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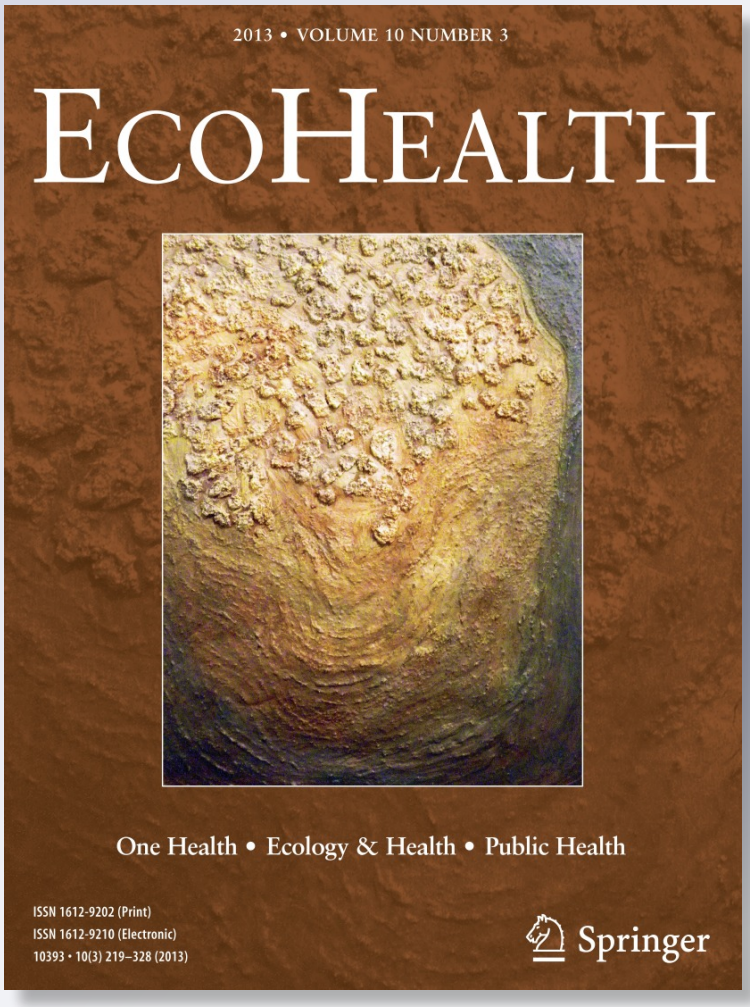

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Short Communication

Duration of Plague (*Yersinia pestis*) Outbreaks in Black-Tailed Prairie Dog (*Cynomys ludovicianus*) Colonies of Northern Colorado

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Abstract: Plague, caused by the bacterium *Yersinia pestis*, triggers die-offs in colonies of black-tailed prairie dogs (*Cynomys ludovicianus*), but the time-frame of plague activity is not well understood. We document plague activity in fleas from prairie dogs and their burrows on three prairie dog colonies that suffered die-offs. We demonstrate that *Y. pestis* transmission occurs over periods from several months to over a year in prairie dog populations before observed die-offs.

Keywords: Prairie dog, plague, disease outbreak, flea

Highly lethal pathogens pose unique public-health problems, because they seem to periodically flare into outbreaks before disappearing into long quiescent phases. Plague, caused by the bacterium *Yersinia pestis*, exemplifies this quiescent—outbreak pattern in both human and animal populations (Gage and Kosoy 2005). Introduced to the United States around 1900, plague currently poses a conservation threat to several animal species, including populations of prairie dogs (*Cynomys* spp.) which can be decimated by plague outbreaks such that only a few individuals survive (Antolin et al. 2002; Stapp et al. 2004; Pauli et al. 2006). Plague's impacts upon prairie dog populations can also affect other species, e.g., the endangered black-footed ferret (*Mustela nigripes*) which depends upon large complexes of prairie dog colonies to provide its primary prey, and is itself highly susceptible to plague mortality (Antolin et al. 2002; Matchett et al. 2010). The natural history of plague in prairie dogs illustrates the important and far-reaching implications of wildlife disease for conservation biology. Yet our understanding of the dynamics of plague outbreaks in prairie dog populations remains poorly understood.

Field-based estimates of plague activity in black-tailed prairie dog colonies suggest durations of 2–4 months (e.g., 2 months, 20.5 ha colony, Wyoming (Pauli et al 2006); June–September, Kansas (Cully et al. 2000)). Modeling approaches have suggested outbreak durations of 5–10 weeks (Webb et al. 2006) or outbreaks as a culmination of plague activity lasting for several months to multiple years (Salkeld et al. 2010). Die-offs of white-tailed prairie dogs (*C. leucurus*) and Gunnison' prairie dogs (*C. gunnisoni*) appear to last several months to over a year (Lechleitner et al. 1968; Anderson and Williams 1997; Cully et al. 1997; Ubico et al. 1988; Girard et al. 2004). Understanding

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the temporal dynamics of plague in prairie dog colonies is important as it provides insights into plague ecology and evolution. For example, does *Y. pestis* transmission occur within a colony over a period of several months (or even longer)? Or does *Y. pestis*'s arrival in a prairie dog colony cause a rapid decline in the host population, and persistence of *Y. pestis* at the landscape scale occurs via metapopulation dynamics, i.e., movement of the pathogen from colony to colony after causing temporary local extinctions of the prairie dog host? Interventions to control the spread of *Y. pestis*, such as oral vaccination of prairie dog populations or insecticidal dusting of prairie dog burrows to kill fleas (Abbott et al. 2012), may be optimized with an improved understanding of the timing of plague activity. Here we report on an investigation of three plague outbreaks in black-tailed prairie dog (*Cynomys ludovicianus*) populations to determine the duration of plague activity.

The investigation took place on the Pawnee National Grassland, western Weld County, Colorado where plague is now endemic (Stapp et al. 2004; Salkeld et al. 2007; Tripp et al. 2009 for site details). Fleas were sampled, or "swabbed," using 15 × 15 cm^2 of flannel cloth attached to a flexible plumbing snake (2-m cable, 1.3 cm in diameter), which was inserted into a prairie dog burrow to at least 1 m in depth, and then removed (for details see Ubico et al., 1988; Salkeld et al. 2007). Fleas were identified by light microscopy to the species level, using the method of Stark (1958) and Hubbard (1968), and identification was confirmed at Center for Disease Control and Prevention (CDC), Fort Collins, Colorado. Fleas were screened individually for *Y. pestis* by PCR of the *pla* gene, according to the procedures described in Salkeld et al. (2007). Fleas from captured prairie dogs (see Tripp et al. 2009) were also examined for all three colonies. The period of plague activity is defined as the time from the first detection of plague, i.e., first positive flea or the first *Y. pestis*-infected prairie dog carcass, until the last detection of plague. Protocols were approved by the Institutional Animal Care and Use Committee at Colorado State University (03053A05).

On colony #82, fleas were swabbed from burrows at least once a month from May to November 2005 (number of burrows = 59–649 per month) (Fig. 1). The first dead prairie dog was discovered in mid-August 2005 (*Y. pestis* confirmed as cause of death by CDC), and approximately 90% of prairie dogs were dead by early November 2005. The earliest *Y. pestis*-positive fleas were obtained from burrows on August 12th, 2005 and found consistently in burrows until late November 2005; prevalence of burrows harboring *Y. pestis*-positive fleas ranged from 4 to 19% (Fig. 2; see Table online). In the following year (2006), burrow sampling occurred from February to October, but *Y. pestis*-positive fleas were found only sporadically [in May, July, and the last detection in August (16th) 2006]. The duration of plague activity was approximately, and minimally, 3 months (August–November) with sporadic *Y. pestis* detection extending the estimate to roughly a year. Fleas were obtained from 4,276 burrows, and comprised 88% *O. hirsuta* (15,674/17,753), 6% *Pulex simulans* (1,022/17,753), 2% *O. tuberculata cynomuris* (360/17,753), 4% *Thrassis fotus* (697/17,753).

On colony #84, the first *Y. pestis*-positive flea was detected from a prairie dog in October (25th) 2005. Burrow sampling (number of burrows = 88–799 per month) occurred from April to October 2006, and yielded the first *Y. pestis*-positive flea on April 5th. The prairie dog die-off was obvious in spring 2006, with approximately 40% of the colony dead by April, and 90% of the colony dead by June 1st. Small numbers of prairie dogs—whether survivors or new immigrants—were observed through September 2006. The last detection of *Y. pestis*-positive fleas from animals was in September (5th) 2006, and from burrows in August (30th) 2006, with prevalence of infected burrows ranging from 14 to 18% (April to early June) and subsequently declining to between 0.3 and 4% (Fig. 2; see Table online). The duration of plague activity was minimally 10 months (October 2005–September 2006). Fleas were obtained from 1,868 burrows, and comprised 77% *O. hirsuta* (2,264/2,929), 10% *O. tuberculata cynomuris* (289/2,929), 12% *Thrassis fotus* (349/2,929), and 1% *Pulex simulans* (27/2,929).

The earliest detection of *Y. pestis*-positive fleas on colony #76 was from fleas obtained from prairie dog hosts in October (16th) 2006. Burrows were sampled in October 2006, and February and April 2007 (number of burrows = 30–100), with *Y. pestis*-positive fleas only found in burrows in April (18th) 2007 [2.0% (2/98) of burrows harbored infected fleas]. The die-off of prairie dogs on colony #76 occurred up to February 2007. The duration of plague activity was approximately, and minimally, 6 months (October–April). Fleas were obtained from 195 burrows, and comprised 90% *O. tuberculata cynomuris* (654/725), 8% *O. hirsuta* (59/725), 1% *Thrassis fotus* (8/725), and $<1\%$ *Pulex simulans* (4/725). The higher proportion of *O. tuberculata cynomuris* in colony #76 reflects the sampling periods across the winter months, when *O. tuberculata cynomuris* predominates (Salkeld and Stapp 2008a; Wilder et al. 2008; Tripp et al. 2009).

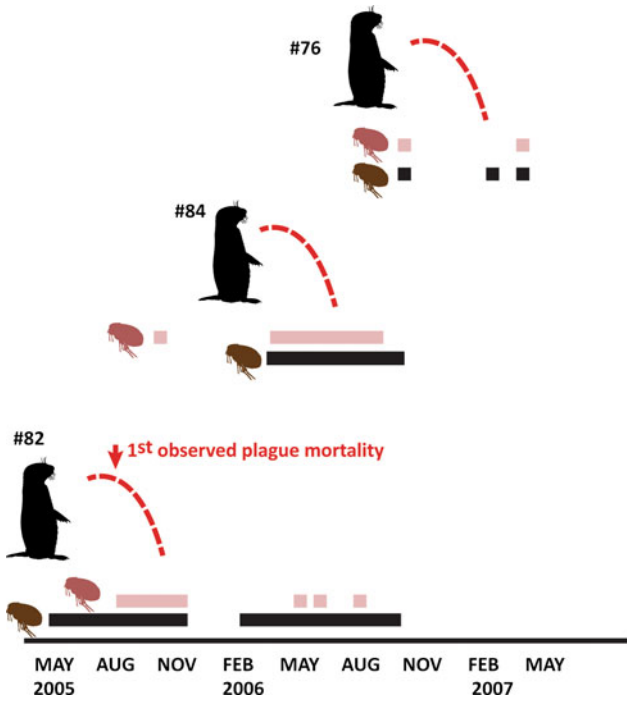

Figure 1. Schematic representation of plague-induced die-offs on black-tailed prairie dog colonies on the Pawnee National Grasslands, Colorado. Flea-sampling periods are marked in *dark gray*; periods with fleas PCR-positive for *Yersinia pestis* are marked in *light pink*. *Dotted lines* represent estimates of timing of obvious prairie dog population declines. See text for additional details (Color figure online).

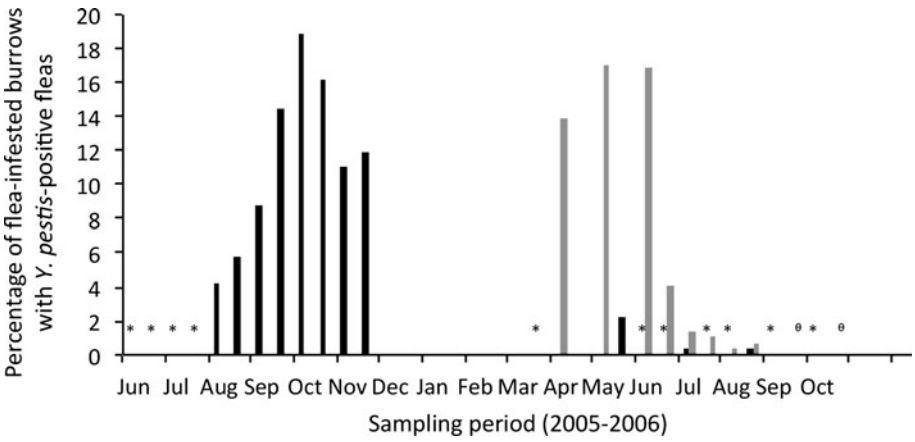

Figure 2. Percentage of flea-infested prairie dog burrows containing fleas PCR-positive for *Yersinia pestis*, on two black-tailed prairie dog colonies: colony #82 (in *black*) and colony #84 (in *gray*). Sampling occasions when no fleas were positive for *Y. pestis* are shown (* for colony #82; θ for colony #84 which was only sampled in 2006).

The prairie dog fleas, *O. hirsuta* and *O. tuberculata cynomuris*, are known vectors of plague (Wilder et al. 2008). Our surveillance efforts demonstrated that up to 18–19% of prairie dog burrows could harbor infected fleas. This observation reflects a previous study of plague activity in South Dakota, which observed roughly 23–26% (range 4.7–43.6%) of burrows containing *Y. pestis* positive fleas (Hanson et al. 2007). Although *T. fotus* was found in some abundance in the burrows, this flea does not appear to feed on prairie dogs (Brinkerhoff et al. 2006; Tripp et al. 2009).

Prairie dog colonies can comprise hundreds of hectares of short-grass prairie habitat, and several thousand individuals. Considering that the majority of prairie dogs probably succumb to plague in their burrows, it is improbable that plague activity is easily and accurately observed by researchers. Our findings suggest that plague activity occurs for several months, but our observations are probably under-estimates given the inherent difficulties of detecting *Y. pestis*. If observations of *Y. pestis*-positive fleas are combined with patterns of *O. hirsuta* infestations on grasshopper mice—a putative signal of plague activity (Stapp et al.

2009)—then periods of plague activity are extended. Increased abundance of *O. hirsuta* occurred on grasshopper mice in June 2005 on colony #82 (Stapp et al. 2009), suggesting plague activity and prairie dog mortality minimally from June to November 2005, and some degree of plague activity from June 2005 to August 2006. On colony #84, increased abundance of *O. hirsuta* occurred on grasshopper mice in July 2005 (Stapp et al. 2009) suggesting plague activity from July 2005 to September 2006. Essentially then, plague activity occurs from months to over a year in black-tailed prairie dog colonies. Transmission rates and duration are likely influenced by factors such as the size of the prairie dog colony (presumably larger populations will take longer to succumb to plague), how and when plague arrives in the colony (e.g., multiple or single introductions), and upon local conditions (e.g., flea populations, the presence of alternate hosts, prairie dog density or behavior etc.). It is important to note that, hypothetically, prairie dog colony extirpation is not the sole outcome of plague's presence; situations probably occur when plague arrives and an outbreak erupts quickly, just as plague may arrive in a colony, smolder slowly and fade-out (Salkeld et al. 2010). However, our findings suggest that periods of *Y. pestis* transmission occur cryptically, i.e., before evidence of a prairie dog die-off, and therefore that spread of the pathogen between prairie dog colonies may occur over a more extended timeframe. This observation lends support to the hypothesis that *Y. pestis* populations can be maintained in prairie dog populations without necessarily invoking the role of an alternate reservoir (Salkeld and Stapp 2008b).

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