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PLAGUE IN A COMPLEX OF WHITE-TAILED PRAIRIE DOGS AND ASSOCIATED SMALL MAMMALS IN WYOMING

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ABSTRACT: Fleas were collected from white-tailed prairie dogs (*Cynomys leucurus*) and other small mammals trapped on six grids during a field study near Meeteetse (Wyoming, USA) in 1989 and 1990 to investigate the dynamics of plague in this rodent population. Fleas were identified and tested for *Yersinia pestis* by mouse inoculation. *Yersinia pestis*-positive fleas were found on prairie dogs and in their burrows. Flea species on prairie dogs changed from spring to late summer. White-tailed prairie dog numbers were significantly lower in the presence of *Y. pestis*-positive fleas; however, affected populations generally recovered 1 to 2 yr following absence of detectable plague. Grids where recovery occurred had a high proportion of juvenile male prairie dogs. Eighteen flea species were identified on small mammals, six of which were infected with *Y. pestis*. Some flea species were associated with a particular small mammal species, while others were found on a broad range of host species. Flea species most important in the potential interchange of *Y. pestis* between associated small mammals and white-tailed prairie dogs were *Oropsylla tuberculata cynomuris*, *Oropsylla idahoensis*, and *Oropsylla labis*. Plague cycled through the white-tailed prairie dog complex in an unpredictable manner. Each summer the complex was a mixture of colonies variously impacted by plague: some were declining, some were unaffected by plague, and others were recovering from plague population declines. These data provide insight into the dynamics of plague in white-tailed prairie dog complexes, but predicting movement of plague is not yet possible and the role of associated mammals in maintenance of plague is not understood.

Key words: *Cynomys leucurus*, epizootiology, fleas, plague, small mammals, white-tailed prairie dog, *Yersinia pestis*.

INTRODUCTION

In recent years, white-tailed prairie dog (WTPD) populations (*Cynomys leucurus*) in Wyoming (USA) have experienced high mortality due to plague, *Yersinia pestis* (Menkens and Anderson, 1991). Clark (1977) reported 85% reduction in a WTPD population in southeastern Wyoming during a single active season. These declines in response to plague were not uniform in all WTPD populations. Both Ubico et al. (1988) and Menkens and Anderson (1991) observed differing population responses to plague in colonies of the Meeteetse Complex of WTPD's in northwestern Wyoming. These population responses ranged from enzootic plague to epizootics characterized by rapid decreases and followed by increases in prairie dog numbers. Apparently, WTPD populations, even during widespread plague epizootics, maintained a remnant of reproductive individuals (Cully, 1989).

A plague epizootic can develop when a population of relatively susceptible individuals, such as prairie dogs, are exposed to infected fleas from septicemic individuals of a relatively resistant species, such as deer mice (*Peomyseus maniculatus*) (Poland, 1989). Fitzgerald (1970) suspected that both deer mice and Richardson's ground squirrels (*Spermophilus richardsonii*) were acting as reservoir species in a Gunnison's prairie dog (*Cynomys gunnisoni*) epizootic. Due to their abundance and increased resistance to plague mortality in comparison to many other rodents, deer mice have been viewed as maintenance hosts in many prairie dog plague epizootics (Karami, 1981). Thomas et al. (1988) suggested that northern grasshopper mice (*Onychomys leucogaster*) might be important in enzootic-epizootic cycles of plague where they occur in conjunction with highly susceptible species.

With the ongoing reintroduction of black-footed ferrets (*Mustela nigripes*),

there is a need to better understand the dynamics of plague in prairie dog populations and the associated small mammal community. Prairie dogs are the main prey for black-footed ferrets and their unexpected reduction due to plague epizootics complicate reintroduction efforts.

Objectives of this study were to determine: (1) the influence of plague on WTPD population parameters by comparing sites with and without plague; (2) flea species density and infection rates of fleas on WTPD's for sites with and without plague; (3) flea species composition, percentage of burrows infested with fleas, mean number of fleas per infested prairie dog burrow (flea index), and prevalence of infection per WTPD colony; (4) the composition and distribution of mammal species associated with WTPD on the Complex; and (5) flea species composition and prevalence of infection in order to characterize the flea fauna of these mammal species.

MATERIALS AND METHODS

The 2,995 ha Meeteetse Complex of WTPDs is composed of 37 colonies (Clark et al., 1986). The Complex is found on the western margin of the Bighorn Basin, 15 km northwest of Meeteetse, in northwestern Wyoming (44°7′ to 44°15′N and 108°56′ to 109°14′W).

The Complex is dominated by long, cold winters and short, hot summers (Bailey, 1980). Average annual precipitation is 28 cm evenly distributed throughout the year (Clark et al., 1986). The area has a mean elevation of 2,083 m. Junegrass (*Koeleria cristata*), wheatgrass (*Agropyron* spp.), needlegrass (*Stipa* spp.), and grama (*Bouteloua* spp.) are the dominant grasses on the Meeteetse Complex (Collins and Lichvar, 1986). They are intermixed with shrubs such as sagebrush (*Artemesia tridentata*) and rabbitbrush (*Chrysothamnus nauseosus*).

Grazing is the major land use, although it differs in intensity both spatially and temporally (Clark et al., 1986). Since the 1950's, oil exploration, and seismic activity associated with it, has had an impact on the Complex.

We established six trapping grids to capture prairie dogs and small mammals: BLM 13, GOULD (G), EAST CORE (EC), PICKETT CREEK (PC), WEST CORE (WC), and 91. Grid baselines were oriented parallel to access roads to facilitate trap movement and placement. Five grids were approximately square (300 m × 270 m) and 8.1 ha in area. BLM-13 was identical in area to the other five grids, but its shape was an elongated rectangle (450 m × 180 m) because of its location on a narrow ridge. The seven rows of each grid, which were parallel to the baseline, were 45 m apart, while the 11 columns of each grid were 30 m apart.

We established grid baselines by sequentially aligning 11 fluorescent orange wooden stakes along a line initiated by a pair of stakes spaced 30 m apart. A right triangle, with sides of 30 and 45 m and a hypotenuse of 54.1 m, was then used to place the first grid row perpendicular to the baseline. Row and column intersections, which represented trap stations, were determined by visual triangulation, and marked using a numbered aluminum tag and a flagged wire.

A single Tomahawk live trap (Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) (42 × 15 × 15 cm), to capture prairie dogs was placed at each trap station on the selected grid for a total of 77 traps. A single Sherman live trap (H.B. Sherman Traps, Inc., Tallahassee, Florida, USA) (8 × 8 × 23 cm) to capture small mammals was placed beside the Tomahawk live trap at every other trap station. The result was an overlaying grid of 24 Sherman traps.

Tomahawk live traps were opened in the early morning (approximately 0500 hr) and baited with rolled oats. Sherman traps were opened and baited with rolled oats in the late morning (approximately 1000 hr) while the larger traps were being checked and closed. Sherman traps were then checked and closed the following morning while larger traps were being opened and baited.

Trapping occurred from 1 June to 13 August in 1989, and from 21 May to 15 August in 1990. Each grid was trapped for five nights twice each summer, with approximately 6 wk separating the two trapping periods. Each prairie dog captured was weighed to the nearest 10 g by using a Pesola scale (Forestry Suppliers, Jackson, Mississippi, USA); the sex, age, and reproductive status of each individual also was determined. An individually-numbered ear tag (National Band and Tag Co., Newport, Kentucky, USA, Monel tag, size 1) was placed in the right ear prior to release to monitor trapping history. Individuals were classified into adult and juvenile age classes using the criteria of overall body size, reproductive status, and weight (Menkens and Anderson, 1989). Adults were those animals over 1 yr of age and juveniles were those born immediately prior to, or during, the present trapping season. The repro-

ductive status of adult female prairie dogs was determined only during June. Females captured during June were considered to have been fecund earlier in the year if their nipples were enlarged. Those that did not breed had small and scaly or completely undeveloped nipples (Menkens and Anderson, 1989).

During 1989, every other small mammal captured in Sherman traps was identified to species, weighed by means of a Pesola scale, sexed, and aged. In 1990, every small mammal captured was processed in this way. Prior to release in both years, every small mammal processed was toe clipped to identify the trapping period in which it was captured.

Desert cottontail rabbits (*Sylvilagus audubonii*), white-tailed jackrabbits (*Lepus townsendii*) and Uinta ground squirrels (*Spermophilus armatus*), were also captured in Tomahawk live traps. Prior to release, each mammal was individually marked in the right ear with a numbered ear tag (National Band and Tag Co.).

Fourteen prairie dog burrow sampling sites were selected to represent a variety of burrow densities and locations throughout the Complex. The baselines of these grids were oriented parallel to roads to provide ease of access. Wooden stakes, painted fluorescent orange for visibility, were placed every 30 m along the 300 m baseline. After placing the initial stake, the other stakes were positioned using 30 m measurements and line-of-sight adjustments.

Transects were sampled by standing at a randomly selected distance along the baseline, determining the perpendicular direction with a compass, and pacing 342 steps (an approximation of the 270 m width of a grid). Transect width was determined with the aid of 2-m long wooden pole that was centered at the midline of the observer. While pacing the transect length, burrows were sampled which were at or within 1 m of the observer. Active burrows were determined by the presence of prairie dog droppings. Fleas were collected from any active burrow overlain by some portion of the pole and that had an entrance greater than 10 cm in diameter. All burrows sampled were mapped on the appropriate data form and marked with a small flag and a numbered aluminum tag. Active burrow density (number of prairie dog burrows per ha) on each grid was estimated by dividing the total number of burrows sampled by the total area of all transects on a grid (0.54 ha).

Fleas were collected from every prairie dog on the first morning of trapping on each grid. Subsequently, fleas were collected from one of six prairie dogs trapped in 1989 and one of five trapped in 1990. In 1989, fleas were captured from every other associated mammal, and in 1990 from every associated mammal. Fleas were not collected from prairie dogs or associated mammals that had already yielded fleas during the 5 day trapping period.

A 5-1 glass canning jar with a clasp-type glass lid was used to anesthetize animals. The lid was modified by filling its hollow interior with cotton held in place by a circular piece of hardware cloth (Barnes and Kartman, 1960). The cotton in the lid was moistened with approximately 2 ml of Halothane (Halocarbon Laboratories, Inc., Hackensack, New Jersey, USA), an inhalant anesthetic. The animal was placed in the jar and the lid was sealed. The animal was left in the jar until all motor movement ceased; then it was removed from the jar, fleas were collected, and the animal released.

Collection of fleas was accomplished by holding the anesthetized animal in an inverted position over a white plastic basin and brushing it from anterior to posterior with a modified toothbrush. The sampled animal was allowed to recover from the anesthetic and was released. Collected fleas, which were also anesthetized, were removed from the basin with a small wooden applicator moistened with saline solution and placed into a vial containing a 2% sodium chloride and 0.001% Tween 80 solution (Quan et al., 1981). The vial was sealed and labeled with the date, a code number, and the number of fleas. All samples collected were refrigerated and shipped every 10 days to a laboratory for plague analysis. In 1989, flea samples were sent to the Centers for Disease Control (CDC; Fort Collins, Colorado, USA) for species identification and determining if they were infected with *Y. pestis*. In 1990, flea samples were sent to the Wyoming State Veterinary Laboratory (University of Wyoming, Laramie, Wyoming, USA).

At the laboratory, fleas were identified to species using keys to the Siphonaptera (Hopkins and Rothschild, 1953, 1956, 1971, 1966, 1971; Stark, 1959, 1970; Johnson, 1961; Lewis et al., 1988) and pooled according to host and location. Pools of 1 to 25 fleas were triturated in 0.5 to 1 ml sterile saline and the suspension was inoculated subcutaneously in the inguinal region of young laboratory mice (NIH General Purpose Stain). Mice were held for 21 days and observed daily for morbidity and mortality. Moribund mice were euthanized. Spleen and liver from dead mice were cultured on Columbia blood agar (Acumedia Manufacturing, Inc., Baltimore, Maryland, USA), incubated at room temperature and at 37 C for 72 hr, and examined daily for growth. Bacteria were identified by colony morphology, growth and Gram negative characteristics, and phage lysis at CDC and Wyoming (Quan et al., 1979). These tests

were done at both labs. In addition, impression smears of liver and spleen were examined by fluorescent antibody staining technique (Quan et al., 1981).

Fleas were collected from the burrows of each grid twice during the season, with 4 to 6 wk separating the collections. Those burrows from which fleas were collected during the first period were resampled during the second period.

Flea collection consisted of swabbing the burrow with a square of white flannel, 20 cm on a side, that was attached by means of an alligator clip to a 2-m section of plumber's snake (Barnes et al., 1972). The snake was extended into the burrow as far as possible and removed. The flannel cloth was detached and placed into two plastic bags, one tied shut inside the other. The outer bag was labeled with the date and the identification code of the burrow.

Sampling cloths were stored in plastic and refrigerated to slow flea movement and to minimize observer exposure to potentially infected fleas. Fleas were removed from the flannel with forceps and stored in vials containing a 2% sodium chloride and 0.001% Tween 80 solution. Fleas collected from burrows were processed in the same manner as fleas sampled from mammals.

Population estimates for WTPDs were computed using Chapman's unbiased version of the Lincoln-Peterson estimator (White et al., 1982). This technique provided estimates of population size with small biases and standard errors (Menkens and Anderson, 1989). White-tailed prairie dog densities were calculated using the naive estimator, which is the population estimate divided by the area of the trapping grid (Menkens and Anderson, 1989).

White-tailed prairie dog density estimates for each grid were compared between years using the Normal test, which considers the amount of confidence interval overlap between estimates (Snedecor and Cochran, 1980). In this case, if the 95% confidence intervals of the estimates failed to overlap, the difference was considered significant at an $\alpha \leq 0.05$.

White-tailed prairie dog sex ratios were compared to a 1:1 ratio using the Chi-square test (Zar, 1984). The two-sample *t*-test was used to determine if a difference existed in the means of the sex ratios for grids with 1990 *Y. pestis*-positive WTPD flea pools and those without (Zar, 1984).

The two-sample *t*-test was also used to compare the means of WTPD age ratios (number of juveniles/adult female) for all grids, both between trapping periods within a year and between years. As with the sex ratios, this test was employed to determine if a difference existed between the means of the age ratios for grids with and without *Y. pestis*-positive WTPD flea pools in 1990.

Both the percentage of WTPD's infected with fleas and the mean number of fleas per infested WTPD (flea index) were compared between trapping periods for each year with the two-sample *t*-test. Additionally, the means of the flea indices were compared for each grid between years and between 1990 plague-positive and plague-free grids. Grids were considered plague-positive if *Y. pestis* was isolated from any flea group from that grid, and were considered plague-free if *Y. pestis* was not isolated from any flea group.

Within each year, unpaired two-sample *t*-tests were used to compare the number of deer mice on plague-positive trapping grids to those that were plague-free (Zar, 1984). Other species were not captured with enough frequency to make comparisons possible. Both the mean number of fleas per infested deer mouse and the percentage of deer mice infested were compared between plague-positive and plague-free grids using the unpaired two-sample *t*-test. Simple linear regression was used to determine if statistically significant relations existed between WTPD density, percent flea infestation, and flea indices as well as comparisons of numbers of fleas on mammals on infected and plague free grids (Neter et al., 1985).

Both the percentage of burrows infested with fleas and the mean number of fleas per infested burrow were compared between sampling periods within a year by means of a paired two-sample *t*-test. The unpaired version of this test was used to compare these two flea population parameters on plague-positive grids to those that were plague-free in both 1989 and 1990. Simple linear regression was employed to determine if a significant relation existed between the percentages of burrows infested with fleas and the mean number of fleas per infested burrow in both 1989 and 1990 (Neter et al., 1985).

RESULTS

In 1989, *Y. pestis*-positive fleas were collected from BLM-13, EC, and PC. Positive fleas from BLM-13 and EC were taken directly from WTPDs, while those from PC were from a WTPD burrow. *Yersinia pestis*-positive fleas were collected throughout the trapping season, indicating that the occurrence of plague was not limited to one period of the spring or sum-

mer. Flea species removed from WTPDs that were infected with *Y. pestis* were *Neopsylla inopina, Oropsylla tuberculata cynomuris, Oropsylla idahoensis,* and *Oropsylla labis.* In 1990, *Y. pestis* was found in EC, G, 91, and WC. Positive fleas were taken both from prairie dogs and burrows on EC, G, and 91.

All fleas from mammals other than prairie dogs in the Meeteetse Complex were negative for *Y. pestis* in 1989. However, in 1990, three species of associated mammals captured on a total of three trapping grids possessed *Y. pestis*-positive fleas. A positive *O. labis* from a desert cottontail was collected on 91 in early summer. Positive fleas were removed from Uinta ground squirrels on G in late spring. Four positive flea species were found on desert cottontails and Uinta ground squirrels: *O. tuberculata cynomuris, O. idahoensis, O. labis,* and *Oropsylla pandorae* (Table 1). Deer mice had *Y. pestis*-positive fleas on both G and WC throughout the late spring and summer. Except for a single *Catallagia decipiens,* all *Y. pestis*-positive fleas from deer mice were *Aetheca wagneri* (Table 1).

Two-hundred fifty individual WTPD's were captured in 1989, while only 177 were captured in 1990. This decrease occurred despite the inclusion of a second trapping period 91 during 1990, which increased the overall trapping effort for that year.

Density estimates of WTPD's were significantly lower in 1990 than in 1989 for EC, G, and 91 ($P \leq 0.05$). Density estimates for these three grids in 1990 were from 79% (G, period 2) to 96% (G, period 1) lower than those in 1989, a mean decrease of 88% (SE = 2.7). BLM-13, PC, and WC all increased in density between 1989 and 1990, although density estimates from only one trapping period per grid were significantly different between years ($P \leq 0.05$). Increases in WTPD density ranged from 13% (WC, period 1) to 488% (BLM-13, period 2), with a mean percent increase of 161% (SE = 70).

White-tailed prairie dog sex ratios (number of males per female) for all trapping grids in 1989 and 1990 were not significantly different from 1:1 ($P \leq 0.05$). Age ratios (number of juveniles per adult female) of WTPD's generally increased within a trapping season between periods 1 and 2, although the means of these ratios over all trapping grids were not significantly different either between trapping periods within a year or between years ($P \leq 0.05$).

Fleas were collected from 109 WTPD's in 1989; 68% were infested with one or more fleas. Infested WTPDs yielded 292 fleas, for a mean flea index of 3.9 fleas per infested WTPD (SE = 0.7). The mean flea index was lower for period 2 than for period 1, but not significantly ($t = 1.42$, 9 df, $P = 0.189$).

Of the 99 WTPD's from which fleas were collected in 1990, 73% were infested with ≥1 flea. Five hundred and three fleas were collected from these infested WTPD's, for a mean flea index of 7.0 fleas per infested WTPD (SE = 0.9). As in 1989, the mean flea index was lower in period 2 than in period 1, but not significantly ($t = 1.42$, 10 df, $P = 0.187$). Mean flea indices were significantly higher for those grids with plague present in 1990 (EC, G, and 91) than for those that were plague-free (BLM-13, PC, and WC) ($t = 2.50$, 10 df, $P = 0.037$). The overall WTPD mean flea index for 1990 was higher than that for 1989, but this difference was not significant ($t = 0.78$, 21 df, $P = 0.444$). For both 1989 and 1990, *N. inopina, O. tuberculata cynomuris, O. idahoensis,* and *O. labis* were the predominant flea species collected from WTPDs (Table 1). Flea species composition changed between years, with *N. inopina* more common in 1989 than in 1990, and *O. tuberculata cynomuris* and *O. idahoensis* more common in 1990 than in 1989.

Flea data from 1990 showed WTPD flea indices were positively related to the percent of WTPDs infested with fleas ($r^2 = 0.68$, $P = 0.001$). No significant relationships were found between WTPD density

TABLE 1. Percentage of flea species found on mammals in the Meeteetse Complex (Wyoming, USA) in 1989 and 1990.

		Flea source					
Flea species	Yr	White-tailed prairie dog	Prairie dog burrow	Deer mice	Desert cottontail	Uinta ground squirrel	Northern grasshopper mice
Aetheca wagneri	1989	3	2	93	9	28	13
	1990	1	0	97[a]	0	78	2
Cediopsylla inaequalis	1989	2	—	—	87	—	—
	1990	0	—	—	65	—	—
Hystrichopsylla dippiei	1989	0	—	0	—	0	—
	1990	1	—	0	—	6	—
Neopsylla inopina	1989	27[a]	18	1	0	4	0
	1990	9[a]	31[a]	0	4	0	10
Neopsylla spp.	1989	1	—	—	—	—	—
	1990	0	—	—	—	—	—
Oropsylla tuberculata cynomuris	1989	20[a]	34	1	0	2	9
	1990	29[a]	18[a]	0	4	0	10[a]
Oropsylla idahoensis	1989	21[a]	14[a]	1	2	—	20
	1990	36[a]	11[a]	0	20	—	6[a]
Oropsylla labis	1989	20[a]	20	1	0	—	7
	1990	18[a]	34[a]	0	8[a]	—	4[a]
Oropsylla pandorae	1989	2	4[a]	—	2	—	51
	1990	0	4	—	0	—	69[a]
Oropsylla tuberculata tuberculata	1989	0	—	0	—	—	—
	1990	0	—	0	—	—	—
Oropsylla spp.	1989	0	0	0	—	—	—
	1990	0	1	0	—	—	—
Pulex irritans	1989	0	—	—	—	—	—
	1990	1	—	—	—	—	—
Pulex spp.	1989	0	—	—	—	—	—
	1990	0	—	—	—	—	—
Rhadinopsylla fraterna	1989	5	5	0	—	4	—
	1990	7	4	1	—	6	—
Catallagia dicipiens	1989	—	6	2	—	—	—
	1990	—	0	1[a]	—	—	—
Catallagia spp.	1989	—	1	1	—	—	—
	1990	—	1	0	—	—	—
Amaradix bitterrootensis	1989	—	—	0	—	—	—
	1990	—	—	0	—	—	—
Callistopsyllus campestris	1989	—	—	0	—	—	—
	1990	—	—	1	—	—	—
Callistopsyllus terinus	1989	—	—	0	—	—	—
	1990	—	—	0	—	—	—
Callistopsyllus spp.	1989	—	—	0	—	0	—
	1990	—	—	1	—	10	—
Epitedia wenmanni	1989	—	—	0	—	—	—
	1990	—	—	0	—	—	—
Merignis shannoni	1989	—	—	0	—	—	—
	1990	—	—	0	—	—	—
Pleochaetis exilis	1989	—	—	3	—	62	—
	1990	—	—	0	—	0	—
Foxella ignota	1989	—	—	—	—	2	—
	1990	—	—	—	—	0	—

[a] Species with *Y. pestis*-positive fleas.

and flea population attributes, or between other flea population attributes.

Species composition of fleas on WTPDs also changed seasonally within the same year. In 1989, *N. inopina* and *O. tuberculata cynomuris* were more abundant in late spring and early summer than in mid-summer (38% versus 15% and 25% versus 15%). *O. idahoensis* and *O. labis*, however, were more abundant in mid-summer than in late spring or early summer (16% versus 35% and 16% versus 33%, respectively). Although flea pools of all four species were positive in late spring and early summer, only pools of *N. inopina* were positive in mid-summer. This seasonal trend was generally the same for 1990, although both *O. idahoensis* and *O. labis* replaced *N. inopina* as late spring and early summer fleas.

The range of estimated active burrow densities (number of burrows per ha) for WTPD towns on the Meeteetse Complex was greater in 1989 (from 33 to 156) than in 1990 (from 15 to 98). Burrow densities declined slightly, though significantly, between sampling periods for some grids in both 1989 (Paired $t = 2.43$, $P = 0.032$) and 1990 (Paired $t = 2.88$, $P = 0.01$). Burrow densities were not significantly different between years for either sampling period 1 (Paired $t = 1.63$, $P = 0.13$) or period 2 (Paired $t = 1.66$, $P = 0.12$). Burrow densities of grids with *Y. pestis*-positive fleas were significantly greater than those that were plague-free in 1990 ($t = 2.67$, 18 df, $P = 0.016$).

In 1989, 163 fleas were collected from 494 burrows during sampling period 1, and 50 fleas were collected from 485 burrows during sampling period 2. The percentage of burrows infested with fleas ranged from 5 at GRAVEYARD (GY) to 33 at BLM-10 during period 1, and from 0 at ROSE CREEK (RC) to 21 at BLM-10 during period 2. There was a significant decline in the percentage of burrows infested with fleas from late spring and early summer (period 1) to mid-summer (period 2) (Paired $t = 3.83$, $P = 0.002$). The mean number of fleas per infested burrow ranged from 1.0 (EC, 91, GY, RC) to 5.3 (BLM-13) during period 1, and from 0.0 (RC) to 1.6 (BLM-13, BLM-10) during period 2. There was a significant decrease in the flea indices between late spring and early summer (period 1) and mid-summer (period 2) (Paired $t = 3.10$, $P = 0.009$). A direct relation did not exist between the percentage of burrows infested with fleas and the mean number of fleas per infested burrow in 1989 ($r^2 = 0.39$, $P = 0.0004$).

Positive fleas were collected from burrows within two WTPD towns in 1989. A single *Y. pestis*-positive *O. idahoensis* was removed from PC in early summer, and an infected *O. pandorae* was collected from LONG HOLLOW (LH) in mid-summer.

In 1990, 169 fleas were removed from 597 burrows during sampling period 1, and 93 fleas were collected from 585 burrows during period 2. The percentage of burrows infested with fleas ranged from 0 at BLM-13, HOGG (H), PUMP STATION (PS), RAWHIDE (RH), and RC to 53 at NEW TOWN (NT) during period 1, and from 0 at BLM-13, PC, and BLM-10 to 23 at NT during period 2. Unlike 1989, the percentage of burrows infested with fleas did not differ between sampling periods (Paired $t = 1.20$, $P = 0.245$). Flea indices ranged from 0.0 (BLM-13, H, PS, RH, RC) to 3.6 (EC) during period 1, and from 0.0 (BLM-13, PC, BLM-10) to 3.8 (NT) during period 2. Flea indices did not significantly differ between sampling periods in 1990 (Paired $t = 0.35$, $P = 0.734$). As in 1989, there was no direct relation between the percentage of burrows infested with fleas and the mean number of fleas per infested burrow in 1990 ($r^2 = 0.47$, $P = 0.0000$).

In 1990, positive fleas were taken from the burrows of five towns on the Meeteetse Complex. A single infected *O. idahoensis* was collected from EC in late spring, as was a single *O. tuberculata cynomuris* from NT. Infected *O. labis* were taken from both G and SC in the early summer, and again from G in mid-sum-

TABLE 2. Mammals other than prairie dogs captured in 1989 and 1990 on the Meeteetse Complex of white-tailed prairie dogs (Wyoming, USA).

Year	Associated mammal species[a]					
	LETO	SYAU	SPAR	PRFA	PEMA	ONLE
1989	1	16	12	2	137	19
1990	1	6	5	2	338	9

[a] LETO = *Lepus townsendii* (white-tailed jackrabbit); SYAU = *Sylvilagus audubonii* (desert cottontail); SPAR = *Spermophilus armatus* (Uinta ground squirrel); PRFA = *Perognathus fasciatus* (olive-backed pocket mouse); PEMA = *Peromyscus maniculatus* (deer mouse); ONLE = *Onychomys leucogaster* (northern grasshopper mouse).

mer. LOT 58 and NT yielded positive *N. inopina* in mid-summer.

Ten flea species were collected from burrows during 1989 and 1990 (Table 1). Four species, *N. inopina, O. tuberculata cynomuris, O. idahoensis,* and *O. labis,* comprised the majority (>80%) of the total flea collection during both years. Except for BLM-13 and PS in 1990, at least one of these four species was collected from every grid during 1989 and 1990.

Deer mice were the most numerous associated mammal in both 1989 and 1990 (Table 2). Desert cottontails, Uinta ground squirrels, and northern grasshopper mice were captured occasionally, while white-tailed jackrabbits (*Lepus townsendii*) and olive-backed pocket mice (*Perognathus fasciatus*) were not commonly captured. Significant differences did not exist between the total number of desert cottontails (Paired $t = 1.33$, $P = 0.24$), Uinta ground squirrels (Paired $t = 1.4$, $P = 0.22$), or northern grasshopper mice (Paired $t = 1.89$, $P = 0.12$) captured in 1989 and 1990. However, there were significantly more individual deer mice captured in 1990 than in 1989 (Paired $t = 6.16$, $P = 0.002$). The number of deer mice did not differ significantly between plague-positive and plague-free trapping grids in 1989 ($t = 1.14$, 4 df, $P = 0.32$) or 1990 ($t = 0.98$, 4 df, $P = 0.38$).

Five hundred and five fleas were collected from 190 mammals, other than prairie dogs, in 1989. In 1990, 1,101 fleas were taken from 361 associated mammals. In both years, the majority of animals from which fleas were collected were deer mice.

We captured 117 deer mice that yielded 333 fleas of 11 species in 1989. In 1990, 969 fleas of 15 species were removed from 301 captured deer mice. Eighteen species of fleas were collected from deer mice in the 2 yr; more than 95% of the fleas were *A. wagneri.*

The flea index, or the mean number of fleas per infested individual, for deer mice ranged from 1.4 (BLM-13 and PC) to 4.6 (G) in 1989. Flea indices on plague-positive grids were not significantly different from those on plague-free grids in 1989 ($t = 1.14$, 4 df, $P = 0.32$). The percentage of deer mice infested with fleas in 1989 ranged from 55 (91 grid) to 90% (EC). As with flea indices, the percentage of deer mice infested with fleas on plague-positive grids was not significantly different from that on plague-free grids ($t = 1.32$, 4 df, $P = 0.26$). These two parameters, the flea index and the percentage infested, were not significantly related to one another in 1989 ($r^2 = 0.10$, $P = 0.54$).

In 1990, flea indices for deer mice ranged from 2.3 (WC) to 4.3 (G). As in 1989, flea indices did not significantly differ between plague-positive and plague-free trapping grids ($t = 0.56$, 4 df, $P = 0.61$). The percentage of deer mice infested with fleas ranged from 73 (WC) to 88% (G) in 1990. Percentage of infested deer mice on plague-positive grids was not significantly different from those on plague-free grids ($t = 0.53$, 4 df, $P = 0.62$). In 1990, flea indices were significantly and positively related to the percentage of deer mice infested with fleas ($r^2 = 0.91$, $P = 0.004$).

Sixteen desert cottontails yielded 71 fleas of four species in 1989, while 26 fleas of five species were collected from six cottontails in 1990. Members of the flea genus *Oropsylla* were more prevalent on cottontails in 1990 than 1989, with *O. labis* providing the only *Y. pestis*-positive flea pool for this host in the Meeteetse Com-

plex (91 grid). Thirteen Uinta ground squirrels were captured in 1989, from which 36 fleas of five species were collected. In 1990, six ground squirrels yielded 87 fleas of six species. All four members of the *Oropsylla* flea genus that were collected from Uinta ground squirrels (*O. tuberculata cynomuris, O. idahoensis, O. labis,* and *O. pandorae*) had *Y. pestis*-positive fleas. Sixty-three fleas of six species were collected from 20 northern grasshopper mice in 1989. Nine grasshopper mice yielded 17 fleas of four species in 1990. All flea samples collected from this host were negative for *Y. pestis.*

White-tailed jackrabbits yielded only one sample of one flea each year. A *Pulex irritans* was removed from a WC jackrabbit in 1989 and a *C. inaequalis* was collected from an EC jackrabbit in 1990. Three olive-backed pocket mice yielded one *Neopsylla inopina* in 1989, while a single pocket mouse provided one *Meringis shannoni* in 1990. Fleas taken from these two mammal species were negative for *Y. pestis* in both years.

Several species of fleas collected in both 1989 and 1990 were limited to only one host species in our study. *Amaradix bitterrootensis, C. decipiens, Catallagia* spp., *Callistopsyllus campestris, Callistopsyllus terinus, Epitedia wenmanni, Opisocrostis* spp., and *O. tuberculata tuberculata* were collected only from deer mice. The northern grasshopper mouse was the only host for *Foxella ignota.*

Several other flea species on the Meeteetse Complex were moderately host-specific and were limited only to members of the Cricetidae, Leporidae, or hosts of a similar size examined in our study. *Callistopsyllus* spp., *Hystrichopsylla dippiei, P. exilis,* and *R. fraterna* were found only on deer mice and northern grasshopper mice. Deer mice and olive-backed pocket mice (*Perognathus fasciatus*) were the only hosts of *M. shannoni. Cediopsylla inaequalis* was collected from desert cottontails and white-tailed jackrabbits, but was also found on carnivores. Uinta ground squirrels and desert cottontails, two of the larger associated mammal species on the Complex, hosted the flea species *O. pandorae.*

A few of the flea species collected on the Meeteetse Complex were found on several species of mammals, and so could be considered to possess low host specificity. *Neopsylla inopina* was found on every mammal species except the white-tailed jackrabbit over the 2 yr of flea sampling. With nearly as wide a range of hosts, *A. wagneri* and *O. tuberculata cynomuris* were collected from WTPD, desert cottontails, Uinta ground squirrels, deer mice, and northern grasshopper mice. The two remaining *Oropsylla* species, *O. idahoensis,* and *O. labis,* were removed from WTPD, desert cottontails, Uinta ground squirrels, and deer mice.

DISCUSSION

In 1989 and 1990, plague occurred throughout the late spring and summer in various WTPD towns in the Meeteetse Complex. The distribution of plague was widespread and sporadic, and changed dramatically between years. Plague was not identified in other small mammals in 1989; however, desert cottontails, Uinta ground squirrels, and deer mice had *Y. pestis*-positive fleas in 1990.

Plague directly influenced the density of WTPD's on the Meeteetse Complex. Trapping grids from which *Y. pestis*-positive WTPD fleas were collected in 1990 had much lower prairie dog densities than in 1989, while those that were plague-free had higher densities. Grids that were plague-free in 1990, especially BLM-13 and PC, showed rapid WTPD population increases within the season. Menkens and Anderson (1991) observed similar rapid recovery in the Meeteetse Complex; in their earlier study low density populations completely recovered in 1 to 2 yr. This rapid recovery may be due to higher natality rates of individual survivors or immigrants, higher overall survival, or increased immigration from surrounding ar-

eas (Menkens and Anderson, 1991). The high proportion of juvenile males on BLM-13 and PC in mid-summer tends to support immigration as the major source of population increases within low density WTPD towns.

Menkens and Anderson (1991), noting the apparently unequal responses of several exposed Meeteetse WTPD populations, concluded that as a result of the great temporal variation in WTPD population attributes, the impact of plague on population dynamics versus impacts associated with other sources of mortality was indistinguishable. The results of this study, on the other hand, indicate that density of WTPD populations in Meeteetse uniformly declined up to 96% during plague epizootics. However, those towns without plague always increased in density between years, inferring that this disease impacted the numbers of WTPD's in the population.

Sex and age differences in mortality during a plague epizootic have been reported for WTPD's (Clark, 1977). However, these results may have been confounded by varying rates of adult emergence (Rayor, 1985). In the present study, WTPD populations affected by a plague epizootic in 1990 had approximately the same number of males and females. Although there were fewer juveniles per female on plague-positive grids than on plague-free grids, this was more likely the result of overall plague mortality among the large population of available juveniles rather than a difference in susceptibility between the age groups.

Attributes of the WTPD flea population changed both seasonally and in response to prairie dog plague epizootics. These fluctuations were especially apparent in the flea indices, which were higher both earlier in the summer and on those grids with plague. All of the major flea species found on WTPD's in this study reached their highest population levels in late spring and early summer, which probably contributes to the high indices observed during this part of the season (Kartman et al., 1962).

The percentage of WTPD's infested with fleas was positively related to flea indices during 1990. It is possible that as the host population decreases due to a plague epizootic, displaced fleas would not only increase the flea index on survivors, but also the proportion infected with fleas. Grids such as BLM-13 in 1989 and 91 in 1990 epitomize this trend.

Flea species most important in the transfer of *Y. pestis* from one WTPD to another in the Meeteetse Complex were *N. inopina, O. tuberculata cynomuris, O. idahoensis,* and *O. labis.* Ubico et al. (1988) also observed that each was a plague vector in the Meeteetse Complex, but considered only *O. tuberculata cynomuris* and *O. labis* of major importance in WTPD plague. However, our results indicated both *O. idahoensis* and *N. inopina* were important in plague transmission among WTPDs in 1990.

The seasonal shift in flea species composition, with *O. idahoensis* and *O. labis* replacing *N. inopina* and *O. tuberculata cynomuris* as prevalent summer fleas, may have had a bearing on the seasonal course of plague. The potential of *O. idahoensis* passing plague was considered to be poor because it is primarily a ground squirrel flea, thus its increase may signal a decline in the number of effective plague transmissions (Ecke and Johnson, 1952). Alternatively, an increase in *O. labis,* a nest flea, may provide a means for plague to overwinter in the body of the flea and for the epizootic to reinstate in the spring (Ecke and Johnson, 1952).

The flea species we encountered on WTPD's in the Meeteetse Complex may have provided clues about the initiation and maintenance of plague epizootics in these populations. Both *O. idahoensis* and *N. inopina* were common ground squirrel fleas, and could have transmitted plague from these populations to WTPD's (Lechleitner et al., 1968; Ubico et al., 1988). Other flea species, such as *A. wagneri, C.*

inaequalis, H. dippiei, O. pandorae, P. irritans, and *R. fraterna,* were accidental on WTPD's.

White-tailed prairie dog towns in the Meeteetse Complex that had a burrow density of less than 60 burrows per ha failed to yield *Y. pestis*-positive flea pools from burrows. In general, low burrow density corresponds to low prairie dog and associated mammal density, a scenario unfavorable to the maintenance of a plague epizootic.

Deer mice, due to their overwhelming abundance and wide array of flea species, could act as both reservoir hosts and disseminators of *Y. pestis* on the Meeteetse Complex. Since abundance of deer mice remained high on those trapping grids with *Y. pestis*-positive fleas, these populations may have been relatively resistant to plague mortality. Although WTPD's and deer mice did not share any *Y. pestis*-positive flea species, they did occasionally harbor flea species that were common to the other. The transfer of a plague infected, and infective flea from a deer mouse to a susceptible WTPD is not unlikely.

Uinta ground squirrels, although irregularly distributed throughout the Meeteetse Complex, produced several *Y. pestis*-positive flea pools. Ground squirrels and WTPDs shared several of these infected flea species: *O. tuberculata cynomuris, O. idahoensis,* and *O. labis.* Their role may be to transport infected fleas from resistant to susceptible species.

Desert cottontails, like Uinta ground squirrels, had a patchy distribution and tended to decline in numbers during a plague epizootic. They also may act as hosts that transport *Y. pestis*-infected fleas over long distances through their widespread wanderings. Northern grasshopper mice did not appear to be directly involved in the WTPD epizootic on the Meeteetse Complex. All fleas gathered from this species were plague-free. Because few white-tailed jackrabbits and olive-backed pocket mice were captured during this study, little is known of their role in plague ecology for the Meeteetse Complex.

In overview, plague apparently cycled through various WTPD towns in the Meeteetse Complex, causing epizootics in those with sufficient host density and vectors. Transport of *Y. pestis*-infected fleas by dispersing prairie dogs or wide-ranging carnivores may introduce *Y. pestis* into unaffected towns, providing new epizootic foci and increased plague distribution (Barnes, 1982). Plague epizootics in WTPDs were curtailed by seasonal climate changes, host hibernation, and low density of hosts (Kartman et al., 1966). Because observations from this study and that of Menkens and Anderson (1991) indicate that Meeteetse WTPD populations rebound rapidly from low densities, plague is probably able to reestablish itself in a WTPD town every 3 to 5 yr.

We feel that it is nearly impossible to predict the movement of plague in the Meeteetse Complex. Any town with a moderate (three WTPD's/ha) to high (six WTPD's/ha) population density and any combination of the four flea species were probably susceptible to a plague epizootic. Although towns closer to active epizootics were more likely to experience an introduction of plague, none were immune to a potential outbreak. The distribution of plague in the Complex changed rapidly from year to year, suggesting either very active transport or long-term maintenance of infected fleas.

We do not understand the importance of mammal species in the maintenance of plague in prairie dog colonies over long periods of time. Although deer mice, grasshopper mice, and ground squirrels are all described as maintenance hosts because of their variable resistance to plague mortality, there is no direct field evidence to support these conclusions.

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