Movements and burrow use by northern grasshopper mice as a possible mechanism of plague spread in prairie dog colonies

JOHN P. KRAFT AND PAUL STAPP*
Department of Biological Science, California State University, Fullerton, CA 92831, USA
* Correspondent: pstapp@fullerton.edu

Northern grasshopper mice (Onychomys leucogaster) have been implicated as a potential reservoir for plague, which causes local extinction of black-tailed prairie dog (Cynomys ludovicianus) colonies. To identify mechanisms by which grasshopper mice could facilitate plague spread, we measured burrow use, movements, and flea burdens of mice in colonies in northern Colorado. At the microhabitat scale, powder-tracked mice (n = 41) used both prairie dog mounds and burrows extensively, entering an average of 5.3 burrows per 100 m traveled. Burrow use did not differ between active and inactive mounds, or vary with mouse age, sex, or reproductive status. Radiotracking revealed that mice occupied larger ranges (X = 3.84 ha) than reported off colonies, which we estimated would overlap 12–23 prairie dog coterie territories. Mice also harbored high flea burdens (8.1 fleas/mouse), including fleas associated with prairie dogs, which we attributed to their frequent use of burrows. Our results support the contention that, at high population densities observed in colonies, grasshopper mice facilitate plague spread by transporting infected fleas between burrows across prairie dog social boundaries represented by coterie territories.

Key words: Cynomys ludovicianus, disease transmission, fleas, host behavior, multihost pathogen, Onychomys leucogaster, vector-borne diseases, Yersinia pestis

© 2013 American Society of Mammalogists
DOI: 10.1644/12-MAMM-A-197.1

The spread of vector-borne diseases during outbreak (epizootic) events can be strongly influenced by the behavior and movements of vectors and hosts (e.g., Loehle 1995; Böhm et al. 2009; Watts et al. 2009; Hoye et al. 2010). For studies of multihost pathogens, researchers must consider not only movements of the primary, amplifying host, but also those of secondary hosts whose behavior may alter the rate of disease spread across the landscape. Plague, a disease of rodents caused by the bacterium Yersinia pestis and transmitted primarily by bites of fleas, can wipe out entire colonies of black-tailed prairie dogs (Cynomys ludovicianus) in the Great Plains of North America (Stapp et al. 2004). Prairie dogs are highly social, living in small, extended family groups called coterie, with widespread sharing of burrows (Hoogland 1995) that may facilitate transmission of Y. pestis between coterie members. On the other hand, coterie territories tend to be socially distinct and defended against intruders (Hoogland 1995), which may reduce spread of plague among coterie across a colony. The observation that plague can extirpate a colony within what appears to be a matter of weeks (Webb et al. 2006), however, is inconsistent with the idea that social barriers reduce the rate of disease spread.

Through intensive field studies, we recently determined that another rodent, the northern grasshopper mouse (Onychomys leucogaster), may be involved in spread of plague in prairie dog colonies in northern Colorado. Grasshopper mice are infected with Y. pestis during prairie dog epizootics (Stapp et al. 2008), but do not suffer the same population declines (Stapp et al. 2009), possibly because some individuals are resistant to plague mortality (Thomas et al. 1988). Although interspecific sharing of fleas is not uncommon in flea–rodent host interactions (Marshall 1981; Krasnov 2008), grasshopper mice are the only local rodents to share fleas with prairie dogs to any significant extent, and prairie dog fleas combed from grasshopper mice have been shown to be infected with Y. pestis (Stapp et al. 2009; Franklin et al. 2010). In addition, colonies with large numbers of grasshopper mice appear to be more susceptible to plague epizootics, and epizootics tend to follow years of high grasshopper mouse abundance (Stapp et al. 2009).
Grasshopper mice are wide-ranging, with home ranges off of prairie dog colonies varying from 1.3 to 2.2 ha (Stapp 1999), presumably reflecting the species’ carnivorous diet. Grasshopper mice also regularly use burrows of other animals, either for refuge, for dust-bathing, or in search of food (Stapp 1997). If grasshopper mice are involved in spread of plague to prairie dogs, individual variation in movements and burrow use could influence rate of disease transmission. Moreover, if burrow use differs among subsets (age classes and sexes) of grasshopper mouse populations, then those subsets that have the greatest probability of transferring infected fleas from burrow to burrow may be more involved in spread of plague across a colony. For example, wide-ranging adult males may enter into more burrows than other subsets of the mouse population, and thus may be responsible for a disproportionate number of infections. Conversely, reproductive females may enter fewer burrows because parental care is focused on 1 or a few natal burrows (Frank and Heske 1992). The types of burrows used also may influence contact between grasshopper mice and prairie dogs. Because mice likely enter burrows to forage for arthropod prey (Stapp 1997), their use of burrows might reflect differences in prey availability. Arthropod distributions in prairie dog burrows depend on the amount of friable soil and organic matter (Wilcomb 1954); therefore, mice may prefer burrows with large amounts of organic matter, for example, inactive burrows no longer maintained by prairie dogs.

We studied flea burdens, movements, and use of prairie dog burrows by grasshopper mice in north-central Colorado to estimate the potential for contact between grasshopper mice, the fleas of prairie dogs, and prairie dogs themselves. We hypothesized that grasshopper mice could increase rate of spread of plague during outbreaks by visiting burrows and transporting infected fleas, as well as their own infected tissues, across social boundaries represented by prairie dog coteries. We used a combination of fluorescent-powder tracking and radiotelemetry to examine burrow use and movements of grasshopper mice in prairie dog colonies, and to estimate number of burrows and coteries visited by grasshopper mice. This information could be useful to parameterize models of plague dynamics, which could clarify the roles of grasshopper mice in plague outbreaks in prairie dogs.

**Materials and Methods**

**Study area and livetrapping methods.**—Our study area was the Pawnee National Grasslands (PNG), which includes the Central Plains Experimental Range (CPER), the primary research area of the Shortgrass Steppe Long-Term Ecological Research Project. Vegetation is shortgrass steppe and the climate is semiarid. Although prairie dogs were relatively uncommon on the PNG and CPER during the 1970s and 1980s, prairie dog colonies have increased dramatically over the past 2 decades (Stapp et al. 2004) and now cover approximately 2% of the 781-km² PNG.

Small mammals were trapped on 2.25-ha grids consisting of 100 Sherman live traps (Sherman Trap Company, Tallahassee, Florida), with traps spaced 15 m apart. In 2006, trapping grids were placed on 5 prairie dog colonies that were ≥1 km from each other and had no recent history of plague. Colonies CPER105, CPER127, and CPER129 had 2 grids per colony spaced at least 100 m apart, whereas PNG78 and PNG76 had only 1 grid each, resulting in a total of 8 trapping grids. Each grid was trapped twice between 1 June and 8 August 2006, with trapping sessions approximately 4 weeks apart.

Each grid was trapped for 4 consecutive nights during a trapping session. Traps were baited with a mixture of peanut butter and oatmeal. Raw wool was provided to prevent hypothermia. Traps were set 1 h before sunset and checked at dawn. All animals except those used for tracking were released immediately at their capture location. Upon 1st capture, each individual was weighed; identified to sex, age (adult and nonadult based on mass and pelage), and reproductive status (reproductive: scrotal males, pregnant or lactating females); measured; and marked with a uniquely numbered aluminum ear tag (National Band and Tag Company, Newport, Kentucky). Mice were briefly and lightly anesthetized with isoflurane (Abbott Laboratories, Chicago, Illinois) and fleas were combed from mice to estimate flea burdens. Because grasshopper mice tend to live at low population densities, we used the number of unique individuals trapped per 100 trap-nights (TN) as an index of relative abundance on each grid (Stapp 2007). Total number of trap-nights was adjusted by subtracting 0.5 trap-nights for every trap that was sprung (tripped and empty). We averaged the abundance estimates from both trapping sessions to estimate abundance for each grid.

**Fluorescent-powder tracking.**—Grasshopper mice selected haphazardly for tracking were held until approximately 1–2 h before sunset, then dusted with colored fluorescent paint pigment (Radiant Color, Inc., Richmond, California) and released at their capture location. Because mice often switched burrows before dark, their last known daytime locations were marked just before sunset to ensure all recorded movements were nocturnal. Starting 3–4 h after dark, powder trails were tracked using a lantern with an ultraviolet lightbulb (General Electric Co., Cincinnati, Ohio). We marked trails at 1-m intervals with flagged nails and attempted to track each mouse for 100 m. Every burrow that the mouse entered was flagged to determine the number and type of burrows entered. We used ratio of net displacement (straight-line distance between the path’s start and end) to total path length (RND) as a measure of tortuosity of path.

Marked trails were mapped by taking a compass bearing from each nail toward the next nail. We recorded microhabitat type (grass, bare ground, or burrow mound) at each flagged nail. To estimate available microhabitat in the area of each path, we recorded microhabitat type at 1-m intervals along a 50-m random transect on the same day that paths were mapped. Transects were placed within 5 m of the starting point and the direction was determined by a random compass bearing. To determine availability of burrows of different types, burrow densities were estimated by counting the number of burrow
estimates should be considered underestimates of actual home
all locations for each mouse. Because of the relatively short
range area was calculated as the minimum convex polygon of
were plotted in ArcView 9.1 (ESRI, Redlands, California), and
accuracy of about 3 m. Global positioning system locations
obtaining 5 locations per animal per night. Global positioning
system coordinates were taken at each location, with an
locate mice approximately every 30 min, with the aim of
tracked on foot using a Custom Electronics, Inc. (Urbana,
mice (26–36 g) were anesthetized with isoflurane and fitted
(PNG70), using the methods described above. A subset of adult
were sampled 2–7 times, with 20 burrows swabbed per
fleas on 18 active colonies between 2004 and 2006. Colonies
abundance of fleas in prairie dog burrows (Salkeld and Stapp
mice encountered prairie dog fleas (Oropsylla hirsuta
estimate the number of prairie burrows entered per night by
burrow within the first 100 m of movement path. On average,
tor age classes, or by reproductive status (t-tests,
however number of burrows entered did not differ between sex
Grasshopper mice used prairie dog burrows regularly. Of 41
entrances in a 50 × 5-m belt transect along 1 side of the random
transact. Within the transect, all burrows, including those of
prairie dogs, Ord’s kangaroo rats (Dipodomys ordii), threeline
ground squirrels (Ictidomys tridecemlineatus), and pocket
squirrels (Thomomys talpoides), were counted. Prairie dog
burrows were categorized as follows: active burrows that had
fresh digging or scat, or both, and were frequently used by
prairie dogs; usable burrows with entrances lacking vegetation
but with no sign that would indicate frequent use of prairie
dogs; and inactive burrows that were clearly not usable by
prairie dogs because of thick vegetation around the entrance or
because the entrance had collapsed.
Research on live animals was approved by the Institutional
Animal Care and Use Committee at California State University
Fullerton, under scientific collecting permits to P. Stapp from
the Colorado Division of Wildlife, and performed in a humane
manner following guidelines of the American Society of
Mammalogists (Sikes et al. 2011).
Radiotracking.—In July and August 2008, grasshopper mice
were captured on 4 grids on 1 large prairie dog colony
(PNG70), using the methods described above. A subset of adult
mice (26–36 g) were anesthetized with isoflurane and fitted
with BD-2C radiocollars (Holohil Systems Ltd., Carp, Ontario,
Canada). Mice were released at their capture location and
tracked on foot using a Custom Electronics, Inc. (Urbana,
Illinois) receiver and yagi 3-element antenna. We sought to
locate mice approximately every 30 min, with the aim of
obtaining 5 locations per animal per night. Global positioning
system coordinates were taken at each location, with an
accuracy of about 3 m. Global positioning system locations
were plotted in ArcView 9.1 (ESRI, Redlands, California), and
range area was calculated as the minimum convex polygon of
all locations for each mouse. Because of the relatively short
period of time we tracked mice, our minimum convex polygon
estimates should be considered underestimates of actual home
ranges.

### Table 1.—Path attributes of northern grasshopper mice (Onychomys leucogaster) powder-tracked on black-tailed prairie dog (Cynomys ludovicianus) colonies (n = 41; 22 males, 19 females). Path tortuosity is the ratio of net displacement to total path length (RND). Prairie dog burrows/100 m is the mean number of prairie dog burrows entered per 100 m of path. Other burrows/100 m is the mean number of other burrows, that is, of species other than prairie dogs, entered per 100 m of path. Microhabitat classifications are: % mound = percentage of path on prairie dog mounds, % bare ground = percentage of path on bare ground. Prairie dog burrows were categorized as active, usable, or inactive based on visual inspection. Means are shown as ± 1 SE, with sample size in parentheses.

<table>
<thead>
<tr>
<th>Group (n)</th>
<th>Tortuosity (RND)</th>
<th>Prairie dog burrows/100 m</th>
<th>Other burrows/100 m</th>
<th>% mound</th>
<th>% bare ground</th>
<th>% active burrows</th>
<th>% usable burrows</th>
<th>% inactive burrows</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males (22)</td>
<td>0.50 ± 0.05</td>
<td>4.8 ± 0.5</td>
<td>0.3 ± 0.1</td>
<td>10.1 ± 0.7</td>
<td>41.3 ± 3.3</td>
<td>25.0 ± 6.2</td>
<td>27.9 ± 4.8</td>
<td>47.1 ± 6.9</td>
</tr>
<tr>
<td>Reproductive adults (6)</td>
<td>0.67 ± 0.02</td>
<td>4.6 ± 1.3</td>
<td>0</td>
<td>8.6 ± 1.1</td>
<td>32.3 ± 6.5</td>
<td>12.4 ± 7.9</td>
<td>35.9 ± 13.8</td>
<td>51.7 ± 10.8</td>
</tr>
<tr>
<td>Nonreproductive adults (11)</td>
<td>0.45 ± 0.06</td>
<td>5.3 ± 0.6</td>
<td>0.5 ± 0.3</td>
<td>12.3 ± 0.9</td>
<td>42.2 ± 3.7</td>
<td>27.8 ± 8.9</td>
<td>26.5 ± 3.4</td>
<td>45.7 ± 10.1</td>
</tr>
<tr>
<td>Juveniles (5)</td>
<td>0.40 ± 0.11</td>
<td>4.2 ± 0.7</td>
<td>0.2 ± 0.2</td>
<td>7.0 ± 1.0</td>
<td>18.2 ± 8.1</td>
<td>34.0 ± 17.3</td>
<td>21.3 ± 12.2</td>
<td>44.7 ± 18.7</td>
</tr>
<tr>
<td>Females (19)</td>
<td>0.40 ± 0.05</td>
<td>5.9 ± 0.6</td>
<td>0.3 ± 0.2</td>
<td>10.3 ± 1.2</td>
<td>43.6 ± 3.3</td>
<td>25.4 ± 4.4</td>
<td>20.9 ± 4.6</td>
<td>48.6 ± 6.2</td>
</tr>
<tr>
<td>Reproductive adults (7)</td>
<td>0.38 ± 0.06</td>
<td>6.2 ± 1.4</td>
<td>0.3 ± 0.3</td>
<td>12.6 ± 0.9</td>
<td>55.4 ± 3.1</td>
<td>31.1 ± 6.5</td>
<td>29.7 ± 7.0</td>
<td>39.2 ± 7.8</td>
</tr>
<tr>
<td>Nonreproductive adults (5)</td>
<td>0.53 ± 0.11</td>
<td>6.2 ± 0.8</td>
<td>0.4 ± 0.4</td>
<td>10.9 ± 2.1</td>
<td>42.7 ± 6.5</td>
<td>28.0 ± 8.9</td>
<td>28.7 ± 11.8</td>
<td>43.3 ± 10.8</td>
</tr>
<tr>
<td>Juveniles (8)</td>
<td>0.35 ± 0.07</td>
<td>5.0 ± 1.2</td>
<td>0.3 ± 0.2</td>
<td>7.8 ± 2.4</td>
<td>13.1 ± 4.6</td>
<td>19.0 ± 7.7</td>
<td>8.4 ± 4.3</td>
<td>60.2 ± 11.8</td>
</tr>
<tr>
<td>Total (41)</td>
<td>0.45 ± 0.03</td>
<td>5.3 ± 0.4</td>
<td>0.3 ± 0.1</td>
<td>10.2 ± 0.7</td>
<td>42.4 ± 2.4</td>
<td>25.2 ± 3.9</td>
<td>24.6 ± 3.4</td>
<td>47.8 ± 4.7</td>
</tr>
<tr>
<td>Adults (28)</td>
<td>0.49 ± 0.04</td>
<td>5.6 ± 0.5</td>
<td>0.3 ± 0.1</td>
<td>11.5 ± 0.6</td>
<td>44.0 ± 2.7</td>
<td>26.3 ± 4.4</td>
<td>29.5 ± 4.0</td>
<td>44.2 ± 5.1</td>
</tr>
<tr>
<td>Juveniles (13)</td>
<td>0.39 ± 0.06</td>
<td>4.6 ± 0.7</td>
<td>0.2 ± 0.1</td>
<td>7.6 ± 1.4</td>
<td>39.1 ± 4.4</td>
<td>22.9 ± 7.6</td>
<td>14.8 ± 5.2</td>
<td>55.1 ± 9.3</td>
</tr>
</tbody>
</table>

Potential interactions with prairie dogs and their fleas.—To estimate the number of prairie burrows entered per night by grasshopper mice, we combined our estimates of movement speed and number of burrows entered per meter of path with an estimate of nightly activity time from a previous radiotracking study (Stapp 1999). To estimate the likelihood that grasshopper mice encountered prairie dog fleas (Oropsylla hirsuta) in burrows, we used data from studies of prevalence and abundance of fleas in prairie dog burrows (Salkeld and Stapp 2008). In those studies, prairie dog burrows were swabbed for fleas on 18 active colonies between 2004 and 2006. Colonies were sampled 2–7 times, with 20 burrows swabbed per sampling event. We calculated mean prevalence (proportion of burrows occupied), load (number of fleas per burrow), and intensity (number of fleas per infested burrow) of O. hirsuta in burrows (see Salkeld and Stapp [2008] for details). We compiled published values of area of prairie dog coterie territories to estimate the number of coterie territories that a grasshopper mouse would overlap in the course of its nightly movements.

### RESULTS

**Burrow use, small-scale movements, and flea burdens.**—Grasshopper mice used prairie dog burrows regularly. Of 41 powder-tracked mice (♂:♀: 22:19), only 1 did not enter a burrow within the first 100 m of movement path. On average, mice entered 5.3 (SD = 2.6) burrows per 100 m of path; however, number of burrows entered did not differ between sex or age classes, or by reproductive status (t-tests, t_{40} < 1.576, P ≥ 0.123; Table 1). Burrow densities ranged from 117.1 to 192/ha, with a mean of 131.1/ha (SD = 25.6/ha, n = 8). Mice used different types of prairie dog burrows in proportion to their availability (paired t-tests for each burrow type, t_{40} < 0.24, P > 0.811), but entered burrows of other small mammals less often than expected (t_{40} = 3.15, P = 0.003; Fig. 1). In addition,
mice spent a significantly higher proportion of their time on prairie dog mounds (\( \bar{X} \pm SE; 10.2\% \pm 0.7\% \)) than expected based on random transects (1.5% \( \pm \) 0.3%; paired \( t_{40} = 11.46, P < 0.001 \)). Use of other microhabitat types did not differ significantly between sites, sexes, or by age classes, or by reproductive status (Table 1). Mean path tortuosity (RND = 0.45 \( \pm \) 0.03, range = 0.36–0.69, \( n = 41 \)) did not differ between age or sex classes of mice (analysis of variance [ANOVA], \( F_{3,38} = 1.52, P = 0.226; \) Table 1). Among adult mice, reproductive males had significantly straighter paths than did reproductive females (ANOVA, \( F_{3,25} = 3.28, P = 0.038; \) Table 1). The proportion of path spent on prairie dog mounds differed between age classes, with adults using more mounds (11.5% \( \pm \) 0.6%) than juveniles (7.6% \( \pm \) 1.4%; \( F_{1,40} = 8.12, P = 0.006; \) Table 1).

A total of 1,186 fleas, representing 7 different species, were combed from grasshopper mice in 2006. The most common flea species was Plecochaeis exilis (69.1%), followed by Thrassis fotsus (21.0%), a flea associated with the thirteen-lined ground squirrel (Hubbard 1968). The remaining 9.9% consisted of Meringis parkeri (6.7%), a flea of kangaroo rats; Foxella ignota (0.8%), a flea of pocket gophers; and Aetheca wagneri (0.5%) and Orchopeas leucopus (0.1%), which are both commonly found on deer mice (Peromyscus maniculatus—Hubbard 1968). Prairie dog fleas (O. hirsuta) represented 1.9% (\( n = 22 \)) of the total fleas removed and were found on 12.3% of the 148 grasshopper mice examined, with load of O. hirsuta of 1.3 per infested host. Combining all species, flea burdens of grasshopper mice ranged from 0 to 35 fleas per individual (8.1 \( \pm \) 0.5 fleas per individual, \( n = 148 \)). Flea prevalence on grasshopper mice was extremely high: 97% (144) had at least 1 flea and 62% of mice had 2–10 fleas. Flea burdens, both in terms of fleas per mouse and flea species richness, were not related to subsequent burrow use (\( r < 0.08, P > 0.631 \)).

Although grasshopper mice were the most abundant rodents on our grids, we also caught Ord’s kangaroo rats, deer mice, and silky pocket mice (Perognathus flavus). Relative abundance of grasshopper mice in 2006 varied considerably between sites, ranging from 1.0 to 5.2 individuals per 100 trap-nights. Grasshopper mouse abundance was not related to prairie dog burrow density (\( r = 0.38, P = 0.348 \)). The use of burrows by mice tended to increase with mouse abundance (\( r = 0.67, P = 0.069; \) Fig. 2). Path tortuosity was not correlated with number of burrows entered (\( r = 0.12, P = 0.447 \)) or mouse abundance (\( r = -0.14, P = 0.731 \)).

Radiotracking.—Mouse abundance in July–August 2008 was 1.0–2.0 individuals per 100 trap-nights, somewhat lower than that on most grids in 2006 (Fig. 2). A total of 21 (\( \ddot{c}:\ddot{v}:12:9 \)) grasshopper mice were fitted with radiocollars; 9 mice (\( \ddot{c}:\ddot{v}:5:4 \)) were located \( > 20 \) times over 6 or more nights (range: 6–23 nights). Mice were tracked between 2100 and 0100 h, with locations 47.5 min (SD = 7.2 min, \( n = 9 \)) apart. Omitting distances between locations of < 3 m, we estimated that mice moved an average of 53.7 m/h (SD = 13.1 m/h) or 0.89 m/min.

Mean range area (minimum convex polygon) of 9 mice with \( > 20 \) locations was 3.84 ha (SD = 1.64 ha; Fig. 3). Female mice had larger mean ranges (3.92 \( \pm \) 0.70 ha) than did males (3.77 \( \pm \) 0.88 ha), but the difference was not statistically significant (\( t_{8} = 0.13, P = 0.90 \)).
Potential interactions with prairie dogs and their fleas.—Stapp (1999) estimated that grasshopper mice were active aboveground for approximately 350 min per night during summer. Assuming that activity time is similar on prairie dog colonies, and using our mean estimates for burrow use (5.3 burrows/100 m) and movement speed (0.89 m/min), we estimated that a grasshopper mouse enters roughly 17 burrows each night. At higher population densities (Fig. 2), mice might enter up to 22 burrows per night.

Mean prevalence of *O. hirsuta* in burrows was 0.34 (SD = 0.14, *n* = 18 colonies—Salkeld and Stapp 2008), suggesting that the probability that a grasshopper mouse encountered a prairie dog flea in a burrow was 34%. On average, burrows harbored a load of 1.4 (SD = 0.9) *O. hirsuta*, with infested burrows containing 3.8 (SD = 1.4) fleas. Therefore, a grasshopper mouse may encounter approximately 22–31 prairie dog fleas in burrows per night. This estimate is likely to be conservative because grasshopper mice probably are more attractive to fleas than a flannel swab and may visit more burrow chambers, where they encounter more fleas.

Estimates of area of coterie territories of black-tailed prairie dogs from the literature ranged from 0.17 to 0.31 ha (Table 2). Assuming that coterie territories are contiguous and that these values are applicable to our study area, we estimated that the average range (3.84 ha) of a grasshopper mouse could encompass 12–23 adjacent coterie territories.
Table 2.—Mean and range of coterie territory area (ha) of black-tailed prairie dogs (*Cynomys ludovicianus*).

<table>
<thead>
<tr>
<th>Location</th>
<th>̅(ha)</th>
<th>Range (ha)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>South Dakota</td>
<td>0.31</td>
<td>0.05–1.01</td>
<td>Hoogland (1995)</td>
</tr>
<tr>
<td>South Dakota</td>
<td>0.29</td>
<td>0.16–0.37</td>
<td>King (1955)</td>
</tr>
<tr>
<td>South Dakota</td>
<td>0.17</td>
<td>0.08–0.42</td>
<td>Calculated from Newby (2005)</td>
</tr>
<tr>
<td>Colorado</td>
<td>0.20</td>
<td>0.12–0.61</td>
<td>Tileston and Lechleitner (1966)</td>
</tr>
</tbody>
</table>

**Discussion**

Our estimates of range area are conservative, but they clearly show that northern grasshopper mice are wide-ranging for their small body size and capable of moving relatively long distances quickly. As in mixed grassland areas where pocket gopher mounds are the primary source of burrows (Stapp 1997), grasshopper mice used prairie dog mounds and burrows often during nocturnal movements, presumably for hunting prey, dust-bathing, or as a source of refuge. Although ranges of grasshopper mice tended to be larger on prairie dog colonies than in grassland areas (Stapp 1999), at smaller, microhabitat scales, movements of mice on prairie dog colonies were more tortuous, and they entered more burrows than mice in mixed grassland areas (grassland: RND = 0.61 ± 0.08, burrows per 100 m = 3.0 ± 1.1, n = 13 [Stapp 1997], spring and summer). These differences likely reflect differences in the spatial patterning of prairie dog and gopher disturbances; prairie dog burrows are relatively uniformly distributed and therefore readily encountered, whereas gopher mounds tend to be aggregated and more dispersed, requiring more linear movements between clusters of mounds (Kraft 2009). Assuming that small-scale movements can be linked to population-level processes (e.g., Morales et al. 2010), the more circuitous movements of grasshopper mice on prairie dog colonies might help explain why grasshopper mice tend to be abundant on prairie dog colonies (Agnew et al. 1986; Lomolino and Smith 2003; Stapp 2007).

The extensive use of burrows of prairie dogs, pocket gophers, and other mammals potentially exposes grasshopper mice to a diversity of prey, but also to ectoparasites. Nearly all (97%) grasshopper mice had fleas and most suffered very high flea burdens (8.1 fleas per mouse). Most fleas (69.1%) were *P. exilis*, a species commonly associated with grasshopper mice (Hubbard 1968), but in our study grasshopper mice hosted a total of 7 flea species, including those associated with other common small rodents at our sites. For comparison, in similar studies from 2004 to 2007 at our study area (Franklin et al. 2010; P. Stapp, in litt.), prevalence of fleas on thirteen-lined ground squirrels was 50%, with 2.8 fleas per squirrel, 99.6% of which were *T. fotus* (*n* = 1,044 squirrels and 2,910 fleas), whereas prevalence of fleas on deer mice was 35%, with 0.8 fleas per mouse, 85.4% of which were *A. wagneri* (*n* = 452 mice and 342 fleas). The mechanisms that permit grasshopper mice to tolerate such high flea burdens and such a high diversity of fleas (Thomas 1988) are unknown, but such a response would seem to be adaptive, given the carnivorous, commensal lifestyle of this species.

Grasshopper mice also were infested with prairie dog fleas (*O. hirsuta*), with 12.3% of mice carrying at least 1 flea and mean load of 1.3 *O. hirsuta* per infested host. Although *O. hirsuta* is normally not common on grasshopper mice, both prevalence and loads of *O. hirsuta* increase dramatically during plague outbreaks, as fleas from dead and dying prairie dogs seek live hosts; for example, during an outbreak in 2005, 81% of mice were infested with *O. hirsuta*, with a mean load of 3.8 of these fleas (Stapp et al. 2009). Importantly, *O. hirsuta* is extremely rare on other rodent species, even during epizootics (prevalence < 0.4%; 4 singletons on 1,092 hosts—Stapp et al. 2009). Molecular genetic and stable isotope analyses show that *O. hirsuta* both feeds on grasshopper mice and carries *Y. pestis* (Stapp and Salkeld 2009; Franklin et al. 2010), providing a mechanism by which the plague pathogen can be transmitted between prairie dogs and grasshopper mice. The large number of prairie dog burrows entered by grasshopper mice each night provides ample opportunities for mice to pick up and transport *O. hirsuta* between burrows. This behavior also might expose grasshopper mice to infected carcasses of prairie dogs, which can be an additional source of infection via scavenging (Boone et al. 2009; Kraft 2009).

The extensive use of burrows by grasshopper mice, combined with their propensity to move long distances, creates a potential avenue for *Y. pestis* to be transported across prairie dog social boundaries represented by coterie territories. Using published estimates of coterie territory area from other grasslands in the central Great Plains, we estimated that a grasshopper mouse with an average range of 3.84 ha would overlap 12–23 coterie territories. We emphasize that our estimates of range area were taken only over a 2-month period in summer and thus are conservative, suggesting that overlap may be greater. Estimates of coterie territory area and dispersion and the extent of intercoterie movements of prairie dogs from our study area would allow us to quantify the degree of overlap more precisely. Although it is still unclear whether grasshopper mice can serve as a long-term reservoir for plague in prairie dog colonies (Stapp et al. 2009), our results suggest that grasshopper mice can play an important role in spread of plague during epizootics by increasing the odds that a source of infection moves from being confined to 1 or a few coteries, to a colony-wide outbreak. In addition, the fact that the number of burrows used tends to increase with grasshopper mouse abundance (Fig. 2) may help explain why local outbreaks often occur on colonies with large numbers of grasshopper mice and during periods when grasshopper mice are abundant (Stapp et al. 2009). We speculate that, through their individual movements, grasshopper mice increase functional connectivity among burrows, flea populations, and prairie dog coteries, making outbreaks more likely and increasing the probability of extinction of a colony. The incorporation of information on the spatial dispersion and movements of amplifying and alternate hosts and vectors into models of plague has led to new insights about the dynamics of plague transmission and persistence in both prairie dogs (Salkeld et al. 2010) and gerbils (Reijniers et al. 2012).
ACKNOWLEDGMENTS

We greatly appreciate the assistance of M. Lindquist, D. Salkeld, G. McMichael, and especially C. Cardinal, with fieldwork and logistics. B. Flynn plotted global positioning system coordinates of locations in ArcView and calculated range areas. Our research was supported by grants from the National Science Foundation (EID-0327052, DEB-0217631) and funds from the Department of Biological Science at California State University Fullerton.

LITERATURE CITED


Submitted 2 August 2012. Accepted 22 May 2013.

Associate Editor was Richard D. Stevens.