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DYNAMICS OF PLAGUE IN A GUNNISON'S PRAIRIE DOG COLONY COMPLEX FROM NEW MEXICO

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ABSTRACT: A plague (*Yersinia pestis*) epizootic spread through Gunnison's prairie dogs (*Cynomys gunnisoni*), and possibly other rodent species, in the Moreno Valley in north-central New Mexico between winter 1984–1985 and autumn 1987. We observed the progress of the epizootic and subsequent population recovery at four prairie dog towns within the valley during this period. At two towns (Midlake and Val Verde) the prairie dogs were marked prior to the epizootic. At two additional towns (Vega and South Entrance) prairie dogs were marked following the epizootic. In 1988, a second epizootic occurred at Vega. One hundred thirty-nine serum samples were collected from prairie dogs and other rodents and 1,750 fleas were collected from animals and burrows. Fleas infected with *Y. pestis* were collected from prairie dogs, deer mice (*Peromyscus maniculatus*), and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*). Prairie dog fleas included *Oropsylla hirsuta, O. labis* and *O. tuberculata*; deermouse associated fleas were *Aetheca wagneri* and *Rhadinopsylla sectilis,* and *Oropsylla bacchi* was associated with thirteen-lined ground squirrels. All of the above flea species were collected from prairie dog burrows. All rodent species shared some flea species. Thirteen-lined ground squirrels disappeared shortly before plague was identified in prairie dogs at Midlake. Meadow voles were rare following the epizootic at Vega in 1986, became abundant in 1987, and disappeared at the time of the second prairie dog epizootic in summer 1988. Although we collected serum from Gunnison's prairie dogs, thirteen-lined ground squirrels, deer mice, and meadow voles (*Microtus pennsylvanicus*), we identified elevated serum titers against *Y. pestis* only in Gunnison's prairie dogs. Prairie dog mortality at all towns affected by plague was in excess of 99%. Serum antibody titers indicate that more than 40% of the few prairie dogs left to establish colonies following epizootics survived plague infection.

Key words: *Cynomys gunnisoni*, epizootiology, fleas, interspecific transmission, plague, population dynamics, *Yersinia pestis*.

INTRODUCTION

Plague (*Yersinia pestis*) was first discovered in New Mexico (NM; USA) in Gunnison's prairie dogs (*Cynomys gunnisoni*) near Zuni in 1938 (Link, 1955). Plague is now found throughout the state, and by 1982 had been reported in 31 of 33 counties (Barnes, 1982). In NM, 21 species of rodents and 16 species of fleas have been found infected with *Y. pestis* (Weber, 1978). Plague was first recorded in the Moreno Valley, Colfax County, NM, in August 1949 when it was found in Gunnison's prairie dogs (Link, 1955). There were no further observations of plague there until 1983 when a teen-age boy from the town of Eagle Nest (NM) became ill with the disease and died. The NM Environmental Improvement Division (NMEID, Santa Fe, NM, USA) collected fleas from prairie dog and ground squirrel burrows around the town of Eagle Nest and found *Y. pestis* positive *Oropsylla bacchi,* fleas that associate with thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), *O. hirsuta* and *O. labis,* flea species associated with Gunnison's prairie dogs, and *Rhadinopsylla sectilis,* a deer mouse (*Peromyscus maniculatus*) flea (NMEID, unpublished records).

Gunnison's prairie dogs are highly susceptible to plague, and three attempts to study the species' social behavior were interrupted by the disease (Lechleitner et al., 1962; 1968; Fitzgerald, 1970; Rayor,

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1985). Mortality in Gunnison's prairie dogs as a result of plague has been described, but those reports have not followed the recovery of prairie dog populations subsequent to plague. In this paper, we describe a wave-like plague epizootic that swept through a 100 km^2 complex of Gunnison's prairie dog towns in the Moreno Valley, NM, between spring 1985 and summer 1987; we also document the course of recovery of the prairie dog populations subsequent to the epizootic. Additionally, we attempt to analyze the dynamics of the plague epizootic, including both intraspecific and interspecific transmission of the disease in the Moreno Valley.

METHODS

The Moreno Valley, elevation 2,560 m, is located in the Sangre de Cristo Mountains (36°30′N, 105°15′W) Colfax County, NM (Fig. 1). The bottom of the Moreno Valley supports a variety of grasses and shrubs; plant cover and productivity are high. Suitable prairie dog habitat in the Moreno Valley covers approximately 100 km^2. The land is mostly privately owned cattle ranches. Cattle grazing is limited to summers because winters are very cold with mean daily temperatures of −5 C in January. The warmest month is July with a mean daily temperature of 18 C. The heaviest precipitation usually occurs during July and August (NM Office of the State Climatologist, 1984), although winter snow also is important to the range vegetation.

Two geographic features in the Moreno Valley bound the plague-affected areas. Six-mile Creek flows east from the forest into Eagle Nest Lake, approximately 4 km south of the town of Eagle Nest (Fig. 1). The valley formed by this stream contains mesic grassland with the water table close to the surface. Prairie dogs did not dig burrows in this habitat, and they rarely ventured into it more than 5 to 10 m. The grass was usually high enough to obstruct a prairie dog's view of its surroundings. The second boundary was Jackson Hill, a ridge that crosses the valley approximately 7 km south of Six-mile Creek. The ridge is covered by shallow soil and xeric grassland similar to that of uplands throughout the valley. Prairie dog colonies were present both north and south of Jackson Hill, but were separated by approximately 1 km.

The first study area (Midlake) was located adjacent to Eagle Nest Lake in October 1984,

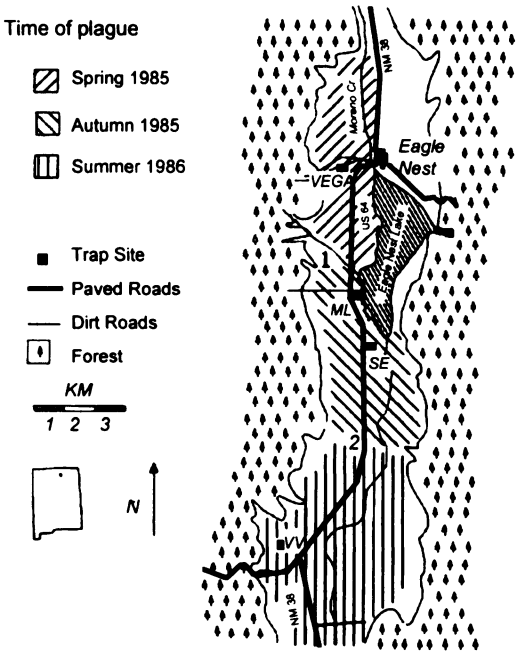


FIGURE 1. Map of the Moreno Valley showing the locations of the study areas (ML = Midlake, SE = South Entrance, VV = Val Verde), and the progress of plague during the period March 1985 to November 1986. Plague probably began in prairie dogs north and east of Eagle Nest during the summer of 1983. The shading shows the course of plague during the period winter 1985–summer 1987. The three regions were separated by boundaries at Six-mile Creek (1) and Jackson Hill (2).

and consisted of 9 ha in the middle of a prairie dog town that covered approximately 100 ha (Fig. 1). The Val Verde site was identified at the south end of the valley in October 1985. Both sites were established in advance of the plague epizootic. After plague eliminated prairie dogs at Midlake, the Vega study site was established in March 1986, at the north end of the valley 2 km west of the town of Eagle Nest, and South Entrance was identified in June 1987, near the south end of Eagle Nest Lake approximately 2 km south of the original Midlake study site.

Prairie dogs were trapped in small Tomahawk live traps (14 × 14 × 40 cm) baited with rolled oats. When captured, prairie dogs were weighed on a triple beam balance, sexed, aged to juvenile or adult age class by weight and pelage color (Cully, 1997), uniquely marked by toe clip or numbered fingerling tags attached to the ear, and individually marked with commercial hair dye. We attempted to trap all of the prairie dogs at the study sites. Visual observations of

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fur marks combined with recaptures in traps indicated that more than 90% of prairie dogs at the staked study sites at Midlake, Vega and South Entrance were marked. At Val Verde approximately 50% of the active prairie dogs were captured on the 1 ha area trapped. Mark recapture trapping was inappropriate during population declines because the high rates of mortality would bias the analysis.

In 1988 at Vega, South Entrance, and Val Verde, prairie dog populations were estimated by visual scan counts (Fagerstone and Biggins, 1986; Menkens and Anderson, 1993). At Vega and South Entrance, 2 ha plots were marked with wood stakes; the grids were 100 × 200 m with stakes placed at 20 m intervals. The stakes made it possible to systematically count prairie dogs on areas of known size during periods when it was not possible to trap animals or when the populations were changing rapidly. Visual counts were made from a car parked approximately 100 m from the prairie dog towns. Counts were made with the aid of 10× binoculars and a 30× spotting scope three or four times in the morning while prairie dogs were most active above ground. The highest count was used for the population or density estimate.

During 1985, blood samples were collected from toes when the animals were marked by toe clipping. This method was satisfactory only during warm weather when the wounds bled freely. Consequently, beginning in April 1986, blood samples were collected by cardiac puncture. Newly captured animals were anesthetized with ether to reduce stress during handling, and to simplify collecting fleas which also were anesthetized by the ether. All sera were tested for antibodies to *Y. pestis* using the passive hemagglutination test (World Health Organization, 1970). Sera with titers ≥ 1:16 were considered positive.

Beginning in July 1985, fleas and blood samples were collected from newly captured prairie dogs. Fleas were brushed from the anesthetized animals during the handling procedure. Fleas also were collected from prairie dog burrows by swabbing the burrows with a square of flannel attached to the end of a sewer cable. The swab was inserted 1 to 2 m into burrows. Fleas were immediately removed with forceps and placed in a 2% NaCl solution in a small vial. If no fleas were captured on the first swab, another burrow was selected. If the swab collected fleas, the burrow was swabbed repeatedly until fleas were no longer captured. Burrows were selected from throughout the marked portions of the study sites, and represent a cross section of the burrows in the colony. Fleas from burrows that were close together and shared by individuals within social groups of prairie dogs were often combined in the same vial for submission to the Centers for Disease Control (CDC, Plague Branch, Division of Vector-borne Infectious Diseases, Ft. Collins, Colorado, USA). Fleas were identified and analyzed for *Y. pestis* at CDC.

In the laboratory, fleas were individually examined microscopically and identified to species following the classification of Traub et al. (1983) or Hopkins and Rothschild (1962). After identification, fleas were pooled by collection site, host species (or social group), and flea species. Fleas collected from different social groups or towns were kept separate as described above. Flea pool size never exceeded 25 individuals. Flea pools were triturated in a small amount of physiological saline and 0.1 ml aliquots were inoculated subcutaneously into 6-wk-old mice. The mice that died within 21 days of inoculation were necropsied and liver and spleen tissues were removed for bacteriological analysis to verify that plague was the cause of death as described by Quan et al. (1981).

Rodents other than prairie dogs were trapped at Midlake, Val Verde, and Vega to determine which species were present and to collect fleas and serum samples for plague analysis. Small rodents were trapped at study areas on three or more occasions between September 1985 and September 1988. Folding aluminum 8 × 9 × 23 cm Sherman Live Traps were set in parallel rows of 10 with 10 m between traps. The number of rows set varied between trap sessions at the three areas. Traps were baited each evening and examined in early morning and at least two times during the day. Because of high mortality during blood collection, (blood was collected from these species by cardiac puncture in order to obtain adequate sized samples for antibody analysis), mark-recapture population estimation was not appropriate for deer mice and meadow voles (*Microtus pennsylvanicus*). Relative population estimates, based on captures per trap-night effort, were calculated.

RESULTS

Plague occurred in the Moreno Valley between autumn 1984 and summer 1987 (Table 1, Fig. 1). The epizootic occurred in three spatially and temporally distinct phases. In winter-spring 1985, plague-killed prairie dogs in the northern third of the valley west of Moreno Creek and Eagle Nest Lake, north of Six-mile Creek (Fig. 1). From July 1985 to July 1986

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TABLE 1. Chronological list of plague events in the Moreno Valley (New Mexico, USA) during the 1984 to 1987 plague epizootic in Gunnison's prairie dogs as they occurred in the north, middle and south thirds of the valley.

Date	North (Vega)	Middle (Midlake, South Entrance)	South (Val Verde)
8/83	Human plague case. Plague positive fleas from GPD, TLGS, DM[a]		
9/84	GPD abundant	GPD and TLGS abundant	GPD abundant
11/84–2/85	Hibernation	Hibernation	Hibernation
4/85	Few GPD active	GPD breeding activity, TLGS rare	GPD breeding activity
5/85	GPD numbers decline	GPD numbers steady	GPD numbers steady
6/85	Last known GPD colony disappears	Juvenile GPD's emerge, last TLGS trapped	
7/85		Begin collecting fleas	
8/85		Plague positive fleas at Midlake	
9/85		<25 GPD observed at Midlake	GPD numbers high
10/85–2/86		Hibernation	Collect fleas and blood samples at Val Verde; negative for *Y. pestis*
3/86	Vega GPD colony forms. Trap DM and MV for fleas and blood	7 GPD captured at Midlake. Trap DM and MV for fleas and blood	
6/86	Juveniles emerge at Vega	1 litter emerges at Midlake. Disappears 2 wk later. Collect plague positive fleas from burrows	Trap DM and MV for fleas and blood; negative for *Y. pestis*
7/86		Last GPD disappears at Midlake	GPD's disappear from portion of Val Verde, collect blood and fleas. Fleas not tested, blood negative for *Y. pestis*
8/86			GPD population collapse, few remnants at local sites within colony; fleas positive for *Y. pestis*
9/86	Adult GPD's hibernate	Identify GPD colony at South Entrance	
4/87	≈50 GPD's emerge from hibernation	9 GPD's at South Entrance	Scattered GPD's present
6/87	Juvenile GPD's emerge	Juvenile GPD's emerge at South Entrance	No juvenile GPD's observed, *Y. pestis* positive fleas in burrows and blood contains antibodies to *Y. pestis*
6/88	>500 GPD's at Vega	≈25 GPD's at South Entrance	≈28 GPD's with young present
7/88	GPD population decline at Vega		
9/88	1 GPD remains at Vega, plague positive fleas collected from burrows		

[a] GPD = Gunnison's prairie dog; TLGS = thirteen-lined ground squirrel; DM = deer mouse.

TABLE 2. Results of blood samples collected from mammals at the Moreno Valley (New Mexico, USA).

Area	Species	1985	1986	1987
Midlake Study Area	*Cynomys gunnisoni*	5[a]	7	
	Spermophilus tridecemlineatus		1	1
	Peromyscus maniculatus		4	2
Val Verde	*Cynomys gunnisoni*	3	23	2 (2)[b]
	Spermophilus tridecemlineatus		12	1
	Peromyscus maniculatus		13	
	Microtus pennsylvanicus		4	1
Vega	*Cynomys gunnisoni*		15 (2)	1
	Spermophilus tridecemlineatus		4	4
	Peromyscus maniculatus			1
	Microtus pennsylvanicus		16	9
South Entrance	*Cynomys gunnisoni*			5 (2)
	Spermophilus tridecemlineatus			3
Total		8	99 (2)	32 (4)

[a] Number of samples analyzed. Underline indicates that samples were collected during epizootic.
[b] Number of samples with antibodies against *Y. pestis* in parentheses.

plague-killed prairie dogs in the middle of the valley between Six-mile Creek and Jackson Hill. Plague occurred between June 1986 and July 1987, south of Jackson Hill.

There was no evidence of plague in prairie dogs in the middle of the valley until July 1985. Visual observations indicated that the density of Gunnison's prairie dogs was similar throughout the valley in October 1984. The density estimate based on trapping at Midlake in October 1984, was 30/ha, and in July 1985, was 28/ha. On 24 July 1985, an adult male died in a trap. He had been in the trap for <2 hr when found, and at that time he was moribund. Two hr later he was dead. A blood sample obtained from this animal was sero-negative for *Y. pestis*; however, Gunnison's prairie dogs die so quickly from plague that they may fail to develop measurable antibodies before death; this also is true for laboratory mice (Quan et al. 1981). On 6 August 1985, the first *Y. pestis* positive fleas were collected from burrows at Midlake (see below). By September the population had declined noticeably, and by early October 1985, approximately 25 prairie dogs remained where 168 had been marked. At the same time the population declined similarly throughout the central third of the valley. At the Midlake study area only 7 to 10 animals emerged from hibernation in April 1986, where there had been approximately 90 one year earlier. One litter of three juveniles and a single adult 200 m south were all that remained on 14 June 1986. None of these animals was captured, but flea samples collected from burrows used by the juveniles were positive for *Y. pestis*. On 5 July 1986, there were no longer any prairie dogs at Midlake.

There were no indications of plague at the south end of the valley until June 1986. Three antibody negative serum samples and eight *Y. pestis* negative flea samples were collected in October 1985 (Tables 2, 3) from 18 prairie dogs trapped at Val Verde. The first indication of plague at the south end of the valley occurred between 1 and 14 June 1986, when prairie dogs disappeared from a 2 ha field adjacent to US Highway 64 at Val Verde. From 4 to 6 July 1986, 30 prairie dogs were trapped and marked at a 1 ha area near the center of the Val Verde Town. Visual counts of marked and unmarked animals at the trap area indicated that about half of the prairie dogs were marked so the

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TABLE 3. Fleas from Gunnison's prairie dog burrows in the Moreno Valley (New Mexico, USA).

Area	Year[a]	Number of burrows/number sampled	OH[b]	OL[b]	OTC[b]	OB[b]	AW[b]	CD[b]
Midlake	1985	16/78[c]	56 (6/10)[d]	18				
	1986	12/41[c]	58 (2/6)	22 (2/6)		1		
	1987	4/25		13				
Val Verde	1985	7/21	18	1				
	1986	20/59	235 (2/19)	143 (3/11)			1 (1/1)	
	1987	12/35[c]	109 (1/3)	77 (1/6)		2		
	1988	1/25						4
Vega	1986	15/108	79					
	1987	4/25	11					
	1988	15/25	96 (5/6)	8 (3/3)	2 (2/2)	4 (1/2)		
South Entrance	1987	2/25		7	7	6		

[a] Underline indicates year when plague was active in prairie dogs.
[b] OH = *Oropsylla hirsuta*, OL = *Oropsylla labis*, OTC = *Oropsylla tuberculata cynomuris*, OB = *Oropsylla bacchi*, AW = *Actheca wagneri*, CD = *Catallagia decipiens*.
[c] Additional samples were collected, but the number of burrows without fleas was not recorded.
[d] Number of fleas collected (number of plague positive pools/total number of pools).

population at that time was approximately 50 per ha. The colony covered approximately 200 ha and consisted of 5,000–10,000 prairie dogs. Four blood samples tested from that time had negative antibody titers to *Y. pestis*. Fleas were collected and identified, but not assayed for *Y. pestis*. By 11 August 1986, there had been a massive die-off and only 4 to 5 prairie dogs remained at the center of the colony. There were scattered prairie dogs across the town, and a concentration of approximately 100 on a ridge 400 m to the northwest that was separated from the rest of the town by mesic habitat with deep grass that was little used by prairie dogs. By mid-September 1986, there were no active prairie dogs at the central areas of the Val Verde town where densities had been highest in mid-summer, and the population was noticeably reduced at the peripheral area. In July 1987, we trapped four prairie dogs from the center of the town and all were nulliparous adult females. The duration of the epizootic at the south end of the valley was approximately 1 yr. However, more than 90% of the mortality occurred between 8 July and 11 August 1986.

Between September 1984 and May 1987, the Gunnison's prairie dog population in the Moreno Valley was reduced from more than 100,000 animals to between 250 and 500. This represents a minimum mortality rate of ≥99.5%. This mortality estimate is conservative because the survivors included animals born during 1986 and 1987, after the epizootic at the north end of the valley.

At Midlake in October 1984, thirteen-lined ground squirrels were released from traps without marks, so we cannot estimate their density beyond noting that they were nearly as frequently captured as prairie dogs. During spring 1985, only three thirteen-lined ground squirrels were caught at Midlake compared to 77 prairie dogs. Thirteen-lined ground squirrels disappeared from Midlake by the end of June 1985, but whether they had plague is not known. Limited trapping at Midlake indicated that the deer mouse population there was high (0.12/trap night) during October 1985, at the peak of the prairie dog epizootic (Table 4). Also at that time, one meadow vole without fleas and with a negative antibody titer to *Y. pestis* was trapped. In later trap sessions the deer

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TABLE 4. Results of live-trapping deer mice and meadow voles in the Moreno Valley (New Mexico, USA).

Area	Year[a]	Trap nights	*Peromyscus maniculatus*		*Microtus pennsylvanicus*	
			Captures	Per trap night	Captures	Per trap night
Midlake	1985	200	23	0.1150	1	0.0050
	1986	120	6	0.0500	0	
	1987	80				
Val Verde	1985	80	6	0.0750	0	
	1986	360	24	0.0667	8	0.0400
Vega	April 1986	120	0		1	0.0083
	September 1986	80	0		33	0.4125
	1987	560	6	0.0107	37	0.0661
	1988	300	0		5	0.0167

[a] Underline indicates year when plague was active in prairie dogs.

mouse density dropped to 0.5/trap night, <one half that in October 1985, and no more voles were captured there (Table 4).

At Val Verde, no obvious change in thirteen-lined ground squirrel numbers preceded the epizootic in prairie dogs, but since little trapping occurred there prior to June 1986, it is unlikely that we could have detected a reduction if one had occurred. At the south end of the valley, deer mouse populations were consistently low throughout the period October 1985 to October 1987. Voles were first captured at Val Verde in August 1986, and were still present there in 1987 (Table 4).

Rodents other than prairie dogs were not trapped at Vega until 1986, 1 yr after the plague epizootic there. Thirteen-lined ground squirrels were present in low numbers until summer 1988, when they disappeared simultaneously with the disappearance of the prairie dogs. In March and April 1986, voles and deer mice were uncommon. Later that year the vole population increased and stayed high through 1987. In September 1988, when the prairie dogs disappeared at Vega, the vole population was again low (Table 4). Deer mice were present at Vega in low numbers in August 1987 and September 1988.

The population densities of the different species varied at each area over time. In most cases there was no predictable relationship between the number of rodents and the subsequent plague phenology at the local prairie dog towns. Exceptions to this generalization were: (1) the absence of voles in the meadow near Vega in Spring 1986 after the plague epizootic, and the growth and subsequent decline of the vole population prior to the disappearance of prairie dogs at Vega in 1988; and (2) the disappearance of thirteen-lined ground squirrels prior to the prairie dog plague epizootic at Midlake, and concurrent with the epizootic at Vega in 1988.

One hundred thirty-nine serum samples were collected and tested for antibody titers, 61 from prairie dogs (six antibody positive), 26 from thirteen-lined ground squirrels (zero positive), 20 from deer mice (zero positive), and 30 from meadow voles (zero positive; Table 2). Although sera were collected before, during, and after the epizootic, all positive sera were collected 1 yr or more after the epizootic. Two positive prairie dog sera from Vega in April 1986, and two from Val Verde in July 1987, had titers of 1:256; the two positive samples from South Entrance taken in May 1987, had titers of 1:128. At Vega only two of 15 post-epizootic samples were positive while at South Entrance two of five were positive and at Val Verde two of two were positive.

One thousand seven hundred fifty fleas were collected from prairie dogs burrows (Table 3), prairie dogs (Table 5), thirteen-lined ground squirrels, meadow voles, and deer mice (Table 6). The highest number

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TABLE 5. Number of fleas collected from Gunnison's prairie dogs in the Moreno Valley (New Mexico, USA).

Area	Year[a]	Number of hosts	OH[b]	OL[b]	OTC[b]	OB[b]	RS[b]	MV[b]
Midlake	1985	3/16[c]	15	6				
	1986	4/4	12 (1/3)[d]	3		3		
Val Verde	1985	8/8	63	9		1		
	1986	19/30[e] 13/13	40[e] 80	27[e] 3		1[e] 1		
	1987	1/1	6	1				
Vega	1986	9/43 ?/21	59	6	27	4	1	1
	1987	54	126	4	2			
South Entrance	1987	5	18	2	7			

[a] Underline indicates year in which plague was active.
[b] OH = *Oropsylla hirsuta*, OL = *Oropsylla labis*, OTC = *Oropsylla tuberculata cynomuris*, OB = *Oropsylla bacchi*, RS = *Rhadinopsylla sectilis*, MV = *Monopsylla vison*.
[c] Number with fleas/number examined.
[d] Number of fleas collected (number of plague positive pools/total number of pools).
[e] Indicated samples from July 1986 were not assayed for plague.

of fleas taken from any animal was 25 from a prairie dog at Val Verde in October 1985, prior to the epizootic there. The highest number from burrows was 98 from a burrow at Val Verde on 30 June 1987, 1 yr after the epizootic. Twenty-seven flea pools were collected directly from prairie dogs; one (4%), taken at Midlake during the epizootic was positive for *Y. pestis* (Table 5). One hundred of 370 censused burrows contained fleas. Among infested burrows, mean numbers of fleas were 3.9 (n = 8, SD = 2.6) at Midlake, 4 (n = 2, SD = 1.4) at South Entrance, 17.3 (n = 31, SD = 26.7) at Val Verde, and 5.0 (n = 29, SD = 5.9) at Vega. Other flea samples were collected, but the number of burrows without fleas were not counted regularly until June 1986. Ninety pools collected from prairie dog burrows during or following epizootics were analyzed for *Y. pestis*, and of these 37 (41%) were positive. The percentage of *Y. pestis* positive fleas was lower than the number of positive pools because a single positive flea would make the entire pool positive and most pools consisted of more than one flea. The minimum field infection rates among flea species in burrows varied: 100% (n = 1) for *A. wagneri*, 9% (n = 6 burrows) for *O. bacchi*, 4% for *O. labis* (n = 38 burrows), and 3% (n = 58 burrows) for *O. hirsuta*, the most abundant flea species.

On 6 August 1985, NMEID collected *Y. pestis* positive fleas from prairie dog burrows at Midlake. During the epizootic at Midlake in August and September 1985, 21 fleas were collected from three of 16 prairie dogs examined. An additional 18 fleas were collected from four prairie dogs in 1986, and one pool of *O. hirsuta* was positive for *Y. pestis*. On 14 June 1986, one litter of juvenile prairie dogs which we were unable to trap was present at Mid-

TABLE 6. Number of fleas collected from rodents other than prairie dogs in the Moreno Valley (New Mexico, USA).

Species	n	EW[a]	OH	OL	OTC	OB	OS	RS	AW	MT	CN	CD	MAB	MAS
Spermophilus tridecemlineatus	23		2	6	2	98		1	4	1	1			
Peromyscus maniculatus	32	8	2	2		3	6		64	10		5		
Microtus pennsylvanicus	37	1											2	26

[a] EW = *Epitidea wenmani*, OH = *Oropsylla hirsuta*, OL = *Oropsylla labis*, OTC = *Oropsylla tuberculata cynomuris*, OB = *Oropsylla bacchi*, OS = *Oropsylla stanfordi*, RS = *Rhadinopsylla sectilis*, AW = *Aetheca wagneri*, MT = *Malaraeus telchinus*, CN = *Catallagia newcyi*, CD = *Catallagia decipiens*, MAB = *Megabothris abantis*, MAS = *Megabothris asio*.

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lake. We collected 66 fleas from the burrows they were using; seven of 15 pools were positive including five of eight *O. hirsuta*, two of six *O. labis* and 0 of one *O. bacchi*.

At Midlake four species of fleas were taken from thirteen-lined ground squirrels including 1 prairie dog flea and one deer mouse flea (Table 5). Only one vole was caught at Midlake, and it had no fleas. Deer mice yielded 24 fleas, including one *O. labis*, a species typically found on prairie dogs (Table 6).

On 24 to 26 October 1985, at Val Verde, eight flea samples were collected from prairie dogs, and seven were collected from burrows. All were negative for *Y. pestis*. We flagged burrows for fleas at Val Verde on 14 June 1986, and took flea and blood samples from prairie dogs on 6 to 7 July. Ten flea pools taken from burrows in June were not infected. At Val Verde in July 1986, 30 prairie dogs were sampled for fleas at the beginning of the epizootic (mean = 2.2 fleas/prairie dog, SD = 2.5, range 0–8). Fleas collected in July were identified to species but were not checked for plague. Those samples included *O. hirsuta*, *O. labis*, and *O. bacchi*. By 11 August, the prairie dog population at the center of Val Verde had crashed. Five of 18 flea pools collected from burrows at the center of the town on 12 August 1986, were positive for *Y. pestis*. Prairie dogs at the small satellite colony that was isolated by mesic habitat from the rest of the Val Verde town was still at high density. We collected five flea pools from burrows there on 13 August 1986, and all were negative for *Y. pestis*. In June 1987, three of 10 pools from prairie dog burrows at the center of the town, including *O. hirsuta*, *O. labis*, and *A. wagneri* were positive for *Y. pestis*.

Deer mice, meadow voles, and thirteen-lined ground squirrels were trapped at Val Verde. There were no fleas on meadow voles. Thirteen-lined ground squirrels were mostly infested with *O. bacchi*, although they also carried two species of prairie dog flea, *O. hirsuta* and *O. labis*, and *A. wagneri*, a deer mouse flea (Table 5; Thomas, 1988). Deer mice at Val Verde had the highest diversity of fleas with eight species (Table 6).

At Vega, fleas were collected from 14 adult prairie dogs in spring 1986. All were negative for *Y. pestis*. The mean number of fleas per host was 3.6 (range 0–18, SD = 4.9). The flea species present on prairie dogs at Vega were *O. hirsuta*, *O. labis*, *O. tuberculata cynomuris*, *Rhadinopsylla sectilis*, and *Ceratophyllus vison*; the last two species are deer mouse fleas (Haas et al., 1973).

Deer mice captured at Vega had no fleas. However, we did find deer mouse fleas in prairie dog burrows there (Table 3). Thirteen-lined ground squirrel flea samples from Vega included its specialist, *O. bacchi*, the three prairie dog fleas, and *Catallagia neweyi*. Meadow voles yielded fleas only at Vega. These included the apparent vole specialists, *Megabothris abantis* and *M. asio*; the prairie dog flea, *O. hirsuta*; and a deer mouse flea, *Epitidia wenmani* (Thomas, 1988).

We collected fleas from all four rodent species in the valley, and only found *Y. pestis* positive fleas on prairie dogs or in prairie dog burrows. It is important to note that three species that were not prairie dog fleas, *O. bacchi*, *R. sectilis* and *A. wagneri* were found to be plague-infected in prairie dog burrows. *Yersinia pestis* positive fleas were collected at a gravel pit on the east side of Eagle Nest by NMEID in August 1983: one pool of nine *O. bacchi* and one pool of one *O. hirsuta* from thirteen-lined ground squirrel burrows and one pool of seven *O. labis*, and one pool of two *O. hirsuta* from prairie dog burrows. Later, on 1 November 1983, one pool containing one *R. sectilis*, one pool of 48 *O. hirsuta* and one pool of eight *O. labis* were found positive at the same area (NMEID, CDC, unpublished records).

Prairie dog population recovery following plague was variable. Subsequent to the epizootic at the north end of the valley in

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late summer 1985, late summer 1986 near South Entrance, and late summer 1987 in the vicinity of Val Verde, there were individual prairie dogs or small aggregations. In spring 1986, Vega consisted of 17 animals in two groups that occupied approximately 2 ha. When the juveniles emerged in June 1986, the population increased to nearly 70 animals, but hunters killed about 20 in August 1986. Approximately 50 prairie dogs entered hibernation in September and October, and visual counts in April 1987 indicated that nearly all survived the winter. In April 1987, the population had spread over 8 ha and when juveniles emerged in June 1987, there were approximately 200 animals. These animals again had good over-winter survival and when they emerged in Spring 1988, the town's area had increased in size to approximately 15 ha and was coalescing with another small colony to the south. When the juveniles emerged in June 1988, a visual count of prairie dogs on a marked two ha plot at Vega found 180 prairie dogs on 19 June (Cully, 1997).

Beginning in July, the prairie dogs at Vega began a steady decline in numbers. On 4 July 1988, there were 143 prairie dogs on the 2 ha grid; on 10 August, there were 80; on 28 August, there were four, and on 8 September, there were none. Fleas were collected from burrows at Vega on 10 September 1988, and 11 of 13 flea pools were positive for *Y. pestis*. The positive pools included *O. hirsuta, O. labis, O. t. cynomuris,* and *O. bacchi*. The two negative pools consisted of 25 *O. hirsuta* and 3 *O. bacchi* (Table 3).

In the middle of the valley there were fewer small towns recovering than in the north. At the south end of Eagle Nest Lake two prairie dogs were located on 1 September 1986. The following spring there were 10 prairie dogs at the South Entrance town. This population numbered approximately 25 in September 1987, and was still approximately 25 in spring 1988, although at that time prairie dogs were spread over a larger area, approximately 25 ha. Because we only trapped on about 1.5 ha of the South Entrance colony, an accurate estimate of the population could not be made at that time.

At Val Verde the population consisted of three widely separated groups in July 1987. One group consisted of six nulliparous females and produced no offspring. We were unable to determine the composition of the two other groups. In July 1988, where the six females had been present the year before, there were approximately 28 prairie dogs, both adults and pups. The two other groups appeared to be of similar size; however, again we were unable to get a clear count of prairie dogs at those areas. There were also other small isolated prairie dog colonies at the south end of the valley in July 1988.

DISCUSSION

The source of plague in the Moreno Valley is unknown. It could have entered in at least three ways. First, it is possible that plague is enzootic in the Moreno Valley in rodent species other than prairie dogs, but goes unnoticed. Plague was previously recorded there in 1949 by NMEID, and another epizootic in the mid-1960's was described by ranchers. Second, plague may have been introduced by raptors or mammalian predators that carry fleas from other areas where plague is active outside the Moreno Valley. Third, plague may be introduced from outside the Moreno Valley by other rodent species that maintain enzootic plague. *Yersinia pestis*-positive fleas associated with thirteen-lined ground squirrels, meadow voles and deermice were all collected from prairie dog burrows in the Moreno Valley.

At the time of the epizootic in the Moreno Valley, another plague epizootic was underway 40 km west near Taos and Tres Piedras, NM (J. F. Cully, Jr., pers. obs.). If that epizootic was the source of plague in the Moreno Valley thirteen-lined ground squirrels and meadow voles could not have been the origin because their species ranges do not overlap the plague sites outside

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the Sangre de Cristo Mountains. The deermouse has a continuous distribution that does overlap both sites, and is a possible source of plague. Deermice have been implicated a reservoir species for plague in NM (Holdenried and Quan 1956) and Colorado (Barnes, 1982).

It took a minimum of 3 yr for plague to progress the length of the Moreno Valley in Gunnison's prairie dogs. The epizootic had three geographic and temporal phases during this study. Each phase was isolated from the others by natural geographic and vegetative boundaries that appeared to function as temporary barriers to the spread of the epizootic. At the north and middle sections of the valley the epizootic took about 1 yr to extirpate prairie dogs from affected colonies. This was similar to the progress in South Park, (Colorado, USA; Lechleitner et al., 1968; Fitzgerald, 1970). At Val Verde the initial mortality event lasted about 1 mo, similar to the rate in Gunnison County (Colorado, USA; Rayor, 1985). At the height of the epizootic at Midlake, in addition to residents, unmarked prairie dogs were caught that may have been moving as a result of the disruptions caused by collapsing populations. We speculate that it was usually prairie dogs dispersing from plague-destroyed towns that carried plague across the inhospitable habitat of the barriers to the prairie dog populations to the south. Those same barriers, combined with geographic isolation of recovering prairie dog towns, apparently restricted the backward dispersal of plague into previously affected areas so that recovering populations were not immediately reinvaded by plague from other prairie dog towns to the south.

At all areas, samples included non-prairie dog fleas on prairie dogs or in prairie dog burrows. The differences between flea species at Vega and the other two areas probably reflect seasonal differences in flea abundance and activity because the Vega samples were collected in spring while the others were collected in late summer.

Most of the plague transmission within towns reported here probably resulted from infected prairie dog fleas, *O. hirsuta, O. labis* and *O. tuberculata cynomuris* that were transferred between prairie dogs during close social contact or when burrows were shared and fleas jumped onto new hosts. The spread of plague among towns may occur if dispersing prairie dogs or wide ranging camivores (Barnes, 1993) carry infected fleas from infected to naive towns. *Oropsylla hirsuta, O. labis,* and *O. tuberculata cynomuris* were the predominant fleas found on prairie dogs; all three species were found on other rodent species as well. *Oropsylla hirsuta* and *O. labis* were the species most often *Y. pestis* positive. *Oropsylla labis* and *O. tuberculata cynomuris* were active during different seasons, *O. labis* in summer and *O. tuberculata cynomuris* in the late fall-early spring. These flea species were also involved in prairie dog plague epizootics in Gunnison's prairie dogs in South Park (Lechleitner et al., 1968; Fitzgerald, 1970, 1993) and Gunnison County (Rayor, 1985), and among white-tailed prairie dogs (*Cynomys leucurus*) near Meeteetse (Wyoming, USA; Ubico et al., 1988). At South Park and Meeteetse *Oropsylla idahoensis,* a species not found in the Moreno Valley, was important. *Oropsylla hirsuta,* the dominant prairie dog flea species in the Moreno Valley, was present in small numbers at South Park, and was not reported at Meeteetse. At the Gunnison County site *O. hirsuta* and *O. labis* were important.

With the high rates of mortality recorded among Gunnison's prairie dogs in the Moreno Valley and at sites in Colorado (Lechleitner et al., 1962; 1968; Fitzgerald, 1970; Rayor, 1985; Barnes, 1993). Gunnison's prairie dog is an unlikely maintenance host species for plague between epizootics. There are simply not enough animals alive after an epizootic. Many other mammal and flea species are involved with sylvatic plague world-wide. Seventy-three genera and more than 200 species of rodents have been found naturally infected

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(Poland and Barnes, 1979). In NM, Weber (1978) listed 14 flea species, including *O. hirsuta*, *A. wagneri*, and *O. bacchi*, but did not report *O. tuberculata cynomuris*, or *R. sectilis*. Weber (1978) also identified 20 rodent species, two rabbit species, and six wild carnivore species that have been implicated by infection or antibodies to *Y. pestis* in NM. Multiple rodent species probably maintain plague in NM, with Gunnison's prairie dog serving as an amplification species.

Thirteen-lined ground squirrels may also be involved in the plague cycle in the Moreno Valley. Thirteen-lined ground squirrel populations appeared to be as unstable as prairie dogs. The mortality of thirteen-lined ground squirrels at Midlake prior to the epizootic in prairie dogs, combined with *Y. pestis* positive *O. bacchi* fleas at two sites points to the potential involvement of thirteen-lined ground squirrels. Furthermore, thirteen-lined ground squirrels were found in the deep mesic grasslands along stream courses more frequently than prairie dogs. Poorly drained wetland habitats along Six-mile Creek, between the north and middle thirds of the valley, and between the main portion of the Val Verde colony and its outlier appeared to slow the progress of the epizootic among prairie dogs. It is possible that thirteen-lined ground squirrels were less inhibited from crossing Six-mile creek, and introduced plague from the north to the middle of the valley. *Oropsylla bacchi* was the most abundant flea on thirteen-lined ground squirrels, and also was the flea species most often found on alternate hosts.

Prairie dogs and thirteen-lined ground squirrels exchanged fleas; thirteen-lined ground squirrels frequently used prairie dog burrows for refuge from predators, and at Midlake, thirteen-lined ground squirrels disappeared shortly before the plague epizootic in prairie dogs. In August 1983, a positive *O. bacchi* pool was collected from a thirteen-lined ground squirrel burrow and in September 1988 another was collected from a prairie dog burrow at Vega. The discovery of a *Y. pestis* positive thirteen-lined ground squirrel flea (*O. bacchi*) in a prairie dog burrow in September 1988, combined with frequent collection of *O. bacchi* from prairie dogs (Tables 2, 4), supports this route for the interspecific spread of plague.

The two other rodent species, meadow voles and deer mice, also were potential maintenance hosts for plague. The apparent population cycle of meadow voles at Vega with low populations at the times of the epizootics in prairie dogs in 1985 and 1988 and high populations in between could have resulted from plague. California voles (*Microtus californicus*) are an enzootic host for *Y. pestis* at plague foci in California (USA; Goldenburg et al., 1964; Hudson et al., 1964). However, at this time we have no other evidence that meadow voles were involved with plague in the Moreno Valley. The presence of *Y. pestis* positive *R. sectilis* and *A. wagneri* from prairie dog burrows provides evidence for a route of transmission between deer mice and prairie dogs. Near Santa Fe (NM) deer mice were found to be moderately resistant to plague and therefore were considered a possible enzootic host for plague there (Holdenried and Quan, 1956). *Oropsylla bacchi*, *R. sectilis* and *A. wagneri* were not prairie dog fleas, but were all found to be *Y. pestis* positive in the Moreno Valley. Positives of each species were found in prairie dog burrows, and two species also were collected from the prairie dogs themselves. Thus, each flea species was in an excellent position for interspecific transmission of plague.

Following the epizootics, a large proportion of the surviving Gunnison's prairie dogs in the Moreno Valley tested positive for *Y. pestis* antibodies (13% at Vega, 40% at South Entrance, and 100% at Val Verde), and their titers were high. At Vega and South Entrance there may have been reproduction following the epizootic, so that *Y. pestis* positive individuals might have been among a smaller number of adults which had established the popula-

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tion a year earlier. Some of the animals that tested negative at Vega may have been yearlings which had not been through the epizootic in spring 1985; at Vega unmarked yearlings could not be distinguished from adults. The presence of *Y. pestis* antibodies in a large proportion of survivors of the epizootics indicates that these animals were exposed to *Y. pestis*, survived, and presumably were immune to plague. At South Park, one of nine (Lechleitner et al., 1968) and none of nine (Fitzgerald, 1970) sera from Gunnison's prairie dogs had *Y. pestis* antibodies. Likewise, 0 of 37 white-tailed prairie dogs had antibodies to *Y. pestis* (Ubico et al., 1988). Such low seroprevalence is similar to results from the Moreno Valley during epizootics. All positive titers in the Moreno Valley were taken from prairie dogs present after the epizootic passed.

At Vega and South Entrance the population growth rate, λ, increased from 0.8 before the epizootic to 2.9 following the epizootic (Cully, 1997). If such a high rate of growth were maintained, the original population in the Moreno Valley could recover in between 6 and 7 yr. At Vega the prairie dogs experienced a second epizootic 4 yr after the first and populations throughout the valley are hunted. In July 1996, prairie dog colonies were present throughout the Moreno Valley, but the population was a fraction of what it was in 1984.

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