Flea Diversity and Infestation Prevalence on Rodents in a Plague-Endemic Region of Uganda

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Abstract. In Uganda, the West Nile region is the primary epidemiologic focus for plague. The aims of this study were to 1) describe flea–host associations within a plague-endemic region of Uganda, 2) compare flea loads between villages with or without a history of reported human plague cases and between sampling periods, and 3) determine vector loads on small mammal hosts in domestic, peridomestic, and sylvatic settings. We report that the roof rat, Rattus rattus, is the most common rodent collected in human dwellings in each of the 10 villages within the two districts sampled. These rats were commonly infested with efficient Y. pestis vectors, Xenopsylla cheopis and X. brasiliensis in Arua and Nebbi districts, respectively. In peridomestic and sylvatic areas in both districts, the Nile rat, Arvicanthis niloticus, was the most abundant rodent and hosted the highest diversity of flea species. When significant temporal differences in flea loads were detected, they were typically lower during the dry month of January. We did not detect any significant differences in small mammal abundance or flea loads between villages with or without a history of human plague, indicating that conditions during inter-epizootic periods are similar between these areas. Future studies are needed to determine whether flea abundance or species composition changes during epizootics when humans are most at risk of exposure.

INTRODUCTION

Plague is a flea-borne bacterial zoonosis that is often fatal if appropriate antibiotic treatment is inadequate or delayed.1 In recent decades, the majority of human plague cases have been reported from Africa.2,3 Within Uganda’s West Nile Region, which represents the primary epidemiologic focus for plague in that country,4,5 ~223 human cases were reported annually from 1999 to 2007 to the Ugandan Ministry of Health.6 There is a paucity of quantitative data on flea–host associations in this area; thus, little is known about how the etiologic agent of plague, Yersinia pestis, is maintained in zoonotic cycles or by which fleas the bacterium most likely is transmitted to humans.

In many parts of East Africa, rodents that are susceptible to Y. pestis infection include the roof rat (Rattus rattus), the multimammate mouse (Mastomys natalensis), the Nile rat (Arvicanthus niloticus), gerbils (Tatera spp.), groove-toothed rats (Otomys spp.), and the striped grass mouse (Lemniscomyys striatus).7–10 These rodents are often infested with flea species that are capable of transmitting plague bacteria including Xenopsylla cheopis, X. brasiliensis, Dinopsyllus lypusus, Ctenophthalmus cabirus, and occasionally Ctenocephalides felis.11,12,13

In this study, we sought to 1) describe flea–host associations within a plague-endemic region of Uganda, 2) compare flea loads between villages with or without a history of reported human plague cases and between sampling periods, and 3) determine vector loads on small mammal hosts in domestic, peridomestic, and sylvatic settings. Such information is critical for defining Y. pestis transmission cycles and for providing evidence-based recommendations on plague prevention and control activities in this plague-endemic region.

MATERIALS AND METHODS

Description of study area. Our sampling efforts focused on two counties in the West Nile Region of northwestern Uganda from which the majority of reported human plague cases have been reported in recent decades.21 These were Vurra County in Arua District (mean elevation, 1,140 m; range, 762–1,573 m) and its southern, higher-elevation neighboring county, Okoro (mean elevation, 1,160 m; range, 953–1,927 m), in Nebbi district (Figure 1). The region experiences two periods of rainfall; the earlier and less reliable rain occurs from March to June and heavier and more reliable precipitation typically occurs from late August through November.8,21

Field evaluation of flea infestations of small mammals. Each district was sampled roughly every other month on an alternating schedule (i.e., Arua was sampled 1 month and then Nebbi the next) from January through August 2006. Using the available historical human plague data from the Uganda Ministry of Health, the Uganda Virus Research Institute, and the US Centers for Disease Control and Prevention, five villages with a consistent history of plague cases were matched with five villages without such a history. The villages were paired with respect to elevation (using Global Positioning System receivers), population size (based on 2002 census data), and agricultural practices (qualitatively measured, but typical crop types included cassava, beans, groundnuts, sesame seeds, millet, and maize). Permission was given by the village leaders and the residents to carry out the study.

In Arua district, sampling was conducted in two villages that reported human plague cases in the past (Olii and Pomosi) and two villages from which plague had not been reported previously (Kaza and Pembeleku). Similarly, in Nebbi district, three villages with a history of human plague cases (Agore, Sokonzi, and Uyaru-Agadu) and three villages without such a history (Anyiku, Gbiala, and Monkweroco) were sampled (Figure 1). The median elevation of villages sampled in Arua district was 1,374 m (range: 1,306–1,442 m), whereas the median elevation of villages sampled in Nebbi district...
was 1,560 m (range: 1,430–1,636 m). In this region, the standard criteria for diagnosing plague are sudden onset of fever, chills, malaise, headache, or prostration accompanied by either coughs and hemoptysis or hematochezia (septicemic), or painful regional lymphadenopathy (bubonic), hemateme-
ter of the village, one Tomahawk and one Sherman trap were set every 20 m for 300 m away from the edge of villages in each of the four cardinal directions (i.e., a total of 15 Sherman and 15 Tomahawk traps were set along the northern trap line, and this design was repeated for the eastern, southern, and western directions). Traps within residences, which were earthen structures with thatch roofing and dirt floors, are referred to as “domestic,” whereas those placed within 20 m of the home are termed “peridomestic.” All others are considered “sylvatic.” These sylvatic areas represent a mixture of agricultural plots (primarily cassava, beans, groundnuts, sesame seeds, millet, and maize), fallow fields, and natural vegetation.

During each trapping session, traps were operated for two nights, with animals recovered in the early mornings. On capture, animals were killed by overdose of inhalation anesthetic (halothane), identified to species based on morphologic measurements (e.g., length of body, tail, ear, hind foot, weight), and combed to recover fleas. All fleas collected from small mammals were stored in individual glass collection tubes containing 2% saline with Tween 80 and later identified to species following published taxonomic keys. Data were analyzed using JMP statistical software (SAS Institute, Cary, NC), and comparisons were considered statistically significant when \( P < 0.05 \).

**RESULTS**

**Flea–host associations within a plague-endemic region of Uganda.** Live rodent trapping from January to August 2006 yielded a total of 1,633 rodents and shrews belonging to 17 species. A total of 3,346 fleas (at least 9 species) were collected from 15 species of small mammals (Table 1). No fleas were recovered from two species of rodents (Crestomys gambianus and Thamnomyss spp.). Only five fleas could not be identified. Examination of voucher specimens showed that Ctenophthalmus spp. samples comprised two species: *C. cabirus* and *C. bacopus*. These fleas commonly infest the same range of hosts and are presumed to serve similar ecologic roles.

The most frequently encountered fleas on small mammals included four confirmed or likely vectors of *Y. pestis*: *D. lypusus*, which were typically associated with *A. niloticus* or *M. natalensis*; *Xenopsylla brasiliensis*, most commonly encountered on *A. niloticus* or *R. rattus*; *Ctenophthalmus* spp., which were most abundant on *A. niloticus*; and *X. cheopis*, which were most commonly collected from *M. natalensis* or *R. rattus* (Table 1). Although each of these four flea species infests a wide range of incidental hosts and additional flea species were recovered from the above-mentioned hosts (Table 1), subsequent analyses will focus primarily on these four vectors and three small mammal hosts for which sample sizes were sufficient for statistical analysis.

With regard to rodent infestation, Nile rats (*A. niloticus*) were the most heavily infested small mammals; 50% of the total flea fauna on the small mammals was recovered from Nile rats alone, followed by roof rats (*R. rattus*; 21%) and multimammate mice (*M. natalensis*; 10%). Other hosts each harbored about two percent of the fleas (Table 1).

**Spatial and temporal trends in flea loads.** For each of the four main flea species of interest, we compared flea loads on *A. niloticus*, *M. natalensis*, and *R. rattus* between Arua and Nebbi districts using Mann-Whitney *U* tests. Results of individual comparisons are presented in Figure 2. With the
except for X. cheopis, when flea loads differed between districts they were typically higher in Nebbi district than Arua district. Arvicanthus niloticus collected in Nebbi district harbored significantly more Ctenophthalmus spp., D. lypusus, and X. brasiliensis than A. niloticus collected in Arua district. In contrast, X. cheopis loads were significantly higher on A. niloticus captured in Arua district compared with those trapped in Nebbi district. With the exception of D. lypusus loads on M. natalensis, which were higher in Nebbi district than Arua district, flea loads on this host species were similar between the two districts. Ctenophthalmus spp. and D. lypusus loads were similar on R. rattus collected in Arua and Nebbi districts. However, X. brasiliensis loads were significantly higher on R. rattus from Nebbi district, whereas the opposite trend was observed for X. cheopis (Figure 2).

Focusing again on the four main flea species and three hosts, we observed that Ctenophthalmus sp. loads decreased with increasing elevation (flea load = 2.269 – 0.001 × elevation; \( r^2 = 0.01, F = 7.80, df = 1,1023, P = 0.005 \)). Likewise, X. cheopis loads decreased with increasing elevation (X. cheopis loads = 4.545 – 0.003 × elevation; \( r^2 = 0.04, F = 37.31, df = 1,1023, P < 0.0001 \)). In contrast, D. lypusus and X. brasiliensis loads both increased with elevation (D. lypusus = –0.874 + 0.001 × elevation; \( r^2 = 0.04, F = 4.02, df = 1,1023, P = 0.045 \); and X. brasiliensis = –6.516 + 0.005 × elevation; \( r^2 = 0.04, F = 38.97, df = 1,1023, P < 0.0001 \), respectively).

In general, infestation rates were either similar between sampling periods or lower in January than other months (Mann-Whitney U tests; Table 2). Median numbers of fleas per host examined were similar between villages with a history of human plague and villages that had not reported a human plague case (Mann-Whitney U tests, \( P > 0.05 \) for each of the four vectors and three hosts examined and for all fleas on all hosts combined).

**Flea loads on rodents in domestic, peridomestic, and sylvatic settings.** In Arua and Nebbi districts, R. rattus accounted

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Table 2: Seasonal trends in flea infestation by host species and district

<table>
<thead>
<tr>
<th>Flea species</th>
<th>Host species</th>
<th>Arua</th>
<th>Nebbi</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. lylysus</em></td>
<td><em>M. natalensis</em></td>
<td>0.16 (37) a [0.0]</td>
<td>1.74 (62) b [1.0]</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.33 (33) a [0.0]</td>
<td>1.64 (70) b [0.0]</td>
</tr>
<tr>
<td><em>M. natalensis</em></td>
<td></td>
<td>0.05 (19) a [0.0]</td>
<td>0.21 (28) a [0.0]</td>
</tr>
<tr>
<td><em>X. brasiliensis</em></td>
<td></td>
<td>0.00 (37) a [0.0]</td>
<td>0.11 (62) b [0.0]</td>
</tr>
<tr>
<td><em>A. niloticus</em></td>
<td><em>M. natalensis</em></td>
<td>3.27 (59) a [0.0]</td>
<td>1.22 (90) a [1.0]</td>
</tr>
<tr>
<td><em>R. rattus</em></td>
<td></td>
<td>0.02 (50) a [0.0]</td>
<td>0.38 (69) b [0.0]</td>
</tr>
<tr>
<td><em>Ctenophalum spp.</em></td>
<td><em>A. niloticus</em></td>
<td>0.16 (37) a [0.0]</td>
<td>2.64 (62) b [2.0]</td>
</tr>
<tr>
<td></td>
<td><em>X. cheopis</em></td>
<td>0.00 (19) a [0.0]</td>
<td>1.40 (28) b [0.0]</td>
</tr>
<tr>
<td></td>
<td><em>R. rattus</em></td>
<td>0.2 (50) a [0.0]</td>
<td>0.85 (69) b [0.0]</td>
</tr>
</tbody>
</table>

NS = not sampled.

Since the surveys conducted by Hopkins in the 1930s, when the epidemiologic focus for plague was in the southern portion of Uganda rather than the current focus in the northwest, the host and flea community structure has changed in the West Nile region. Most notably, despite intensive sampling efforts during 1937–1938, only a single *R. rattus* was reported from the West Nile region. During that time, *M. natalensis* was the most common rodent in human dwellings, *X. cheopis* was the most abundant flea species, and *X. brasiliensis* was rarely observed. In contrast, in our study, *R. rattus* seems to have replaced *M. natalensis* as the rodent most closely associated with human dwellings and was also quite common in peridomestic and sylvatic areas. Although epidemiologic studies have not been conducted in this area to determine where humans are at greatest risk of exposure to *Y. pestis*–infected fleas, in many of the world’s plague foci, human infections are most commonly associ-
Among infected host to mobile susceptible host, *Y. pestis* can move rapidly across a landscape. Our data showed that, within sylvatic areas, flea-sharing between *A. niloticus*, *M. natalensis*, and *R. rattus* could allow *Y. pestis* to be maintained among these three host species. *A. niloticus* hosted the highest diversity of flea species and was the most abundant rodent in sylvatic and peridomestic settings; thus, these rats may be important for transporting potentially infected fleas between sylvatic and peridomestic areas. Within the peridomestic domain, *R. rattus* is the second most abundant rodent, and *R. rattus* and *A. niloticus* share *X. cheopis* in Arua district and *X. brasilienensis* in Nebbi district. Once *Y. pestis* is introduced into an *R. rattus*–*Xenopsylla* spp. cycle, there is potential for infected fleas to invade human dwellings on *R. rattus*. As hosts succumb to infection within or around the home, the likelihood that infected rat fleas will feed on humans increases. *D. lypusus* may also be important bridging vectors because they have been shown to feed on human blood. This species was collected primarily from *A. niloticus*, which was dominant in peridomestic areas, but occasionally forages within human dwellings. Abundance of *D. lypusus* may be underestimated because they are believed to spend much of their time off of hosts within burrows. A previous study conducted in these same villages revealed that cat fleas (*C. felis*) are the most abundant host-seeking fleas in human dwellings during inter-epizootic periods and are capable of transmitting *Y. pestis* at low rates by early-phase transmission. Because cat fleas were rarely recovered from rodents, they are not likely to be maintained among these three host species.

### Table 3

<table>
<thead>
<tr>
<th>Setting</th>
<th>Small mammal species</th>
<th>No. hosts examined</th>
<th>No. hosts infested (%)</th>
<th>Total (average) no. fleas recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td>Domestic</td>
<td><em>Arvicanthis niloticus</em></td>
<td>4</td>
<td>4 (100)</td>
<td>19 (4.75) 16 (4.00) 17 (4.25) 0 (0.00) 26 (4.00)</td>
</tr>
<tr>
<td></td>
<td><em>Mastomys natalensis</em></td>
<td>2</td>
<td>4 (100)</td>
<td>0 (0.00) 0 (0.00) 17 (8.5) 5 (2.5)</td>
</tr>
<tr>
<td></td>
<td><em>Rattus rattus</em></td>
<td>72</td>
<td>29 (43)</td>
<td>1 (0.01) 0 (0.00) 48 (0.67) 6 (0.08)</td>
</tr>
<tr>
<td>Peridomestic</td>
<td><em>Arvicanthis niloticus</em></td>
<td>46</td>
<td>39 (85)</td>
<td>85 (1.85) 122 (2.65) 37 (0.80) 2 (0.04)</td>
</tr>
<tr>
<td></td>
<td><em>Mastomys natalensis</em></td>
<td>17</td>
<td>9 (53)</td>
<td>7 (0.41) 2 (0.12) 65 (3.82) 2 (0.12)</td>
</tr>
<tr>
<td></td>
<td><em>Rattus rattus</em></td>
<td>20</td>
<td>8 (40)</td>
<td>1 (0.05) 0 (0.00) 37 (1.85) 4 (0.20)</td>
</tr>
<tr>
<td>Sylavtic</td>
<td><em>Arvicanthis niloticus</em></td>
<td>71</td>
<td>58 (82)</td>
<td>108 (1.52) 157 (2.21) 12 (0.17) 5 (0.07)</td>
</tr>
<tr>
<td></td>
<td><em>Mastomys natalensis</em></td>
<td>64</td>
<td>34 (53)</td>
<td>47 (0.73) 10 (0.16) 50 (0.78) 5 (0.08)</td>
</tr>
<tr>
<td></td>
<td><em>Rattus rattus</em></td>
<td>19</td>
<td>11 (58)</td>
<td>1 (0.05) 1 (0.05) 27 (1.42) 6 (0.32)</td>
</tr>
</tbody>
</table>

Average number of fleas recovered is the total number of fleas collected divided by the total number of rodents examined.

### Table 4

<table>
<thead>
<tr>
<th>Setting</th>
<th>Small mammal species</th>
<th>No. hosts examined</th>
<th>No. hosts infested (%)</th>
<th>Total (average) no. fleas recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td>Domestic</td>
<td><em>Arvicanthis niloticus</em></td>
<td>9</td>
<td>8 (89)</td>
<td>9 (1.00) 10 (1.11) 0 (0.00) 36 (4.00)</td>
</tr>
<tr>
<td></td>
<td><em>Mastomys natalensis</em></td>
<td>2</td>
<td>1 (50)</td>
<td>1 (0.50) 0 (0.00) 0 (0.00) 0 (0.00)</td>
</tr>
<tr>
<td></td>
<td><em>Rattus rattus</em></td>
<td>194</td>
<td>103 (53)</td>
<td>20 (0.10) 1 (0.01) 15 (0.08) 262 (1.35)</td>
</tr>
<tr>
<td>Peridomestic</td>
<td><em>Arvicanthis niloticus</em></td>
<td>52</td>
<td>38 (73)</td>
<td>103 (1.98) 45 (0.87) 12 (0.23) 187 (3.60)</td>
</tr>
<tr>
<td></td>
<td><em>Mastomys natalensis</em></td>
<td>10</td>
<td>2 (20)</td>
<td>1 (0.10) 0 (0.00) 0 (0.00) 3 (0.30)</td>
</tr>
<tr>
<td></td>
<td><em>Rattus rattus</em></td>
<td>27</td>
<td>13 (48)</td>
<td>2 (0.07) 0 (0.00) 0 (0.00) 33 (1.22)</td>
</tr>
<tr>
<td>Sylavtic</td>
<td><em>Arvicanthis niloticus</em></td>
<td>88</td>
<td>69 (78)</td>
<td>157 (1.78) 57 (0.65) 1 (0.01) 80 (0.91)</td>
</tr>
<tr>
<td></td>
<td><em>Mastomys natalensis</em></td>
<td>41</td>
<td>19 (46)</td>
<td>42 (1.02) 3 (0.07) 0 (0.00) 3 (0.07)</td>
</tr>
<tr>
<td></td>
<td><em>Rattus rattus</em></td>
<td>12</td>
<td>6 (50)</td>
<td>4 (0.33) 1 (0.08) 0 (0.00) 15 (1.25)</td>
</tr>
</tbody>
</table>

Average number of fleas recovered is the total number of fleas collected divided by the total number of rodents examined.
to play a critical role as bridging vectors to humans but may serve as secondary vectors transmitting \textit{Y. pestis} from a septi-cemic patient to susceptible members of the household if flea infestation rates are sufficiently high.

Our study was conducted during an inter-epizootic period and provides baseline data on vector-host community structure in a plague-endemic region. Human infections are most commonly acquired during plague epizootics, which represent periods when \textit{Y. pestis} spreads rapidly from host to host.\textsuperscript{15} Understanding the factors responsible for transitions from quiescent to epizootic periods is important for informing plague prevention policies. Several studies have identified positive associations between increases in host abundance or flea infestation rates and epizootic activity.\textsuperscript{37–40} In our study, we did not identify any significant differences in flea infestation rates between villages with or without a history of plague. This finding implies that the history of previous epizootics has little long-term impact on the flea community structure. However, flea loads may increase before or during a plague epizootic. During the quiescent period, we observed that flea loads were lowest in January, which represents the end of the plague season. In situations where flea loads differed among time periods, they generally increased during the months of early rains or agricultural harvest periods from March through August as the plague season approached. These changes could be driven by climate, as has been suggested for plague activity in this and other geographic regions.\textsuperscript{41–44} and could prime vector–host communities for plague epizootics, if the pathogen is introduced. The onset of heavy rains in late August, which marks the start of the plague season, could drive rats into human dwellings, which may increase the likelihood of human exposure to infected rats or their fleas.\textsuperscript{45} Future studies are needed to determine whether vector–host associations differ between quiescent and epizootic periods and whether these changes are influenced by weather patterns. Laboratory-based evaluations of vector efficiency and host susceptibility for the key flea and rodent species, respectively, that were identified in this plague-endemic area are necessary to determine 1) the most likely transmission pathways and 2) the critical infestation thresholds required for enzootic maintenance or epizootic spread of \textit{Y. pestis}. Such information could be useful for identifying which host and vector species to focus on for plague prevention campaigns and for setting targets below which vector populations should be maintained to disrupt the transmission cycle and reduce the risk of the initiation of plague epizootics.

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REFERENCES


