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PYRAPERM KILLS FLEAS AND HALTS PLAGUE AMONG UTAH PRAIRIE DOGS

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ABSTRACT—Plague is an introduced bacterial disease whose primary vectors are fleas (Siphonaptera). Utah prairie dogs (*Cynomys parvidens*) are highly susceptible to plague, and entire colonies usually disappear shortly after plague arrives. Infusion of burrows with Pyraperm (an insecticide-dust) kills fleas and immediately halts the spread of plague within colonies. Thus, insecticide-dusts might play an important role in the conservation of prairie dogs.

RESUMEN—La plaga bubónica es una enfermedad bacterial introducida para quien las pulgas (Siphonaptera) son los vectores principales. Los perros de la pradera de Utah (*Cynomys parvidens*) son muy susceptibles a la plaga, y colonias enteras generalmente desaparecen poco después de la llegada de la plaga. La inyección en las madrigueras con Pyraperm (un polvo insecticida) mata a las pulgas y detiene inmediatamente la propagación de la plaga en las colonias. Entonces, es posible que los polvos de insecticidas puedan jugar un papel importante en la conservación de los perros de la pradera.

The plague (''Black Death'') killed about 30% of the human population in Europe between 1347 and 1352 and was perhaps the greatest epidemiological disaster in world history (Gottfried, 1983; Keeling and Gilligan, 2000; Cantor, 2001). Currently plague is having a similar catastrophic effect on prairie dogs (Cully and Williams, 2001).

Plague is caused by the bacterium *Yersinia* (*Pasteurella*) *pestis,* and fleas (Siphonaptera) are the most common vectors. Plague might have arrived naturally in North America during the Pleistocene via the Siberian-Alaskan land bridge. More likely, however, plague arrived about 100 years ago via flea-infested rats from ships coming from Asia and Europe (Pollitzer, 1951; Barnes, 1993; Biggins and Kosoy, 2001).

Plague infects ≥73 genera and >200 species of mammals and is widespread on every continent except Australia and Antarctica (Biggins and Kosoy, 2001). Some species are highly or moderately resistant to plague (Biggins and Kosoy, 2001). Prairie dogs (Sciuridae: *Cynomys*), however, are highly susceptible, probably because they have not had sufficient time to evolve a good defense against an introduced disease (Cully and Williams, 2001). Outbreaks of plague typically kill most, and commonly all, residents within colonies of all 4 species of prairie dogs in the United States: black-tailed prairie dog (*C. ludovicianus*) (Miles et al., 1952; Barnes et al., 1972; Cully et al., 2000), Gunnison's prairie dog (*C. gunnisoni*) (Kartman et al., 1962; Cully, 1997), Utah prairie dog (*C. parvidens*) (Collier and Spillett, 1975; Hasenyager et al., 1988; Turner, 2001), and white-tailed prairie dog (*C. leucurus*) (Ubico et al., 1988; Menkens and Anderson, 1991; Anderson and Williams, 1997; Cully and Williams, 2001). Numerous behavioral ecologists have lost colonies of marked prairie dogs to plague (Lechleitner et al., 1968; Fitzgerald and Lechleitner, 1974; Clark, 1977; Rayor, 1985; Cully, 1997; Hoogland, 1999). Curiously, evidence of plague among Mexican prairie dogs (*C. mexicanus*) is scarce (Varela and Vasquez, 1954; Trevino-Villarreal et al., 1998; D. E. Biggins, pers. comm.; J. F. Cully, pers. comm.), probably because studies of this species are few.

Prairie dogs are herbivorous, colonial, ground-dwelling squirrels that inhabit western North America (Hollister, 1916; Pizzimenti,

1975). Colonies are subdivided into territorial, harem-polygynous family groups (King, 1955; Fitzgerald and Lechleitner, 1974; Clark, 1977; Wright-Smith, 1978; Rayor, 1988; Trevino-Villarreal, 1990; Mellink and Madrigal, 1993; Hoogland, 1995, 1999, 2001; Travis et al., 1996). Because they have a disproportionate effect relative to their abundance (Mills et al., 1993; Power et al., 1996), prairie dogs are keystone species of the western grassland ecosystem (Miller et al., 1994, 2000; Kotliar et al., 1999). Their foraging, for example, decreases the height of vegetation, changes the species composition of vegetation, and increases landscape heterogeneity (Coppock et al., 1983; Weltzin et al., 1997). Prairie dog excavations increase the mixing of topsoil and subsoil and also promote uptake of nitrogen by plants (Holland and Detling, 1990). Further, colonies increase biological diversity and species richness (Clark et al., 1982; Reading et al., 1989). Animals, such as burrowing owls (*Athene cunicularia*), tiger salamanders (*Ambystoma tigrinum*), and myriad insects, depend on prairie dog burrows for shelter. Aerial predators, such as ferruginous hawks (*Buteo regalis*), golden eagles (*Aquila chrysaetos*), northern goshawks (*Accipiter gentilis*), and prairie falcons (*Falco mexicanus*), commonly prey on prairie dogs, as do terrestrial predators, such as American badgers (*Taxidea taxus*), black-footed ferrets (*Mustela nigripes,* specialists that feed almost exclusively on prairie dogs), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) (Knowles et al., 1982; Desmond and Savidge, 1996; Kotliar et al., 1999).

Mainly because ranchers view them as pests that compete with livestock for forage (Jameson, 1973; Randall, 1976*a,* 1976*b*; Zinn and Andelt, 1999), prairie dogs of all species have been targets of intensive eradication programs that involve shooting, poisoning, drowning, and destruction of habitat (McNulty, 1971; Marsh, 1984; Cincotta et al., 1987; Roemer and Forrest, 1996; Vosburgh and Irby, 1998). Sylvatic plague also has killed millions of prairie dogs (Biggins and Kosoy, 2001; Cully and Williams, 2001). Consequently, all 5 species are becoming increasingly rare and occupy <5% of their former range. The Utah prairie dog and Mexican prairie dog are listed as threatened and endangered species, respectively, by the United States Fish and Wildlife Service (1970, 1984), and listing of the black-tailed prairie dog as a threatened species was considered warranted but precluded (United States Fish and Wildlife Service, 2000). The white-tailed prairie dog and Gunnison's prairie dog are currently under consideration for listing as threatened species (Center for Native Ecosystems et al., 2002; Rosmarino, 2004).

For Utah prairie dogs at Bryce Canyon National Park, emergence from hibernation occurs in late February through mid April, copulations occur in mid March through early April, and nearly-weaned juveniles first emerge from natal burrows in late May and June. Gestation is usually 29 or 30 days, and lactation lasts about 5.5 weeks (Hoogland, 2001).

Unlike eradication programs, plague is not under direct human control. Thus, plague might pose the most formidable obstacle for the long-term conservation of prairie dogs (Cully and Williams, 2001). Because fleas are the primary vectors, removal of fleas might protect animals from plague (Barnes et al., 1972). We tested this hypothesis for Utah prairie dogs by using an insecticide-dust to kill fleas within burrows. The incentive for our research was an outbreak of plague at a colony containing eartagged, marked individuals for which we have long-term information on age, reproductive history, and behavioral ecology (Hoogland, 2001).

METHODS—For the last 8 years (March through June, 1995 to 2002), involving >20,000 person-hours of research, we have studied the ecology and social behavior of Utah prairie dogs at Bryce Canyon National Park in south-central Utah (Hoogland, 2001). Our study colony is the Horse Corral Colony at an elevation of approximately 2,700 m. The colony occupies 5.75 ha and contains a mean of 118 (±54.0 *SD*) adults that emerge from hibernation and 148 (±54.9 *SD*) juveniles in late June (1995 through 2002). The study colony contained 139 adults in April 1998 and 137 adults in April 2001.

Methods for capturing, handling, eartagging, marking, and observing Utah prairie dogs are the same as those used in long-term research with black-tailed prairie dogs and Gunnison's prairie dogs (Hoogland, 1998, 2001, 2003). Each year we capture and uniquely mark all the adult and juvenile residents at the study colony. Using binoculars and a 60-power telescope, we watch marked individuals from 4-m high observation towers.

While handling Utah prairie dogs, we comb the sides and back of each individual 10 times and count the number of ectoparasites that fall to the ground

(see Hoogland, 1995). Ticks and mites (Acarina) are rare, and we have never detected a louse (Anoplura). Fleas are common, however, and include the following species: *Hoplosyllus anomalus, Oropsylla* (*Opisocrostis*) *hirsuta, O. labis, O. tuberculata,* and *Thrassis francisi* (Allred, 1952; Stark, 1958; Pizzimenti, 1975). To preclude recounting the same flea or tick, we killed each ectoparasite via submersion into ethanol. Counted ectoparasites probably represented a small but constant percentage of those actually present (Hoogland, 1979).

To kill fleas within burrows of Utah prairie dogs, we used a DR5 air-powered duster (Birchmeier, Baden, Switzerland). We infused burrows with an insecticide-dust called Pyraperm (pyrenone, 4-0.05 permanone 0.5 dust, code 9440; Bayer Environmental Science, Montvale, New Jersey). Pyraperm was formulated specifically to kill fleas within burrows of prairie dogs and other ground-dwelling squirrels, with minimal secondary consequences for other species. We inserted the pointed nozzle of the air-powered duster into every burrow entrance at the study colony and injected dust for approximately 1 s. We detected no evidence that Pyraperm is harmful to prairie dogs.

We found 5 aboveground carcasses that resulted, we suspected, from plague (2 in 1998, 3 in 2001). To verify the presence or absence of plague, we shipped all carcasses to the Center for Disease Control (CDC) in Fort Collins, Colorado.

Gunnison's prairie dogs and Utah prairie dogs that survive infection with plague develop specific antibodies (Cully et al., 1997; D. E. Biggins, pers. comm.). To determine if Utah prairie dogs at the study colony had developed antibodies against plague in 1998, we collected blood samples in May and June 1999 from 70 adults. We shipped all samples to CDC for analysis.

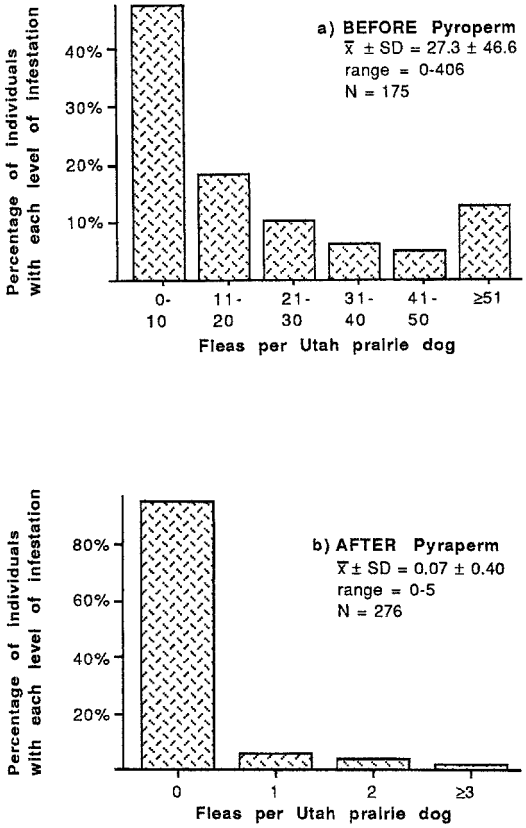

FIG. 1—Number of fleas per Utah prairie dog at the study colony at Bryce Canyon National Park, Utah (a) in March, April, and May 2001, before the infusions of burrow entrances with Pyraperm; and (b) in June and July 2001, after the infusions with Pyraperm. Differences in flea infestation before and after infusions were significant ($P < 0.001$, Mann-Whitney *U*-test).

RESULTS—Nine marked Utah prairie dogs from the same small area (<2 ha) of the study colony died or disappeared in April or May 2001. Five of these 9 moved slowly and seemed disoriented immediately before disappearance, and we observed 3 of these 5 perish aboveground (on 17, 28, and 29 May 2001). All 3 carcasses were plague-positive.

Between 31 May 2001 and 2 June 2001, we infused Pyraperm into every burrow entrance (>1,200) within the colony. Fleas were common on prairie dogs before Pyraperm, but almost completely disappeared afterwards (Fig. 1). Also, no Utah prairie dog showed symptoms of plague or inexplicably disappeared after 31 May 2001. Females at the study colony collectively weaned 163 juveniles in June 2001, and healthy adults and juveniles were evident throughout summer and early autumn 2001 (R. Wallen, Park Biologist, Bryce Canyon National Park, pers. comm.). Further, the number of healthy individuals that emerged from hibernation in 2002 was 121, which is similar to the usual number of emerging adults (mean = 118 ± 54.0 *SD*).

Pyraperm also immediately halted an outbreak of plague at the study colony in 1998. In June 1998, 3 adults and 2 juveniles showed symptoms of plague. The 2 juveniles died aboveground, and CDC confirmed that they were both plague-positive. Immediately after confirmation, one of us (JLH) infused all bur-

row entrances at the study colony with Pyraperm. No more Utah prairie dogs showed symptoms of plague or disappeared after the infusions. Females at the study colony collectively weaned 195 juveniles in June 1998. Healthy adults and juveniles were evident throughout summer and early autumn 1998 (D. Neighbors, Park Biologist, Bryce Canyon National Park, pers. comm.), and 154 healthy individuals emerged from hibernation in 1999. Fleas were common on the Utah prairie dogs before the infusions with Pyraperm in 1998 (mean = 11.0 ± 25.4 *SD* during March through May, $n = 227$), but we did not count fleas after the infusions because we had just marked/remarked all colony residents and our investigation of behavioral ecology was finished for 1998.

All 1999 blood samples ($n = 70$) collected in May and June 1999 from adult Utah prairie dogs at the study colony were negative for plague antibodies, even though many of the samples were from individuals living in the same clan territory, or in an adjacent territory, where plague attacked in June 1998. Evidently, the survivors never contracted plague, even though many frequently interacted with live or dead victims of plague, and several spent the night in the same burrows with live or dead victims.

In both years of plague when the colony was treated with infusions (1998 and 2001), females collectively weaned (insignificantly) more juveniles than in 6 years of no plague and no infusions (mean = 179 ± 22.6 *SD* versus 138 ± 60.0 *SD*; NS, Mann-Whitney *U*-test). Numbers of emerging adults in March and April of 1999 and 2002 (i.e., 8 to 9 months after plague and infusions) were (insignificantly) higher than numbers in March and April following years of no plague and no infusions (mean = 138 ± 23.3 *SD* versus 112 ± 61.4 *SD*; NS, Mann-Whitney *U*-test).

DISCUSSION—Following outbreaks of plague at the study colony in 1998 and 2001, the infusion of Pyraperm into burrow entrances immediately stopped new cases of plague. The cessation was more convincing in 2001 than in 1998 for 2 reasons. First, we obtained estimates of flea infestation of Utah prairie dogs both before and after infusions with Pyraperm in 2001. In 1998, we did not examine individuals for fleas after the infusions, because plague did not appear until the end of the field season. Second, in 2001, we carefully watched marked individuals for additional cases of plague for 6 weeks after the infusions with Pyraperm. In 1998, we watched for new cases of plague for only 1 week after infusions.

Because Utah prairie dogs live in crowded colonies where cannibalism and mouth-to-mouth greetings are frequent (Wright-Smith, 1978; Hoogland, 2001, 2003), direct transmission of plague among individuals seems likely. Our results suggest, however, that fleas are necessary for the continued spread of plague within colonies. If direct transfer of plague occurs via cannibalism of infected carcasses, for example, then additional cases should have appeared in 1998 and 2001 after we killed fleas with Pyraperm.

Plague ravages colonies of all 4 species of prairie dogs within the United States. Mortality from plague is typically >95% and is commonly 100%. Two lines of evidence indicate that prairie dogs occasionally survive exposure to plague. First, white-tailed prairie dogs infected with plague under laboratory conditions sometimes survive (Cully and Williams, 2001). Second, antibodies indicate that small numbers of wild Gunnison's prairie dogs and wild Utah prairie dogs sometimes overcome plague (Lechleitner et al., 1968; Cully et al., 1997; D. E. Biggins, pers. comm.).

It is possible that the stoppage of plague at the study colony was unrelated to infusions with Pyraperm. However, for a species that is highly vulnerable, Pyraperm immediately prevented new cases of plague in 2 years that followed confirmed outbreaks of plague.

It is possible that infusions only temporarily stopped plague and that deaths from plague were common in the months after we stopped studying Utah prairie dogs. However, in both years of plague when the colony was treated with infusions (1998 and 2001), the number of juveniles collectively weaned was insignificantly higher than the numbers weaned in 6 years of no plague and no infusions. Further, throughout the summer and early autumn of 1998 and 2001, park biologists at Bryce Canyon regularly observed numerous aboveground, active prairie dogs (D. Neighbors, pers. comm.; R. Wallen, pers. comm.). In addition, the numbers of emerging adults in March and April of 1999

and 2002 (i.e., 8 to 9 months after plague and infusions) were insignificantly higher than the numbers of emerging adults in March and April following years of no plague and no infusions.

Previous investigators have demonstrated that infusions of insecticide-dust into burrows kill fleas and have hypothesized that infusions therefore protect prairie dogs against plague (Barnes et al., 1972; Beard et al., 1992; Karhu and Anderson, 2000). However, these researchers were unable to verify that prairie dogs in treated colonies were unequivocally exposed to plague. Our results offer clear evidence that infusions protect Utah prairie dogs, and presumably other species of prairie dogs, against plague. Working with black-tailed prairie dogs, Seery et al. (2004) have provided the only other compelling evidence for protection against plague via infusions with insecticide-dust.

Marked Utah prairie dogs were pivotal to our demonstration that Pyraperm immediately stopped the spread of plague in 1998 and 2001. Daily censuses allowed us to document which marked individuals disappeared, the exact dates of disappearances, and that no additional individuals disappeared after infusions. Similar documentation would be difficult without marked individuals.

The Pyraperm that we used in 1998 and 2001 remains active for about 6 weeks after application. Newer insecticide-dusts designed to kill fleas within burrows remain active for ≥24 weeks. Longer-acting insecticide-dusts (such as Deltadust, Bayer Environmental Science, Montvale, New Jersey) should provide better protection against plague (Seery et al., 2004). Probably for this reason, Pyraperm is no longer commercially available.

One person can infuse about 100 burrow entrances per hour with an insecticide-dust such as Pyraperm or Deltadust. Infusing burrows at numerous small colonies or at a few large colonies is thus feasible for a single person or for small teams. At this small scale, and perhaps at larger scales as well, insecticide-dusts might play an important role in the conservation of prairie dogs and the grassland ecosystem.

Sick prairie dogs sometimes transmit plague to humans (Levy and Gage, 1999). Even with current antibiotics, plague among humans is difficult to neutralize and can be lethal (Gottfried, 1983; Keeling and Gilligan, 2000). Pyraperm and other insecticide-dusts help to protect humans against the transfer of plague from prairie dogs and their fleas. This security might be especially valuable when prairie dog colonies occur within boundaries of cities, as they frequently do (e.g., Denver, Colorado; Flagstaff, Arizona; and Laramie, Wyoming).

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Literature Cited

Allred, D. M. 1952. Plague-important fleas and mammals in Utah and the western United States. Great Basin Naturalist 12:67–75.

Anderson, S. H., and E. S. Williams. 1997. Plague in a complex of white-tailed prairie dogs and associated small mammals in Wyoming. Journal of Wildlife Diseases 33:720–732.

Barnes, A. M. 1993. A review of plague and its relevance to prairie dog populations and the black-footed ferret. In: Oldemeyer, J. L., D. E. Biggins, B. J. Miller, and R. Crete, editors. Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of black-footed ferrets. United States Fish and Wildlife Service, Biological Report 93:28–37.

Barnes, A. M., L. J. Ogden, and E. G. Campos. 1972. Control of the plague vector, *Opisocrostis hirsutis,* by treatment of prairie dog (*Cynomys ludovicianus*) burrows with 2% carbaryl dust. Journal of Medical Entomology 9:330–333.

Beard, M. L., S. T. Rose, A. M. Barnes, and J. A. Montenieri. 1992. Control of *Oropsylla hirsuta,* a plague vector, by treatment of prairie dog burrows with 0.5 percent permethrin dust. Journal of Medical Entomology 29:25–29.

Biggins, D. E., and M. Y. Kosoy. 2001. Influences of introduced plague on North American mammals: implications from ecology of plague in Asia. Journal of Mammalogy 82:906–916.

Cantor, N. F. 2001. In the wake of the plague: the

Black Death and the world it made. Free Press, New York.

CENTER FOR NATIVE ECOSYSTEMS, BIODIVERSITY CONSERVATION ALLIANCE, SOUTHERN UTAH WILDERNESS ALLIANCE, AMERICAN LANDS ALLIANCE, FOREST GUARDIANS, T. T. WILLIAMS, ECOLOGY CENTER, AND SINAPU. 2002. Petition to list the white-tailed prairie dog (*Cynomys leucurus*) as a threatened or endangered species and to designate critical habitat under the Endangered Species Act of 1973, as amended.

CINCOTTA, R. P., D. W. URESK, AND R. M. HANSEN. 1987. Demography of black-tailed prairie dog populations reoccupying sites treated with rodenticide. Great Basin Naturalist 47:339–343.

CLARK, T. W. 1977. Ecology and ethology of the white-tailed prairie dog (*Cynomys leucurus*). Publications in Biology and Geology, Milwaukee Public Museum, number 3, Milwaukee, Wisconsin.

CLARK, T. W., T. M. CAMPBELL, D. G. SOCHA, AND D. E. CASEY. 1982. Prairie dog colony attributes and associated vertebrate species. Great Basin Naturalist 42:572–582.

COLLIER, G. D., AND J. J. SPILLETT. 1975. Factors influencing the distribution of the Utah prairie dog, *Cynomys parvidens* (Sciuridae). Southwestern Naturalist 20:151–158.

COPPOCK, D. L., J. K. DETLING, J. E. ELLIS, AND M. I. DYER. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56:1–9.

CULLY, J. F. 1997. Gunnison's prairie dog growth and life-history change after a plague epizootic. Journal of Mammalogy 78:146–157.

CULLY, J. F., A. M. BARNES, T. J. QUAN, AND G. MAUPIN. 1997. Dynamics of plague in a Gunnison's prairie dog colony complex from New Mexico. Journal of Wildlife Diseases 33:706–719.

CULLY, J. F., L. G. CARTER, AND K. L. GAGE. 2000. New records of sylvatic plague in Kansas. Journal of Wildlife Diseases 36:389–392.

CULLY, J. F., AND E. S. WILLIAMS. 2001. Interspecific comparisons of sylvatic plague in prairie dogs. Journal of Mammalogy 82:894–905.

DESMOND, M. J., AND J. A. SAVIDGE. 1996. Factors influencing burrowing owl (*Speotyto cunicularia*) nest densities and numbers in western Nebraska. American Midland Naturalist 136:143–148.

FITZGERALD, J. P., AND R. R. LECHLEITNER. 1974. Observations on the biology of Gunnison's prairie dog in central Colorado. American Midland Naturalist 92:146–163.

GOTTFRIED, R. 1983. The Black Death: natural and human disaster in medieval Europe. Free Press, New York.

HASENYAGER, R. N., T. BALL, AND T. W. CLARK. 1988. Utah prairie dog recovery plan. United States Fish and Wildlife Service, Denver, Colorado.

HOLLAND, E. A., AND J. K. DETLING. 1990. Plant response to herbivory and below ground nitrogen cycling. Ecology 71:1040–1049.

HOLLISTER, N. 1916. A systematic account of the prairie dogs. North American Fauna 40:1–37.

HOOGLAND, J. L. 1979. Aggression, ectoparasitism, and other possible costs of prairie dog (Sciuridae: *Cynomys* spp.) coloniality. Behaviour 69:1–35.

HOOGLAND, J. L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago, Illinois.

HOOGLAND, J. L. 1998. Why do Gunnison's prairie dog females copulate with more than one male? Animal Behaviour 55:351–359.

HOOGLAND, J. L. 1999. Philopatry, dispersal, and social organization of Gunnison's prairie dogs. Journal of Mammalogy 80:243–251.

HOOGLAND, J. L. 2001. Black-tailed, Gunnison's, and Utah prairie dogs all reproduce slowly. Journal of Mammalogy 82:917–927.

HOOGLAND, J. L. 2003. Sexual dimorphism of prairie dogs. Journal of Mammalogy 84:1254–1266.

JAMESON, W. C. 1973. On the eradication of prairie dogs: a point of view. Bios 44:129–135.

KARHU, R., AND S. ANDERSON. 2000. Effects of pyriproxyfen spray, powder, and oral bait treatments on the relative abundance of fleas (Siphonaptera: Ceratophyllidae) in black-tailed prairie dog (Rodentia: Sciuridae) towns. Journal of Medical Entomology 37:864–871.

KARTMAN, L., S. F. QUAN, AND R. R. LECHLEITNER. 1962. Die-off of a Gunnison's prairie dog colony in central Colorado. II. Retrospective determination of plague infection in flea vectors, rodents, and man. Zoonoses Research l:201–224.

KEELING, M. J., AND C. A. GILLIGAN. 2000. Metapopulation dynamics of bubonic plague. Nature 407: 903–906.

KING, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairiedog town in the Black Hills of South Dakota. Contributions from the Laboratory of Vertebrate Biology, University of Michigan 67:1–123.

KNOWLES, C. J., C. J. STONER, AND S. P. GIEB. 1982. Selective use of black-tailed prairie dog towns by mountain plovers. Condor 84:71–74.

KOTLIAR, N. B., B. W. BAKER, A. D. WHICKER, AND G. PLUMB. 1999. A critical review of assumptions about prairie dogs as keystone species. Environmental Management 24:177–192.

LECHLEITNER, R. R., L. KARTMAN, M. I. GOLDBERG, AND B. W. HUDSON. 1968. An epizootic of plague in Gunnison's prairie dogs (*Cynomys gunnisoni*) in south-central Colorado. Ecology 49:734–743.

LEVY, C. E., AND K. L. GAGE. 1999. Plague in the Unit-

ed States, 1995–1997. Infections in Medicine 16: 54–64.

MARSH, R. E. 1984. Ground squirrels, prairie dogs, and marmots as pests on rangelands. In: Proceedings of the conference for organization and practice of vertebrate pest control, 1982 (Hampshire, United Kingdom). Plant Protection Division, Fernherst, United Kingdom. Pp. 195–208.

MCNULTY, F. 1971. Must they die? The strange case of the prairie dog and the black-footed ferret. Doubleday, Garden City, New York.

MELLINK, E., AND H. MADRIGAL. 1993. Ecology of Mexican prairie dogs, *Cynomys mexicanus,* in El Manantial, northeastern Mexico. Journal of Mammalogy 74:631–635.

MENKENS, G. E., AND S. H. ANDERSON. 1991. Population dynamics of white-tailed prairie dogs during an epizootic of sylvatic plague. Journal of Mammalogy 72:328–331.

MILES, V. I., M. J. WILCOMB, AND J. V. IRONS. 1952. Plague in Colorado and Texas. II. Rodent plague in Texas south plains. Public Health Monographs 6:39–53.

MILLER, B., G. CEBALLOS, AND R. P. READING. 1994. The prairie dog and biotic diversity. Conservation Biology 8:677–681.

MILLS, L. S., M. E. SOULE, AND D. F. DOAK. 1993. The history and current status of the keystone species concept. Bioscience 43:219–224.

PIZZIMENTI, J. J. 1975. Evolution of the prairie dog genus *Cynomys*. Occasional Papers of the Museum of Natural History, University of Kansas 39:1–73.

POLLITZER, R. 1951. Plague studies. 1. A summary of the history and a survey of the present distribution of the disease. World Health Organization Bulletin 4:475–533.

POWER, M. E., D. TILMAN, J. A. ESTES, B. A. MENGE, W. J. BOND, L. S. MILLS, G. DAILY, J. C. CASTILLA, J. LUBEHCNCO, AND R. T. PAINE. 1996. Challenges in the quest for keystones. Bioscience 466:9–20.

RANDALL, D. 1976*a*. Shoot the damn prairie dogs. Defenders 51:378–381.

RANDALL, D. 1976*b*. Poison the damn prairie dogs. Defenders 51:381–383.

RAYOR, L. S. 1985. Dynamics of a plague outbreak in Gunnison's prairie dog. Journal of Mammalogy 66:194–196.

RAYOR, L. S. 1988. Social organization and space-use in Gunnison's prairie dog. Behavioral Ecology and Sociobiology 22:69–78.

READING, R. P., S. R. BEISSINGER, J. J. GRENSTEN, AND T. W. CLARK. 1989. Attributes of black-tailed prairie dog colonies in northcentral Montana, with management recommendations for the conservation of biodiversity. In: Clark, T. W., D. Hinckley, and T. Rich, editors. The prairie dog ecosystem: managing for biological diversity. Montana Bureau of Land Management, Wildlife Technical Bulletin 2:13–27.

ROEMER, D. M., AND S. C. FORREST. 1996. Prairie dog poisoning in northern Great Plains: an analysis of programs and policies. Environmental Management 20:349–359.

ROSMARINO, N. J. 2004. Petition to list the Gunnison's prairie dog under the Endangered Species Act. Submitted to the United States Fish and Wildlife Service on behalf of Forest Guardians and 73 co-petitioners on 23 February 2004.

SEERY, D. B., D. E. BIGGINS, J. A. MONTENIERI, R. E. ENSCORE, D. T. TANDA, AND K. L. GAGE. 2003. Treatment of black-tailed prairie dog burrows with Deltamethrin to control fleas (Insecta: Siphonaptera) and plague. Journal of Medical Entomology 40:718–722.

STARK, H. E. 1958. The Siphonaptera of Utah. United States Department of Health, Education, and Welfare, Public Health Service, Washington, D.C.

TRAVIS, S. E., C. N. SLOBODCHIKOFF, AND P. KEIM. 1996. Social assemblages and mating relationships in prairie dogs: a DNA fingerprint analysis. Behavioral Ecology 7:95–100.

TREVINO-VILLARREAL, J. 1990. The annual cycle of the Mexican prairie dog (*Cynomys mexicanus*). Occasional Papers of the Museum of Natural History, University of Kansas 139:1–27.

TREVINO-VILLARREAL, J., I. M. BERK, A. AGUIRRE, AND W. E. GRANT. 1998. Survey for sylvatic plague in the Mexican prairie dog (*Cynomys mexicanus*). Southwestern Naturalist 43:147–154.

TURNER, G. 2001. Recovery of Utah and Gunnison's prairie dog colonies following epizootics of sylvatic plague. Unpublished M.S. thesis, Frostburg State University, Frostburg, Maryland.

UBICO, S. R., G. O. MAUPIN, K. A. FAGERSTONE, AND R. G. MCLEAN. 1988. A plague epizootic in the white-tailed prairie dogs (*Cynomys leucurus*) of Meeteetse, Wyoming. Journal of Wildlife Diseases 24:399–406.

UNITED STATES FISH AND WILDLIFE SERVICE. 1970. Conservation of endangered species and other fish or wildlife (first list of endangered foreign fish and wildlife as appendix A). 35 FR 8491–8498.

UNITED STATES FISH AND WILDLIFE SERVICE. 1984. Endangered and threatened wildlife and plants; final rule to reclassify the Utah prairie dog as threatened, with special rule to allow regulated taking. 49 FR 22330–22334.

UNITED STATES FISH AND WILDLIFE SERVICE. 2000. Endangered and threatened wildlife and plants; 12-month finding for a petition to list the black-tailed prairie dog as threatened. 65 FR 5476–5488.

VARELA, G., AND A. VASQUEZ. 1954. Hallazgo de la peste selvatica en la republica Mexicana. Infec-

cion natural del *Cynomys mexicanus* (perros llaneros) con *Pasteurella pestis*. Revista del Instituto de Salubridad y Enfermedades Tropicales 14: 219–223.

VOSBURGH, T. C., AND L. R. IRBY. 1998. Effects of recreational shooting on prairie dog colonies. Journal of Wildlife Management 62:363–372.

WELTZIN, J. F., S. L. DOWNHOWER, AND R. K. HEITSCHMIDT. 1997. Prairie dog effects on plant community structure in southern mixed-grass prairie. Southwestern Naturalist 42:251–258.

WRIGHT-SMITH, M. A. 1978. The ecology and social organization of *Cynomys parvidens* (Utah prairie dog) in south central Utah. Unpublished M.S. thesis, Indiana University, Bloomington.

ZINN, H. C., AND W. F. AANDELET. 1999. Attitudes of Fort Collins, Colorado, residents toward prairie dogs. Wildlife Society Bulletin 27:1098–1106.

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