these observations were made, and subsequently disappeared entirely. The plant cover around one former population center exhibited distinct concentric zonation. The composition of the vegetation of the area was studied and the stages of secondary plant succession are described in this report. The history of the prairie-dog colony in relation to vegetation changes and land use is discussed.

USE HISTORY OF THE REFUGE

The Wichita Mountains Wildlife Refuge is a tract of 59,099 acres in southwestern Oklahoma which was administered by the U. S. Forest Service from 1901 to 1935, then transferred to the Bureau of Biological Survey which later became the Fish and Wildlife Service. This area consists of rugged low ranges of igneous rock and boulder ridges with intervening valleys and benches of deeply developed soils. The vegetation is an alternation of true prairie and oak savannah.

While a national forest, the area was grazed by cattle under permits to local stockmen, much of it heavily enough to result in serious range depletion. In 1907 the nucleus of a permanent bison herd was brought to the forest and given a pasture of approximately 8,000 acres from which all domestic stock has been excluded since. In 1937 all private grazing permits were terminated. Since that time the refuge has been grazed only by game animals and a herd of longhorn cattle. The estimated numbers of adult grazing animals in 1946 were 512 whitetailed deer, 260 elk, 43 antelope, 476 bison, and 236 longhorns. These amount to 1,137 animal-units [2] using the 59,099 acres of range, a rate of stocking allowing more than 50 acres to the animal-unit. However, the refuge includes approximately 14,000 acres so rough and rocky as to contribute very little of forage value, so that the stocking rate is in effect nearer 40 acres per animal unit.

PRAIRIE-DOGS ON THE REFUGE

When the area was transferred to the Bureau of Biological Survey in 1935, there were several active prairie-dog colonies on it. One, known as the "Grace Mountain town," was chosen to receive complete protection in order that an example of the species might be preserved under natural conditions. A policy of partial control, but not eradication, was adopted for the other colonies, except those near the boundaries of the refuge where they might serve as sources of reinfestation to private lands. These were eradicated.

In 1946 there were five active colonies on the refuge. All except the Grace Mountain town had been partially poisoned from time to time to limit their spread. About half of the area of each town was treated with "1080" bait in May and June 1946, with a reported kill of 80

[1] The assistance of Julian A. Howard, Assistant Refuge Manager, U. S. Fish and Wildlife Service, in the field work is gratefully acknowledged.

[2] Compiled by U. S. Soil Conservation Service.

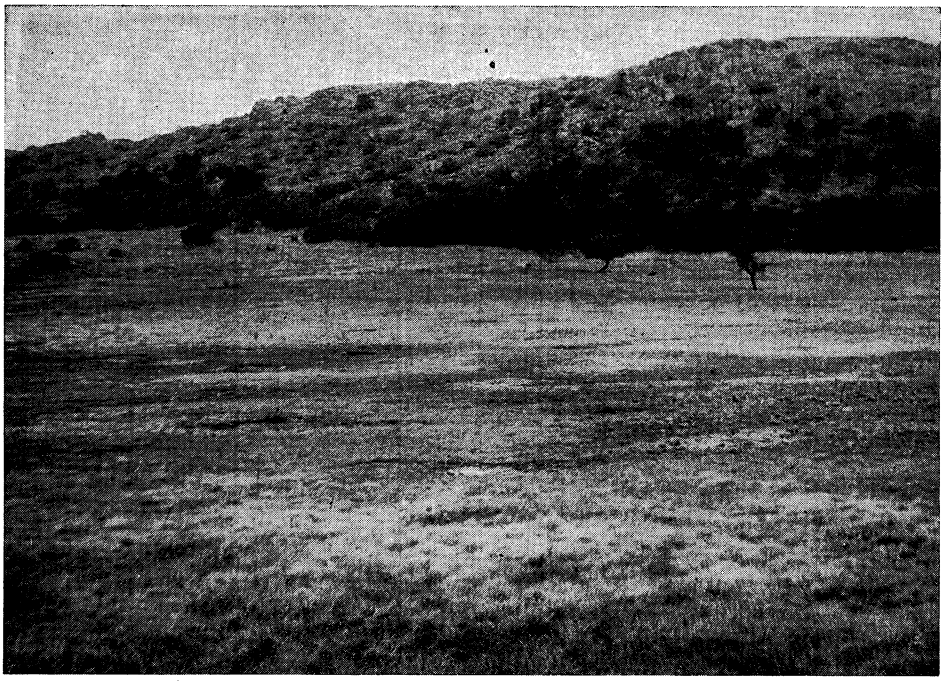

FIG. 1. General view of portion of Grace Mountain prairie-dog town abandoned in the summer of 1946.

per cent. The Grace Mountain town was last poisoned in 1926.

In September, 1946, the Soil Conservation Service, as a part of a training school for its personnel, made a thorough survey of the range vegetation of the refuge, including observations on the relations of wildlife to the vegetation. At this time it was discovered that, in spite of its protection, the Grace Mountain colony had dwindled to a mere remnant while the others had continued to grow. Subsequently, it was reported that the last of this colony of prairie-dogs had disappeared in the summer of 1947.[3]

The Grace Mountain town

The Grace Mountain prairie-dog town was in a narrow valley between Grace Mountain and Baker Peak in the remote northwest corner of the refuge. The "dog-town" area as indicated by the present vegetation was about half a mile long and a thousand feet wide. Its maximum area appears to have been about 50 acres, though it may have extended much farther down the valley in earlier days (figs. 1 and 2).

The area actually occupied by prairie-dogs in 1946 was less than an acre, and the principal effects of their activities were confined to about three acres. About a quarter mile up the valley from this last active nucleus was a second center obviously abandoned within the previous summer. Old burrows indicated that the two centers were once connected by a continuous population.

Around both centers of occupancy were the concentric zones of vegetation which aroused our interest and prompted this study. However, the zonation was more distinct around the upper abandoned nucleus and this one was chosen for intensive investigation.

The valley is a postclimax site within the true prairie. The original natural vegetation was composed of tall and mid

[3] Letter from Ernest J. Greenwalt, dated February 12, 1948.

grasses, with the tall grasses dominating the undisturbed cover. This was evident from remnants surrounding the area disturbed by prairie-dogs. According to information obtained by the Soil Conservation Service in the range survey, the usual proportions of the principal dominants in the climax cover on this site are big bluestem (*Andropogon furcatus*) 30 per cent, little bluestem (*A. scoparius*) 25 per cent, Indiangrass (*Sorghastrum nutans*) 20 per cent, sideoats grama (*Bouteloua curtipendula*) 10 per cent, and switchgrass (*Panicum virgatum*) 8 per cent. The open grassland valley is bounded on either side by a blackjack oak (*Quercus marilandica*) and post oak (*Q. stellata*) savannah which extends up the hillsides.

Methods of Study

Transects were laid out to cross at right angles on a center point in the abandoned prairie-dog town, running lengthwise and crosswise of the valley. The composition of the vegetation was recorded at regular 10-foot intervals along these transects by listing the first 10 plants touching the line beyond each point. The presence of prairie-dog burrows, ant beds, and other modifying influences within 25 feet on either side of the transects was recorded.

By comparing the sequence of species dominating at the various points along the four lines, seven distinct zones were distinguished. These were considered to represent stages of secondary succession from the denuded area in the center of the "last stand" of the prairie-dogs to the relatively undisturbed edge of the valley. The average composition of each zone was expressed as frequencies of occurrence of the species in the combined lists for the points representing the zones along the transects.

To supplement the detailed data along the transects, a sketch map of the study area was made, showing the variations in the aspect of the vegetation to a scale of

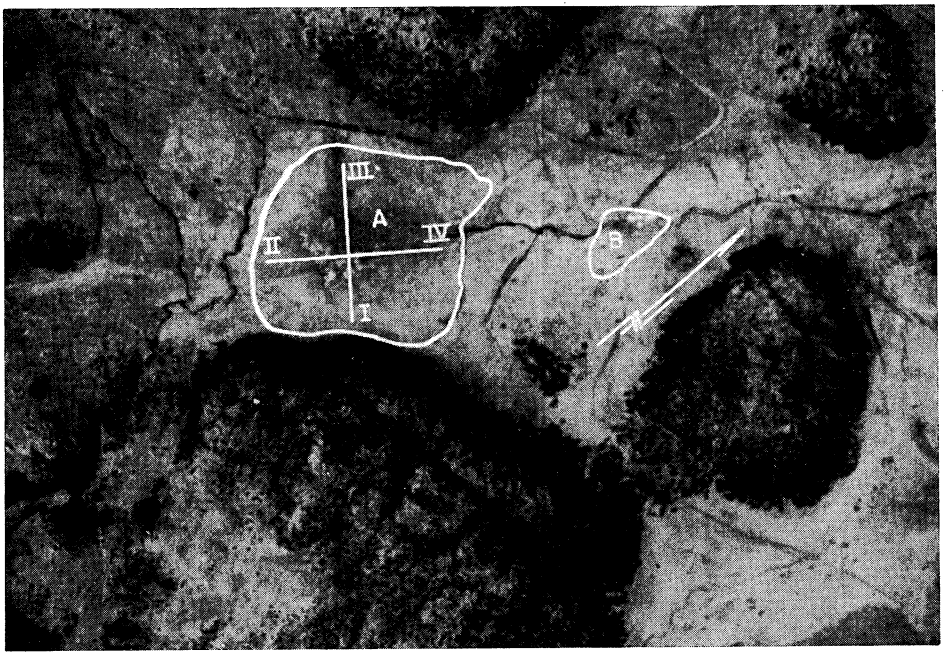

Fig. 2. Aerial photograph of Grace Mountain prairie-dog town area made in 1942. A, Approximate area shown in figure 3, with location of transects; B, Area still occupied by prairie-dogs in September, 1946.

one inch to 100 feet. Range type descriptions of each major zone as recognized by aspect were prepared by the standard reconnaissance method. These were later correlated with the transect data and the vegetation zones delineated as shown in figure 3.

Stages of plant succession

Stages of secondary plant succession may be identified by the species which successively dominate the plant cover of a disturbed area when disturbance ceases. On this basis, stages were recognized in the concentric bands of vegetation on the area abandoned by the prairie-dogs. Since these stages were consistently repeated in order on the four radiating lines, it is concluded that they reflect steps in vegetational development rather than zonation due to soils or other intrinsic site conditions.

Composition of the vegetation in the several zones or stages is shown in table I. Each species is listed under the zone in which it reached its greatest frequency. Its abundance in all zones where it occurred is indicated opposite the species name in the appropriate columns. Plant names are according to Standardized Plant Names (American Joint Committee on Horticultural Nomenclature, '42), except for a few species not included in that book, in which cases authorities are shown after the Latin names.

Table I shows the successive stages as follows:

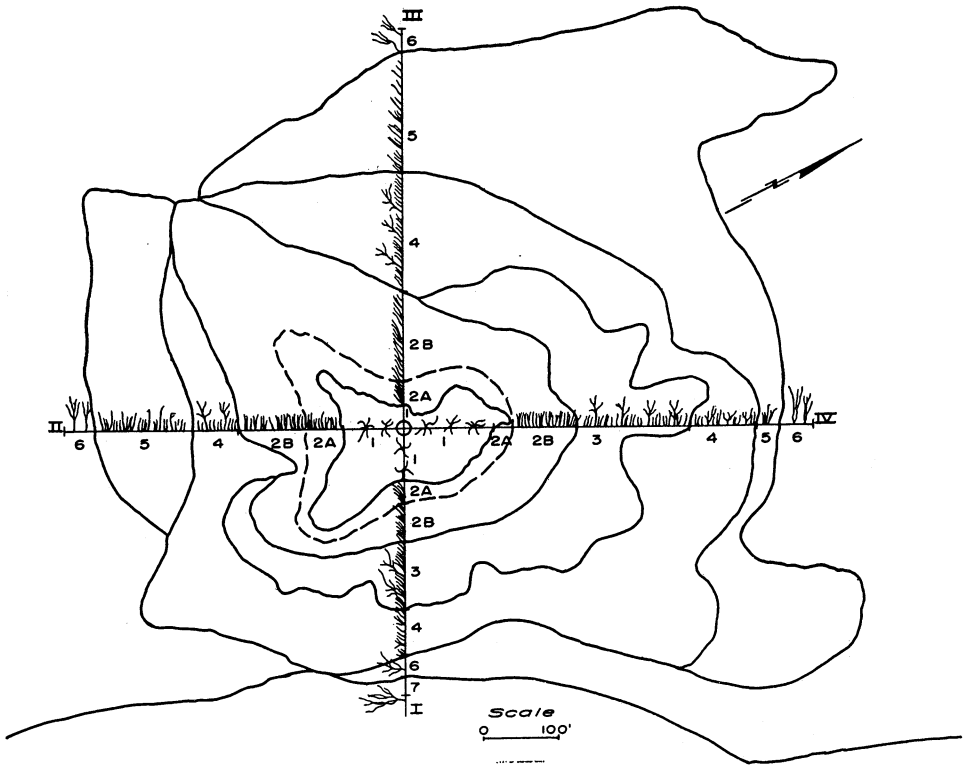

FIG. 3. Detail of plant cover of abandoned portion of Grace Mountain prairie-dog town. O, center point of transects: I, II, III, and IV, end points of transects; 1, barren area and mat forbs; 2A, first-year annual threeawn; 2B, older annual threeawn; 3, threeawn and forbs; 4, threeawn and perennial grasses; 5, short grasses; 6, subclimax mid grasses; 7, climax tall grasses.

TABLE I. *Composition of zones or stages in plant succession in abandoned prairie-dog town. Frequency is expressed as percentage of possible. Each species name appears under heading of stage in which it was most abundant*

Species	Frequency by zones or stages (per cent)						
	1 Mat forbs	2 Three-awn	3 Threeawn and forbs	4 Threeawn and perenn.	5 Short grass	6 Mid grass	7 Tall grass
1. MAT FORB STAGE							
Rushpea *Hoffmanseggia falcaria CAC*	31	T					
Shaggy purslane *Portulaca pilosa*	21	1					
Knotweed *Polygonum neglectum* Besser	15	2		2			
Carpetweed *Mollugo verticillata*	8						
Spotted spurge *Euphorbia maculata*	6	3					
Prostrate amaranth *Amaranthus blitoides*	2						
Scarlet globemallow *Sphaeralcea coccinea*	2						
Yellow oxalis *Oxalis stricta*	1	2	1		T		
Plains milkweed *Asclepias pumila*	1					1	
Bigbract vervain *Verbena bracteata*	T						
Cottonflower *Gossypianthus sheldonii* (Uline and Gray) Small.	T	T					
2. ANNUAL THREEAWN STAGE							
Prairie threeawn *Aristida oligantha*	6	68	24	32	17	11	
Tumblegrass *Schedonnardus paniculatus*		4	1	1			
Gummy lovegrass *Eragrostis curtipedicellata*		4		2		4	
Drummond St. Johnswort *Hypericum drummondii* T & G		1	2				
Thistle *Cirsium* sp.		T					
3. THREEAWN AND FORB STAGE							
Western ragweed *Ambrosia psilostachya*	1	2	26	4	6	12	
Coreopsis *Coreopsis* sp.			12	2	3		2
Spanish clover *Lotus americanus*			3	T			
Japanese brome (?) *Bromus japonicus* (?)			3	2	1		
Carolina canarygrass *Phalaris caroliniana*			1			2	
Little barley *Hordeum pusillum*	T	T					2
Lanceleaf loosestrife *Lythrum lanceolatum* Ell.		1	T				
Branched fleabane *Erigeron divaricatus* Michx.	T	T	T				

T = trace.

TABLE I—*Continued*

Species	Frequency by zones or stages (per cent)						
	1 Mat forbs	2 Three-awn	3 Threeawn and forbs	4 Threeawn and perenn.	5 Short grass	6 Mid grass	7 Tall grass
4. THREEAWN AND PERENNIAL STAGE							
Tumble windmillgrass *Chloris verticillata*		7	3	11	11	3	
Poverty dropseed *Sporobolus vaginiflorus*		T	4	11	T		2
Sedge *Carex* sp.			T	1			
Wright threeawn *Aristida wrightii*				1	1		
Upright prairieconeflower *Ratibida columnaris*		T		2	2		
Curlycup gumweed *Grindelia squarrosa*				1	T	1	
Wild carrot *Daucus carota*				T			
5. SHORT GRASS STAGE							
Blue grama *Bouteloua gracilis*			4	5	36	15	
Buffalograss *Buchloe dactyloides*		5	5	11	12	2	
Fringeleaf paspalum *Paspalum ciliatifolium*		1	1	2	4		
Sand dropseed *Sporobolus cryptandrus*	1	T		T	3	2	
Annual broomweed *Gutierrezia dracunculoides*					2		
Rosering gaillardia *Gaillardia pulchella*					1		
6. MID GRASS STAGE							
Silver bluestem *Andropogon saccharoides*		T			1	23	
Sideoats grama *Bouteloua curtipendula*		T				19	
Hairy grama *Bouteloua hirsuta*						2	
Slimflower scurfpea *Psoralea tenuiflora*						2	
Prairie acacia *Acacia angustissima*						1	
7. TALL GRASS STAGE							
Big bluestem *Andropogon furcatus*							16
Switchgrass *Panicum virgatum*							12
Scribner panicum *Panicum scribnerianum*	T	T	1	6		2	30
Fall witchgrass *Leptoloma cognatum*	1	T	1	4			16
Spikesedge *Eleocharis* sp.			4				10
Longspike triodia *Triodia stricta*			T				6
Rush *Juncus* sp.		T	1	T	T		2
Panicum *Panicum* sp.							1
Tall dropseed *Sporobolus asper*			T	T			T
Total coverage:	25%	50%	40%	50%	50%	60%	75%

1. *Mat forb stage.*—On the central area last occupied by prairie-dogs, annual forbs of mat-forming habit made up approximately 95 per cent of the cover. The principal species and their percentages in the average composition of the zone were rushpea 31 per cent, shaggy purslane 21 per cent, knotweed 15 per cent, carpetweed 8 per cent, and spotted spurge 6 per cent.

Total coverage by vegetation within this zone was progressively greater toward its edges. A small central area was almost completely barren. Where this stage was well developed, the average coverage was about 25 per cent. Including the barren area, this zone was about 200 feet long by 100 feet wide. The condition of the dirt around the burrows, claw marks, feces, and evidence of grazing on plants of the current year's growth showed that the prairie-dogs had used this area until the summer of 1946 (fig. 4).

2. *Annual threeawn stage.*—Surrounding the barren and mat-forb area was a continuous zone dominated by the annual, prairie threeawn, with only minor quantities of other species. Two sub-zones were evident:

a. First-year threeawn. Next to the mat forb area was a distinct band 20 to 50 feet wide of an almost pure stand of prairie threeawn. There was no plant residue on the ground and practically no remains of previous years' plant growth. Prairie-dog burrows were still barren, and there was some evidence of grazing on this year's growth of threeawn.

b. Older threeawn. Outside the first-year band was another of variable width (50 to 120 feet at the transects) in which a natural mulch of previous years' growth of threeawn covered the soil between the current year's plants. In this band, various other species made their appearance with increasing frequency toward the outer limits. Most of the prairie-dog burrows were covered with vegetation, mainly annual weeds.

Total coverage in the annual threeawn zone as a whole ranged from 30 to 60 per cent, with an estimated average of 50 per cent. The principal species were: Prairie

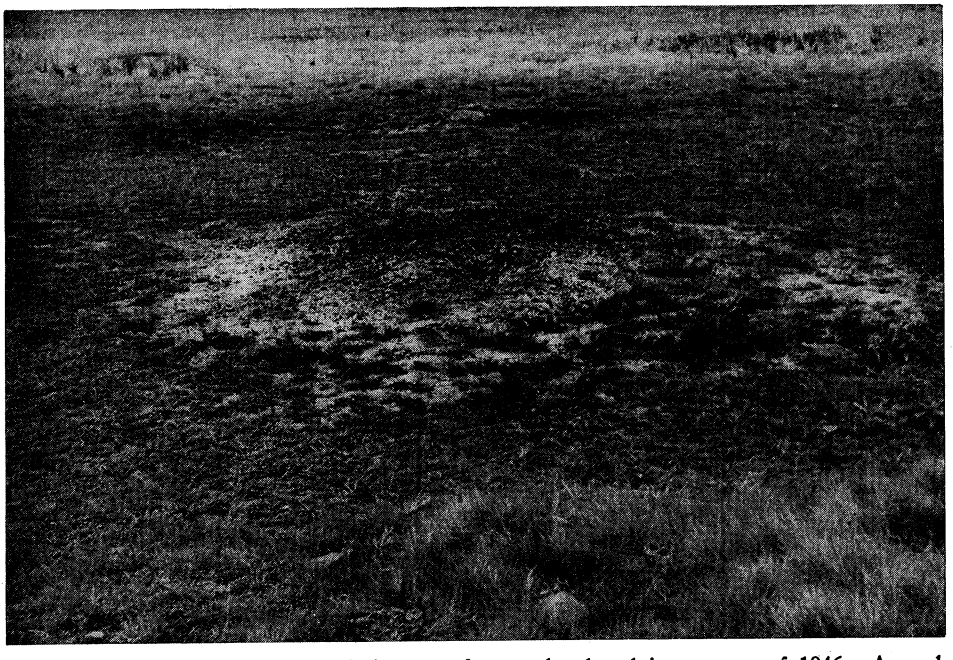

FIG. 4. Barren center and mat-forb zone of area abandoned in summer of 1946. Annual threeawn zone is seen as light-colored area in immediate foreground and background.

threeawn 68 per cent, tumble windmillgrass 7 per cent, and buffalograss 5 per cent.

3. *Threeawn and forb stage.*—In a rather indefinite zone of variable width, outside that completely dominated by prairie threeawn, annual and perennial forbs were prominent in the composition and especially in the aspect. The average composition of this zone as sampled by the transects was: western ragweed 26 per cent, prairie threeawn 24 per cent, and Coreopsis 12 per cent. Total coverage ranged from 20 to 50 per cent, with an average of about 40 per cent. Prairie-dog burrows in this zone were generally covered with vegetation typical of the zone or with pure stands of prairie threeawn.

4. *Threeawn and perennial grass stage.*—Completely surrounding the zones previously described was a band of varying width (50 to 150 feet at the transects) wherein perennial grasses shared dominance with the prairie threeawn. As sampled by the transects, the principal species were: prairie threeawn 32 per cent, poverty dropseed 11 per cent, tumble windmillgrass 11 per cent, buffalograss 11 per cent, Scribner panicum 6 per cent, and blue grama 5 per cent.

Total coverage of this zone ranged from 30 to 70 per cent, with an estimated average of 50 per cent. This zone began just beyond the outer-most prairie-dog burrows or included a few scattered burrows which were completely covered over with vegetation typical of the zone.

5. *Short grass stage.*—Next was a distinct zone in which blue grama and buffalograss made up approximately half the cover, with prairie threeawn occurring in greatly reduced quantity. The principal species were: blue grama 36 per cent, prairie threeawn 17 per cent, buffalograss 12 per cent, tumble windmillgrass 11 per cent, and western ragweed 7 per cent.

The average coverage in this zone was about the same as in the preceding one, estimated at 50 per cent, but was somewhat more uniform. Old burrows were either absent or completely covered over with vegetation typical of the zone.

6. *Subclimax mid grass stage.*—Each line was continued outward from the disturbed area until it sampled the vegetation which appeared least changed from the climax tall grass type. On three lines this was a zone dominated by the subclimax mid grasses, silver bluestem and sideoats grama. Its average composition on the transects included the following principal species: silver bluestem 23 per cent, sideoats grama 19 per cent, blue grama 15 per cent, western ragweed 12 per cent, and prairie threeawn 11 per cent.

Total coverage in this zone was estimated to range from 50 to 70 per cent with an average coverage of 60 per cent. Old prairie-dog holes were present only on the line extending toward the other center of population and these were completely covered over with vegetation typical of the zone.

7. *Climax tall grass stage.*—One line terminated in a narrow zone dominated by big bluestem and switchgrass just outside the woodland on the edge of the valley. An interrupted and irregular margin of these tall grasses along both sides of the valley aparently marked the boundary of the area never seriously modified by the activities of the prairie-dogs. The principal species along the transect were: big bluestem 16 per cent, switchgrass 12 per cent, Scribner panicum 30 per cent, fall witchgrass 16 per cent, a spikesedge 10 per cent, and longspike triodia 6 per cent. By observation of this same zone apart from the transect, little bluestem was noted among the dominants and Indiangrass as a subordinate species. The average coverage was estimated at 75 per cent.

The above-described stages of plant succession closely parallel those described by Smith ('40) on abandoned farmland in the mid grass type of True Prairie in central Oklahoma. He recognized (A) mixed weeds (those usually found on croplands), (B) prairie threeawn, (C) prairie threeawn and forktip threeawn (*Aristida basiramea*), (D) threeawn and

lovegrass (*Eragrostis*), (E) subclimax: silver bluestem, little bluestem, and sideoats grama, and (F) climax: little bluestem and sideoats grama.

Aside from the difference in the climax type, the succession on the abandoned prairie-dog town is characterized by the following differences from that on abandoned farmland: (a) The initial annual weed stage is characterized by prostrate mat-formers capable of growing on the compacted soil around the burrows and of surviving the close grazing by the prairie-dogs; (b) the taller-growing forbs appear after the annual threeawns have modified the unfavorable soil structure produced by trampling and denudation; and (c) a short grass stage results from the increase of grasses which survived the heavy grazing on portions of the area which were never denuded.

Decline of the prairie-dogs

The history of the plant cover may be reconstructed from the evidence. But what of the prairie-dogs? Why did this colony with complete protection decline while the others on the refuge continued to prosper and increase until it was necessary to poison to hold them in check?

Since the fortunes of the Grace Mountain town went almost unnoticed until the population was at a critically low ebb, it is possible only to speculate on what happened to the prairie-dogs from the time this colony was marked for preservation.

However, it is known that the prairie-dog is typically an animal of the short grass plains, or of the Mixed Prairie Association (Clements and Shelford, '39; Carpenter, '40). The population increased following settlement by the white man (Merriam, '02), and spread eastward into the mid grass and tall grass prairies (Schaffner, '26). The history of the spread of one colony from its original site in a mixed grass area into surrounding grass and shinnery oak vegetation under the influence of overgrazing by domestic stock has been traced (Osborn, '42). It seems apparent, then, that the presence of the prairie-dogs on this particular site, where the natural climax cover is dominated by tall grasses, was due to heavy grazing during its use as a cattle range.

Grazing pressure on this area was abruptly eased when the private grazing permits were terminated in 1937. Shortly afterward, the fence was removed from the original "buffalo pasture" on the refuge, and approximately 300 bison and 200 elk were given a range of nearly 30,000 acres, within which the Grace Mountain town was located.

The habit of the bison herds to concentrate in favored spots, grazing local areas closely and leaving others little used, was well known to the refuge staff. The effects of these grazing habits were quite apparent on the refuge when the range survey was made by the Soil Conservation Service. The site of the Grace Mountain prairie-dog town was one of the areas seldom frequented by the bison.

It may be concluded, then, that following the removal of the cattle, the grass cover in this area increased in stature and density in spite of the activities of the prairie-dogs. As the taller forbs and grasses moved in from the edges of the valley, the prairie-dogs retired to a smaller and smaller area. As the colony became overcrowded, some of the prairie-dogs moved out in search of new homes. The concentration resulted in the complete eradication of palatable food plants and final denudation of the central area. Finally, a few individuals found themselves occupying a barren area surrounded by a pure stand of threeawn grass unsuitable for food and too wide to range across to forage on better plants. At last the town was abandoned to the return of a type of vegetation unsuitable as a home for the prairie-dog. The final episode in the disappearance of the colony is recorded in correspondence from Refuge Manager, Ernest J. Greenwalt, as follows:

"On June 28, 1947, we noticed a half dozen young dogs approach the holes with a peculiar stiff-legged gait and they showed reluctance to enter. Some went down a

hole, immediately reappeared and then entered another hole. We investigated and heard a rattlesnake rattle in one hole. We did the same at other holes and located seven rattlers in all by their 'buzzing.' One of the truck drivers broke off a dry mesquite limb, shoved it down a hole a short distance and twisted it around and out came a nice fat rattler. The technique worked on two other holes and we took three rattlesnakes in all. The largest measured 52 inches in length and we guessed the other two at 'about four feet.' I had occasion to visit the town again on August 16, and there was no sign of any live dogs about. Our 'sacred' dog town is depopulated. Perhaps the rattlers were a factor in the final cleanup?"

Another factor suggested as influencing the contraction of the colony is the effects of the improved grass cover from the entire watershed on infiltration of rainfall, reviving the "seeps" along the sides of the valley and forcing the abandonment of some of the burrows. This, however, could have affected only a zone about 50 to 100 feet wide on either side, judging from the present occurrence of plants which indicate "seepy" conditions.

Evidence supporting the theory that plant succession eliminated the prairie-dogs is found in the history of the adjoining Baker's Peak colony, about a mile away on a bench at a higher elevation. This colony has continued to thrive, although subjected to periodic control by poisoning. In May, 1946, half of this colony was baited with the new poison "1080," which was about 80 per cent effective. A month later, a second trial was made after prebaiting. The unpoisoned bait was refused at all colonies where "1080" was used in the first trial. This was true at Baker's Peak, except for a few prairie-dogs on the side nearest the Grace Mountain town. The control agent believed [4] that these had moved in from the Grace Mountain colony since the first baiting, and had never tasted "1080." This confirms our independent conclusion that the prairie-dogs had migrated from the Grace Mountain to the Baker's Peak town, after examination of the study area failed to reveal any evidence of a "die-off."

In this connection, it is significant that there is abundant evidence of grazing by bison on the area occupied by the Baker's Peak colony and that the other prairie-dog towns on the refuge also are in areas regularly used by the big game.

Animal weeds

The concept of "animal weeds," which like certain plants increase with disturbance of the climax cover and decline as the climax is restored, has been advanced by several authors. It is well stated by Taylor, Vorhies, and Lister ('35) in discussing the relation of jack rabbits to grazing in southern Arizona as follows:

"It appears that grazing may also increase the number of insects, jack rabbits, and certain other rodents. Some of the animals behave successionally like the plants. Results of grazing are expressed not only in terms of weeds and annual grasses, but of animal 'weeds' also."

It was on this same wildlife refuge that Weese in 1928 ('39) found grasshopper populations approximately four times as great on the over-grazed cattle range as in the lightly used "buffalo pasture," leading him to suggest that insects could be excluded from a range area with a barbed wire fence. Taylor, Vorhies, and Lister concluded that, "As in the case of Weese's insects, if one could hold stock pressure to a point where sufficient volume of grass is maintained, jack rabbits will be less numerous. To a certain extent one can keep out jack rabbits with a barbed wire fence."

On the basis of the history of the Grace Mountain prairie-dog town, it appears that we are prepared now to add prairie-dogs to the list of animal weeds which can be excluded, at least from the tall grass prairie, with a barbed wire fence.

[4] Letter from A. E. Gray to Ernest Greenwalt.

Summary and Conclusions

The Grace Mountain prairie-dog colony on the Wichita Mountains Wildlife Refuge has been protected since 1935 to preserve an example of this species in its natural habitat. Despite this protection, the colony has waned and finally disappeared.

The plant cover around one population center which was abandoned in the summer of 1946, exhibits distinct concentric zonation. The composition of the vegetation on this area was studied, and the history of the prairie-dog colony traced in relation to vegetation changes and land use.

The climax cover of the site is the tall grass type of the True Prairie, normally dominated by big bluestem, little bluestem and Indiangrass with lesser amounts of other tall and mid grasses.

The stages of secondary plant succession on the abandoned portion of the prairie-dog town, as represented by the concentric zones, are as follows:

1. Mat forbs, dominated by rushpea and shaggy purslane.
2. Annual threeawn, dominated by prairie threeawn.
3. Threeawn and forbs, dominated by prairie threeawn and western ragweed.
4. Threeawn and perennial grasses, dominated by prairie threeawn, poverty dropseed, tumble windmillgrass, and buffalograss.
5. Short grasses, dominated by blue grama and prairie threeawn.
6. Subclimax mid grasses, dominated by silver bluestem and sideoats grama.
7. Climax tall grasses, dominated by big bluestem, switchgrass, and Scribner panicum.

In the tall grass type, prairie-dogs are "animal weeds," and, like grasshoppers and jack rabbits, can be excluded or reduced by the use of a barbed-wire fence to keep out livestock.

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