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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, *Arvicanthus 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 our 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 (*Arvicanthis niloticus*), gerbils (*Tatera* spp.), groove-toothed rats (*Otomys* spp.), and the striped grass mouse (*Lemniscomys striatus*).[7–16] 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*.[7,10–12,14–20]

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.

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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, Gbalia, and Monkwerocoo) 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

FIGURE 1. Villages sampled within Vurra County (Arua District) and Okoro County (Nebbi district), Uganda. Villages with or without a history of human plague cases are indicated as stars or circles, respectively.

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 painful regional lymphadenopathy (bubonic), hematemesis or hematochezia (septicemic), or coughs and hemoptysis (pneumonic). From 1999 to 2005, human plague cases were reported from Olii ($N = 30$), Pomosi ($N = 6$), Agore ($N = 10$), Sokonzi ($N = 20$), and Uyaru-Agadu ($N = 20$). The most recent case reports relative to this study occurred from October to December 2003 for Agore, Pomosi, and Sokonzi villages, whereas cases were reported in February 2004 from Uyaru-Agadu and in December 2005 in Olii. In Arua and Nebbi districts, the majority of human plague cases are reported from late August through early January.[21] Our study included the end of the plague risk season (January–February), a period of low plague activity (March–June), and the beginning of a new risk season (August). We were particularly interested in these periods of time that precede the normal plague season as a means of describing baseline conditions that may prime a community for a plague epizootic and to determine whether there are differences in community structure between villages with or without a history of plague.

Within each village, 10 residences were sampled by placing two Sherman and two Tomahawk traps inside and three Sherman and three Tomahawk traps within 5 m of the outside of each residence. Live traps were baited with equal portions of corn, ground peanuts, and dried fish. Orienting from the center 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),[22] 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.[23–26] 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 *Thamnomys* 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

TABLE 1
Flea infestation of small mammals collected in Arua and Nebbi Districts, Uganda, January–August 2006

	Total no. fleas collected (no. fleas/ hosts examined)									
	Cf	*Cspp*	*Dl*	*Eg*	*La*	*Nspp*	*St*	*Xb*	*Xc*	Total
Aethomys kaiseri (27)	0 (0.00)	3 (0.11)	33 (1.22)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.04)	4 (0.15)	9 (0.33)	50 (1.85)
Arvicanthus niloticus (383)	4 (0.01)	524 (1.37)	703 (1.84)	0 (0.00)	1 (0.00)	0 (0.00)	0 (0.00)	359 (0.93)	82 (0.21)	1673 (4.34)
Crisetomys gambianus (7)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
Crocidura sp. (223)	0 (0.00)	27 (0.12)	34 (0.15)	0 (0.00)	0 (0.00)	1 (0.00)	28 (0.13)	28 (0.13)	54 (0.24)	172 (0.77)
Dasymys sp. (4)	0 (0.00)	13 (3.25)	5 (1.25)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	18 (4.50)
Gerbillus sp. (2)	0 (0.00)	0 (0.00)	5 (2.50)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	5 (2.50)
Lemniscomys striatus (24)	0 (0.00)	32 (1.33)	3 (0.13)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	35 (1.46)
Lophuromys flavopunctatus (53)	0 (0.00)	41 (0.78)	33 (0.06)	0 (0.00)	0 (0.00)	0 (0.00)	4 (0.08)	0 (0.00)	3 (0.06)	81 (1.52)
Lophuromys sikapusi (41)	0 (0.00)	63 (1.54)	53 (1.30)	0 (0.00)	0 (0.00)	0 (0.00)	2 (0.05)	1 (0.02)	1 (0.02)	120 (2.92)
Mastomys natalensis (188)	0 (0.00)	21 (0.11)	143 (0.76)	0 (0.00)	3 (0.02)	0 (0.00)	9 (0.05)	32 (0.17)	132 (0.70)	340 (1.81)
Mus sp. (77)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.01)	1 (0.01)	2 (0.02)	4 (0.04)
Myomys fumatus (27)	0 (0.00)	1 (0.04)	6 (0.22)	0 (0.00)	0 (0.00)	0 (0.00)	5 (0.19)	12 (0.44)	13 (0.48)	37 (1.38)
Oenomys sp. (1)	0 (0.00)	0 (0.00)	1 (1.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (1.00)
Praomys sp. (72)	0 (0.00)	5 (0.07)	6 (0.08)	1 (0.01)	0 (0.00)	0 (0.00)	4 (0.06)	13 (0.18)	30 (0.41)	59 (0.81)
Rattus rattus (453)	3 (0.00)	7 (0.02)	35 (0.08)	123 (0.27)	0 (0.00)	0 (0.00)	0 (0.00)	399 (0.88)	137 (0.30)	704 (1.55)
Tatera sp. (50)	0 (0.00)	4 (0.08)	33 (0.66)	0 (0.00)	0 (0.00)	0 (0.00)	3 (0.06)	2 (0.04)	5 (0.10)	47 (0.94)
Thamnomys sp. (1)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)

Cf = *Ctenocephalides felis*; *Cspp* = *Ctenophthalmus* spp.; *Dl* = *Dinopsyllus lypusus*; *Eg* = *Echidnophaga gallinacean*; *Lspp* = *Leptopsyllla aethiopicus*.; *Nspp* = *Nosopsyllus* spp.; *St* = *Stivalius torvus*; *Xb* = *Xenopsylla brasiliensis*; *Xc* = *Xenopsylla cheopis*.

exception of *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. *Ctenophthamus* 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; $r^2 = 0.004$, $F = 4.02$, 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

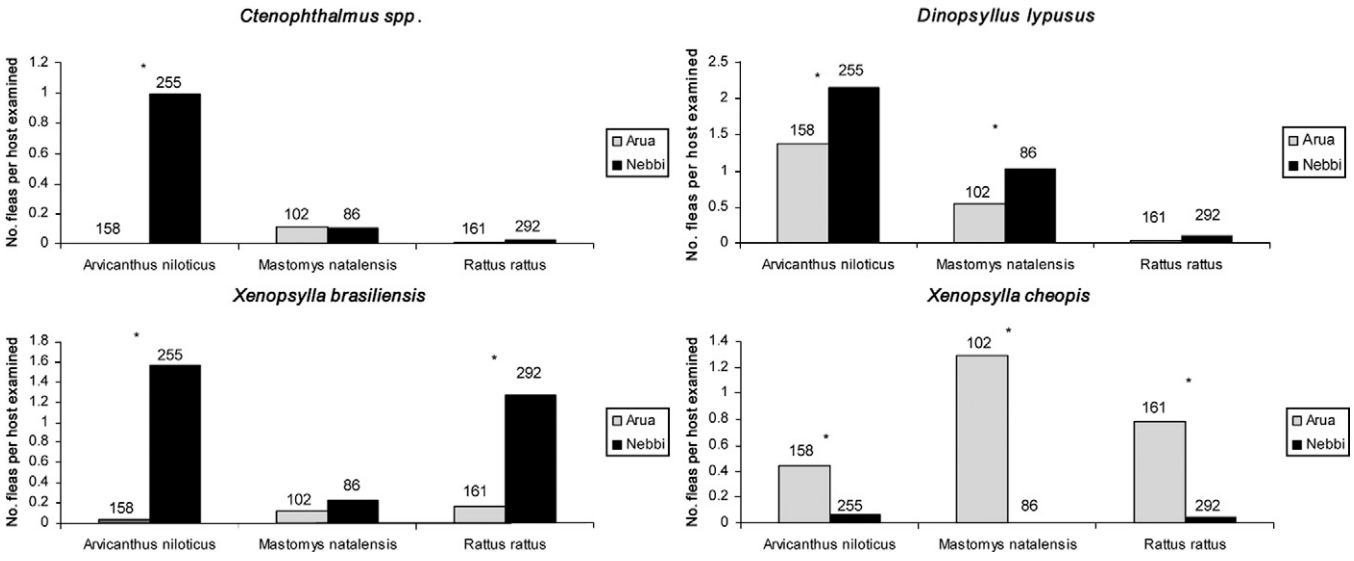

FIGURE 2. Comparison of flea loads on common host species in Arua and Nebbi Districts, Uganda. *Statistically significant differences in median values ($P < 0.05$). Number of hosts examined is shown above each bar.

TABLE 2
Seasonal trends in flea infestation by host species and district

Flea species	Host species	Average no. fleas per host examined (total hosts examined) [median flea load]							
		Arua				Nebbi			
		Jan–Feb	Mar–Apr	May–June	August	Jan–Feb	Mar–Apr	May–June	August
D. lypusus	*Arvicanthus niloticus*	0.16 (37) a [0.0]	1.74 (62) b [1.0]	1.76 (59) b [1.0]	NS	NS	1.47 (59) a [0.0]	2.02 (90) a [1.0]	2.84 (76) a [1.5]
	Mastomys natalensis	0.05 (19) a [0.0]	0.21 (28) a [0.0]	0.87 (55) a [0.0]	NS	NS	1.2 (20) a [0.0]	0.60 (33) a [0.0]	1.33 (33) a [1.0]
X. brasiliensis	*Arvicanthus niloticus*	0.00 (37) a [0.0]	0.11 (62) b [0.0]	0.00 (59) a [0.0]	NS	NS	3.27 (59) a [0.0]	1.22 (90) a [0.0]	0.64 (76) a [0.0]
	Rattus rattus	0.02 (50) a [0.0]	0.38 (69) b [0.0]	0.02 (42) a [0.0]	NS	NS	0.99 (121) a [0.0]	1.70 (112) a [0.0]	1.03 (59) a [0.0]
Ctenophalmus spp.	*Arvicanthus niloticus*	0.16 (37) a [0.0]	2.64 (62) b [2.0]	2.22 (59) b [1.0]	NS	NS	0.96 (59) a [0.0]	0.61 (90) a [0.0]	1.46 (76) b [1.0]
X. cheopis	*Mastomys natalensis*	0.00 (19) a [0.0]	1.40 (28) b [0.0]	1.69 (55) b [0.0]	NS	NS	0.00 (20) a [0.0]	0.00 (33) a [0.0]	0.00 (33) a [0.0]
	Rattus rattus	0.2 (50) a [0.0]	0.85 (69) b [0.0]	1.26 (42) b [0.0]	NS	NS	0.12 (121) a [0.0]	0.00 (112) b [0.0]	0.00 (59) b [0.0]

August represents the start of the plague season, which continues through February.
Values connected by the same letter within each row indicate statistically similar median values (Mann-Whitney *U* tests; $P > 0.05$); Arua and Nebbi districts were tested separately.
NS = not sampled.

for 92% and 95% of small mammals collected in human dwellings (domestic settings), respectively. Examining the number of rodents captured per trap-night from March-June, a period of time when all village locations were monitored, *R. rattus* was significantly more abundant in domestic settings (median, 0.26 *R. rattus* per trap-night; range of 0.13–0.37 for the 10 villages) than in peridomestic or sylvatic locations (median values of 0.02 [range: 0.0–0.05] and 0.0005 [range: 0.0–0.003), respectively; Kruskal-Wallis test with χ^2 approximation $\chi^2 = 23.79$, df = 2, $P < 0.001$). In addition, significantly more *R. rattus* per trap-night were collected in domestic settings in Nebbi district than in Arua district (Mann-Whitney *U* test, $P = 0.03$). All other comparisons of rodent (*R. rattus*, *A. niloticus,* and *M. natalensis*) abundance based on number captured per trap-night separated by trap location were similar between Arua and Nebbi Districts (Mann-Whitney *U* tests). Furthermore, we did not detect any significant differences in rodent abundance between villages with or without a history of plague (Mann-Whitney *U* tests).

In Arua district, *R. rattus* were infested with an average of 0.67 *X. cheopis* per rat, whereas in Nebbi district, *R. rattus* collected in human dwellings were infested with an average of 1.35 *X. brasiliensis* per rat (Tables 3 and 4). In both districts, *A. niloticus* was the most abundant host in peridomestic and sylvatic areas. Within peridomestic setting, *R. rattus* was the next most abundant host species. In sylvatic areas, *M. natalensis* was the second most abundant host (Tables 3 and 4). During March–June for both districts combined, *A. niloticus* were significantly more abundant in peridomestic settings (median of 0.04 *A. niloticus* per trap night, range: 0.008–0.117 among the 10 villages sampled) than in domestic (median of 0.01 *A. niloticus* per trap night, range: 0.00–0.03 among the 10 villages sampled) or sylvatic areas (median of 0.004 *A. niloticus* per trap night, range: 0.00–0.006 among the 10 villages sampled; $\chi^2 = 19.45$, df = 2, $P < 0.001$).

DISCUSSION

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,[8] 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.[8] 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. In Arua district, *X. cheopis* remains the most abundant flea species but has been replaced by *X. brasiliensis* in the higher elevation Nebbi district. These fleas infest a diverse array of host species in both districts. We did not detect any significant differences in small mammal abundance or flea loads between villages with or without a history of plague, indicating that conditions during inter-epizootic periods are similar between these 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-

TABLE 3
Flea infestation data for small mammals collected in domestic, peridomestic or sylvatic areas in Arua District, Uganda (March–June 2006)

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

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

ated with domestic or peridomestic settings.[27–32] Furthermore, because of their high vector efficiency, broad host preferences, and close association with human dwellings, *X. cheopis* and *X. brasiliensis* have been implicated as primary vectors to humans in domestic and peridomestic settings.[7,10,19] Because of the high abundance of *R. rattus* infested with *X. cheopis* or *X. brasiliensis* in and around human dwellings in Arua and Nebbi districts, respectively, it is likely that, during epizootic periods when a high proportion of these fleas may be infected with *Y. pestis*, domestic and peridomestic areas pose the greatest risk to humans.

Our field-derived data on flea–host associations across transects spanning from domiciles to sylvatic areas is valuable for shedding light on how *Y. pestis* might move from sylvatic cycles to human dwellings, as has been suggested previously for other African plague foci.[11,12,33,34] Each of the four primary flea species recovered in our trapping efforts (*Ctenophthalmus* spp., *D. lypusus*, *X. brasiliensis*, and *X. cheopis*) is capable or likely to be capable of transmitting *Y. pestis*.[7,10–12,18,19] Likewise, the three most common rodent species from which these fleas were recovered (*A. niloticus*, *M. natalensis*, and *R. rattus*) are susceptible to infection and have been found to be naturally infected.[7,10,13,14] Infected hosts typically produce very high concentrations of *Y. pestis* in their blood before perishing from the infection. Such high bacterial concentrations ($> 10^6$ cfu/mL) are needed to reliably infect feeding fleas.[35,36] Death of the host forces infected fleas to seek new hosts of the same or different species. As a consequence of this relay of transmission from infectious host to vector 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. brasiliensis* 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.[8] 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.[8] 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.[6] Because cat fleas were rarely recovered from rodents, they are not likely

TABLE 4
Flea infestation data for small mammals collected in domestic, peridomestic or sylvatic areas in Nebbi District, Uganda (March–June 2006)

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

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 *Y. pestis* from a septicemic 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 *Y. pestis* spreads rapidly from host to host.[19] 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.[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,[8,41–44] 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.[12] 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 *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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