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Research article

Host–Parasite Associations in Small Mammal Communities in Semiarid Savanna Ecosystems of East Africa

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Abstract

Despite the established importance of rodents as reservoirs of vector-borne zoonoses in East Africa, there is relatively limited information regarding the infestation parameters and host associations of ectoparasites that vector many such pathogens among small mammals in this region. Between 2009 and 2013, small mammals were live-trapped in the semiarid savanna of Kenya. A subset of these individual hosts, including 20 distinct host taxa, was examined for ectoparasites, which were identified to species. Species of fleas, ticks, mites, and sucking lice were recorded. Based on these data, we calculated host-specific infestation parameters, documented host preferences among ectoparasites, conducted a rarefaction analysis and extrapolation to determine if ectoparasites were adequately sampled, and assessed nestedness for fleas to understand how pathogens might spread in this system. We found that the flea community structure was significantly nested. Understanding the ectoparasite network structure may have significant human relevance, as at least seven of the ectoparasite species collected are known vectors of pathogens of medical importance in the region, including *Yersinia pestis*, *Rickettsia* spp., and *Theileria parva,* the causative agents of plague, spotted fevers and other rickettsial illnesses in humans, and theileriosis, respectively.

Key words: flea, louse, mite, tick, ectoparasite

Rodents and other small mammals are primary reservoirs of many vector-borne pathogens of medical and veterinary significance throughout the world, including the causative agents for Lyme disease, hantaviral diseases, and hemorrhagic fevers (Meerburg et al. 2009, McFarlane et al. 2012, Luis et al. 2013, Han et al. 2015, Morand et al. 2015). In East Africa, important vector-borne pathogens with small mammal reservoirs include *Yersinia pestis* (plague), *Borrelia* spp. (tick-borne relapsing fever), *Rickettsia* spp. (spotted fevers, murine typhus, and other rickettsial illnesses), *Bartonella* spp. (cat scratch disease, trench fever, bacillary angiomatosis, etc.), and *Theileria parva* (livestock theileriosis; Pearse 1929, Roberts 1939, Heisch et al. 1953, Norval et al. 1992, Mediannikov et al. 2010, Zimba et al. 2012, Leulmi et al. 2014). These pathogens have serious social and economic consequences; in 1989, a regional loss equivalent to US$168 million was attributed to theileriosis alone (Mukhebi et al. 1992). The significance of small mammals in the dynamics of disease in these systems will depend strongly on host–vector associations – including the host specificity of the vectors, and the intensity of infestation of these ectoparasites. There have been relatively few studies of such associations in East Africa (Roberts 1936, 1939; Heisch et al. 1953; Schwan 1986; Laudisoit et al. 2007; Oguge et al. 2009; Sang et al. 2011), and none that explores details of host–parasite networks from the woody semiarid savanna ecosystem that dominates much of East Africa.

In this study, we aim to not only document host–ectoparasite associations across a range of taxonomic groups, but also understand

the nested structure of these relationships to shed light on how pathogens might spread in these East African small mammal communities. Nestedness, a pattern in which species composition of small, species-poor assemblages constitutes nonrandom subsets of species occurring in successively larger, species-rich assemblages, is a method for determining whether species live in structured or unstructured assemblages (Atmar and Patterson 1986, Ulrich et al. 2009). Nested patterns are typically attributed to free-living species communities occurring in insular or fragmented habitats (Atmar and Patterson 1986); however, in the case of parasite communities, individual hosts can be considered insular habitats for parasites (Kuris et al. 1980). As a result, nestedness has been previously used as an indicator of parasite community structure, where specialist parasite species parasitize species-rich hosts (i.e., hosts parasitized by several species) and generalist parasites interact with parasite species-rich hosts as well as hosts with fewer parasites (Graham et al. 2009). However, studies have yielded different results and there is still no consensus as to whether parasite communities tend to be structured in a nested pattern (Poulin 1996; Rohde et al. 1998; Matějusová et al. 2000; Krasnov et al. 2005, 2011; Patterson et al. 2009). The lack of consensus on nestedness in parasite communities could be owing to differences in statistical techniques used or the difference in spatial scales at which communities are analyzed (e.g., host individuals vs. host populations; Krasnov et al. 2005).

Nestedness has been suggested to facilitate pathogen transmission across host–parasite communities unless key species-rich hosts in the network have a reduced capacity to facilitate pathogen transmission (Graham et al. 2009). Thus, understanding parasite-sharing structures in networks, such as nestedness, can prove advantageous to understanding the spread of parasites and their associated pathogens in a system (Paull et al. 2011, Pilosof et al. 2015).

Here we examine the ectoparasite communities, including fleas (Siphonaptera), ticks (Ixodidae), mites (Acari), and sucking lice (Phthiraptera: Anoplura), associated with small mammals in a range of natural and human-dominated landscapes in semiarid savanna of Laikipia and Isiolo Counties, Kenya. We first describe host associations and infestations of fleas, ticks, mites, and sucking lice found on small mammals in this area. We then assess nestedness of assemblages for each ectoparasite group across 11 small mammal host taxa with respect to the potential for vector-borne pathogen transmission.

Materials and Methods

Study Site

From 2009 to 2013, small mammals and their ectoparasites were sampled at 98 localities over an approximately 3,000-km^2 area in the semiarid savanna of Laikipia and Isiolo Counties, Kenya. Sampling sites encompassed an array of land uses, including conserved landscapes with abundant large wildlife and a range of anthropogenically disturbed landscapes, consisting of both small-scale and large-scale agriculture, moderate-to-intensive pastoral land use, and human habitation.

Small Mammal Sampling

Most trapping was conducted on a series of ninety-eight 10 by 10-m grids as part of a larger study to understand effects of land-use change on small mammal communities (Young et al. 2015). This trapping was supplemented by additional trapping off site to target a diversity of habitat types (escarpments, riparian habitats, and human habitation) and small mammal species. There were 147–300 trap nights per site.

All trapping was conducted using 8 by 9 by 22-cm Sherman live-traps baited with oats and peanut butter. Traps were opened in the evening and shut in the morning to avoid heat stress to animals. After capture, small mammals were identified using morphological features and were subsequently sampled for ectoparasites (details below). Blood samples were taken to genetically confirm host species identifications using CO1 barcodes when field identification was unclear (Ratnasingham and Hebert 2007). Each animal was then uniquely marked using numbered ear tags to avoid resampling the same hosts. Recaptured hosts were not resampled for ectoparasites or blood; any recaptures were simply recorded and released. After sampling, most hosts were released at the point of capture; however, a subset of hosts were lethally sampled for voucher specimens to verify species identifications. All individual small mammals were identified to species, except those in the genus *Mus* because this species group is morphologically cryptic and it was not possible to obtain CO1 barcodes from all individuals.

Ectoparasite Sampling

Host animals were sampled for ectoparasites by being stretched over a container of 70% ethanol (white plastic polyethylene pan, 51 by 132 by 13 cm, large enough to ensure all ectoparasites were captured) and combed on all parts of the body using a standard flea comb (Krasnov et al. 2003, Seery et al. 2003). Most host animals were fully alert, restrained by the neck scruff and tail to ensure immobility while combing; however, *Acomys* sp. were briefly anesthetized with inhaled isoflurane during handling, as their sensitive skin is prone to tearing. Fleas and any other ectoparasites were then collected using a transfer pipette from the ethanol container, ensuring there were no ectoparasites left in the container before sampling a different host. Subsequent to combing, the ears, face, and genital areas of the animal were visually examined, and any other visible ectoparasites were removed. This protocol was primarily designed for sampling fleas, and as such, the prevalence and infestation intensity data are reliable only for this taxonomic group. However mites, ticks, and sucking lice were also collected in large numbers using this technique. All ectoparasite specimens were preserved in ethanol (70–100%), and all fleas and representative specimens of lice and mites were cleared and slide-mounted to confirm species identity.

From the total of 2,703 mammals captured and sampled for ectoparasites, all ectoparasites from a stratified random sampling by host species were identified. At least 10 individuals of every host (except where <10 individuals of that species had been captured) were included, and the remaining sampling was distributed across land use types to capture the fullest possible range of host–parasite associations present in the landscape (Supp. Table 1 [online only]). Ectoparasites were identified by experts (fleas: Eckerlin and Dittmar, ticks: Robbins, Hedlund, and Allan, lice: Durden, mites: Dowling) using morphological features and taxonomic keys (see Supp. Table 1 [online only]). In some instances where species identification was challenging, multiple researchers independently assessed species identity, a mutual confirmation of which gave confidence as to the identity of ectoparasite species.

For a large subset of the morphologically identified animals (both hosts and ectoparasites), barcodes of the mitochondrial CO1 gene were used to identify potentially cryptic species and confirm the identities of morphological clusters (Ratnasingham and Hebert 2007). Sequences obtained from all screened ectoparasites and hosts are publicly available in the Barcode of Life Project (boldsystems.org), with images available for every individual. Vouchered specimens of every ectoparasite species identified (slide-mounted for

fleas, lice, and mites), except those destroyed in the process of barcoding, are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC.

Infestation intensity was calculated using the total number of individual ectoparasites of each group (flea, tick, mite, and louse) per host only from those hosts that had at least one ectoparasite sampled (Bush et al. 1997). Infestation intensity is reported either as a mean infestation across all hosts for all flea, tick, mite, or louse species, or as mean infestation intensity among specific host–parasite associations. Because the sampling was designed specifically for fleas, prevalence data are only reported for fleas, as zeros recorded for other taxa frequently may be false-negatives.

Data Analysis

Rarefaction analysis

Given the difference in sample sizes of individuals of each host species examined for ectoparasites (e.g., 3 *Gerbillus pusillus* vs. 132 *Gerbilliscus robustus*), rarefaction analyses and Bernoulli product model extrapolations were conducted to estimate expected ectoparasite species richness had all host species been sampled to a greater degree. Rarefaction analyses are a common technique used to assess and compare species richness in data sets with differing numbers of sampling units, and extrapolations can be used to estimate the expected number of species that would be found with increased sampling (Colwell et al. 2012). Bernoulli product model extrapolations (Colwell et al. 2012) provide reasonable results for extrapolations to double or triple the original sample. In this study, the rarefaction analyses and Bernoulli product model extrapolations were computed using the program EstimateS (Version 9, R. K. Colwell, http://purl.oclc.org/estimates).

Rarefaction and extrapolation analyses were performed for each ectoparasite group (fleas, ticks, mites, and lice) with respect to each host species sample size. Only host species where more than one host individual was collected and there was more than one ectoparasite individual collected across the host species were included in the analysis. Results are presented as an estimated species richness (S_{est}) and standard deviation of a tripled sample size for each ectoparasite group across each host species. Results for which S_{est} was $\geq$1 species greater than the originally sampled species richness are highlighted.

Nestedness analysis

Ectoparasite group community structure and nestedness were assessed using weighted nestedness, a metric developed by Galeano et al. (2009). In contrast to other nestedness estimators, the weighted nestedness estimator takes into account the intensity (weight) of each host–parasite interaction in the network as opposed to using presence–absence matrices as a basis for calculating nestedness (Galeano et al. 2009, Ulrich et al. 2009).

Nestedness was calculated for each parasite group (fleas, ticks, mites, and lice). Of the 781 host individuals and 20 taxa for which all ectoparasites were examined, only host species of which at least 10 host individuals were sampled for all ectoparasites were included in the data set (11 host species; Table 1). Data were organized as prevalence matrices in which rows represented host species and columns represented ectoparasite species. Matrices were constructed for each ectoparasite group. Weighted nestedness (WIN) and *P*-values were calculated using *vegan* and *bipartite* packages in R (Dormann et al. 2008, Oksanen et al. 2015, R Core Team 2015), where WIN values of 0 represent a random structure, WIN = 1 represents a perfectly nested structure, and *P*-values $\leq$ 0.05 indicate a nested assemblage.

Table 1. Species and number of individual small mammals examined for ectoparasites

Host species	Host number
Acomys kempi[b]	21
Acomys percivali[b]	14
Aethomys hindei[b]	51
Arvicanthis nairobae[b]	22
Arvicanthis niloticus[b]	38
Elephantulus rufescens[b]	12
Gerbillus pusillus	3
Gerbilliscus robustus[b]	132
Grammomys dolichurus[b]	11
Graphiurus microtis	1
Lemniscomys striatus	9
Mastomys natalensis[b]	77
Mus spp.[a]	5
Myomyscus brockmani	9
Paraxerus ochraceus	1
Rattus rattus	4
Saccostomus mearnsi[b]	458
Taterillus harringtoni[b]	38
Xerus erythropus	4
Zelotomys hildegardeae	8
Total	918

Laikipia and Isiolo counties, Kenya, 2009–2013.
[a] Only identified to genus.
[b] Included in nestedness analysis.

Results

Host–Parasite Associations

In total, 918 mammal specimens (of the 2,703 captured) belonging to 20 taxa of small mammals (including 19 rodents and 1 elephant shrew) were examined for all ectoparasites (Table 1). All 2,703 mammals (belonging to 29 taxa) were examined for total flea prevalence and infestation (Supp. Table 1 [online only]).

Fleas (14 species) were collected from 20 species of small mammals (Table 1) including 2,753 flea individuals that were identified to species. Of the small mammals parasitized by fleas, mean infestation intensity (± standard error [SE]) for all flea species was 4.18 ± 0.23 fleas per host individual, but there was high variation among species in infestation intensity. Of the 14 species of fleas found, seven species exhibited generalist host associations: *Xenopsylla cheopis* (11 hosts), *Dinopsyllus lypusus* (10 hosts), *Dinopsyllus kempi* (9 hosts), *Xenopsylla robertsi* (9 hosts), *Xenopsylla brasiliensis* (9 hosts), *Xenopsylla sarodes* (7 hosts), and *Ctenophthalmus calceatus cabirus* (7 hosts; Table 2). *Ctenophthalmus bacopus* parasitized only one host species, and the remaining six flea species each parasitized between two to five host species (Table 2). Results from the rarefaction analysis and extrapolation suggest that sampled flea species richness was saturated for 12 of the 18 sampled species, but more flea species would be found with additional sampling of *Aethomys hindei*, *Arvicanthis nairobae*, *Grammomys dolichurus*, *Saccostomus mearnsi*, *Taterillus harringtoni*, and *Zelotomys hildegardeae* (Table 6).

Ticks were much less frequently encountered in our sampling (only 65 individuals were sampled) and only eight taxa of ticks were collected from nine host species (Table 3). Owing to difficulty in identification of immature (and typically engorged) ticks, two tick taxa were only identified to genus (*Ixodes* sp. and *Rhipicephalus* sp.), but genetic screening of these taxa confirmed these to be different from other *Ixodes* and *Rhipicephalus* species sampled. Mean infestation intensity (±SE) for the mammals parasitized by ticks was 1.51 ± 0.15 ticks per host individual, but this does not include individuals that

Table 2. Flea (Siphonaptera) infestations of small mammals in Kenya, 2009–2013, showing mean and range values

Host species	*C.f. felis* (M)	*C.f. strongylus*	*C. ansorgei*	*C. bacopus*	*C.c. cabirus* (M)	*D. kempi*	*D. lypusus* (M)
Acomys kempi	1,1[b]	–	–	–	1,1	–	–
Acomys percivali	–	–	–	–	–	–	–
Aethomys hindei	–	–	–	–	1,1	1,1[b]	1.38,1–3
Arvicanthis nairobae	–	–	–	4.5,1–8[b]	–	2.33,1–3[b]	5.75,1–11
Arvicanthis niloticus	–	–	1,1[b]	–	2,2	2,1–4[b]	3,1–9
Elephantulus rufescens	1,1[b]	–	–	–	–	–	–
Gerbilus pusillus	–	–	–	–	–	–	–
Gerbilliscus robustus	1,1[b]	–	–	–	–	1,1[b]	1.44,1–4[b]
Grammomys dolichurus	–	–	–	–	–	1,1[b]	1,1
Graphiurus microtis	–	–	–	–	–	–	–
Lemniscomys striatus	–	–	–	–	4,1–9	1,1[b]	1,1
Mastomys natalensis	–	–	1,1	–	1.42,1–3	1,1[b]	1.81,1–5
Mus spp.	3,3[b]	–	–	–	–	–	–
Myomyscus brockmani	–	–	–	–	–	–	–
Paraxerus ochraceus	–	–	–	–	–	–	–
Rattus rattus	–	–	–	–	–	–	1,1
Saccostomus mearnsi	1,1	1,1[b]	–	–	1.5,1–3	1.2,1–2[b]	1.52,1–5[b]
Taterillus harringtoni	–	–	–	–	–	–	–
Xerus erythropus	–	1.67,1–2[b]	–	–	1,1	–	–
Zelotomys hildegardeae	–	–	–	–	–	1.5,1–3[b]	2,2[b]

Host species	*E. gallinacea* (M)	*P. echinatus*	*X. brasiliensis* (M)	*X. cheopis* (M)	*X. humilis*	*X. nubica*	*X. robertsi*	*X. sarodes*	Number of hosts[a]
Acomys kempi	–	1.33,1–2[b]	–	–	–	–	1.75,1–3	–	21 (8)
Acomys percivali	–	1,1[b]	–	–	–	–	1.33,1–2	–	14 (10)
Aethomys hindei	–	–	24,1–47	1.14,1–2[b]	–	2,2	2,1–11	4,4[b]	51 (39)
Arvicanthis nairobae	–	1,1[b]	2,2b	2.14,1–4	–	–	–	2.67,1–6[b]	22 (16)
Arvicanthis niloticus	–	–	1.33,1–2	2.17,1–13	1,1	–	–	1,1[b]	38 (32)
Elephantulus rufescens	–	–	1,1	–	–	–	–	–	12 (3)
Gerbilus pusillus	–	–	–	–	–	2,1–4[b]	–	–	3 (3)
Gerbilliscus robustus	18.5,8–29[b]	–	1.33,1–3[b]	1.43,1–3[b]	7.83,1–30	2.2,1–6	1,1	1.14,1–2[b]	132 (109)
Grammomys dolichurus	–	–	–	1,1	–	–	–	–	11 (3)
Graphiurus microtis	–	–	–	1,1[b]	–	–	–	–	1 (1)
Lemniscomys striatus	–	–	–	–	–	–	–	–	9 (4)
Mastomys natalensis	–	–	1,1	1.79,1–10[b]	2.33,1–5[b]	–	–	1,1[b]	77 (71)
Mus spp.	–	–	–	–	–	–	1,1	–	5 (2)
Myomyscus brockmani	–	–	–	–	–	–	1.5,1–2	–	9 (2)
Paraxerus ochraceus	–	–	–	1,1[b]	–	–	–	–	1 (1)
Rattus rattus	–	–	8,3–13	1,1	–	1,1	–	–	4 (4)
Saccostomus mearnsi	1,1	–	2,1–5	2.93,1–17[b]	1,1[b]	–	1,1	3.64,1–23	458 (447)
Taterillus harringtoni	–	–	1,1[b]	–	2,1–4	5.83,1–25[b]	1,1	1,1[b]	38 (26)
Xerus erythropus	–	–	–	–	–	–	–	–	4 (4)
Zelotomys hildegardeae	–	–	–	6,6[b]	–	–	1,1	–	8 (5)

Flea species: *Ctenocephalides felis felis, Ctenocephalides felis strongylus, Ctenophthalmus ansorgei, Ctenophthalmus bacopus, Ctenophthalmus calceatus cabirus, Dinopsyllus kempi, Dinopsyllus lypusus, Echidnophaga gallinacea, Parapulex echinatus, Xenopsylla brasiliensis, Xenopsylla cheopis, Xenopsylla humilis, Xenopsylla nubica, Xenopsylla robertsi, Xenopsylla sarodes*.

Mean infestation intensity (mean per infested host) for all hosts that had at least one flea, and infestation range (or a single number if there was no range). Zeros from uninfected hosts excluded. (M) denotes flea species known to vector pathogens of human medical importance.

[a] Total number of hosts examined for all ectoparasites and number of hosts examined parasitized by fleas (in parentheses).

[b] New host association.

were not sampled for ticks. From the collected tick species, *Haemaphysalis leachi* and *Rhipicephalus parvus* parasitized the most host species (six and five, respectively); *Hyalomma truncatum* parasitized three host species; *Rhipicephalus praetextatus* and *Rhipicephalus* sp. parasitized two host species, and the remaining tick taxa each parasitized only one mammalian species (Table 3). Rarefaction analysis and extrapolation results indicate that sampled tick species richness would increase with increased sampling for only one of the nine host species for which ticks were observed: *A. hindei* (Table 6).

Mites were the most diverse group sampled, with 25 species documented from just 248 individual mites, across 16 mammal taxa (Table 4). Mean infestation intensity (± SE) of those individuals parasitized by mites was 1.88 ± 0.12 mites per host individual. Of the 25 collected mite species, *Androlaelaps* nr. *marshalli* and *Androlaelaps theseus* were the most generalist, with each parasitizing five host taxa. At the other end of the spectrum, 13 mite species (five *Laelaps*, three *Echinolaelaps*, and five *Androlaelaps*) were recorded as parasitizing only one host taxon. The remaining mite

Table 3. Tick (Ixodidae) infestations of small mammals in Kenya, 2009–2013

Host species	*H. leachi* (MV)	*H. truncatum* (M)	*Ixodes* sp.	*R. jeanneli*	*R. praetextatus*	*R. parvus* (V)	*R. simpsoni*	*Rhipicephalus* sp.	Number of hosts[a]
Acomys kempi	2,2	–	–	–	–	–	–	–	21 (1)
Aethomys hindei	–	–	–	1,1	1,1	1,1[b]	1,1	2.5,2–3	51 (6)
Arvicanthis niloticus	1,1[b]	–	–	–	–	–	–	–	38 (1)
Elephantulus rufescens	1,1	–	1.2,1–2	–	–	2,1–4[b]	–	–	12 (9)
Gerbilliscus robustus	1.67,1–2	–	–	–	1,1	1.25,1–2[b]	–	1,1	132 (13)
Mastomys natalensis	1.5,1–2[b]	–	–	–	–	–	–	–	77 (2)
Rattus rattus	–	1,1[b]	–	–	–	–	–	–	4 (1)
Saccostomus mearnsi	–	1,1[b]	–	–	–	1,1[b]	–	–	458 (5)
Taterillus harringtoni	1,1	1,1[b]	–	–	–	1,1[b]	–	–	38 (5)

Tick species: *Haemaphysalis leachi, Hyalomma truncatum, Ixodes sp., Rhipicephalus jeanneli, Rhipicephalus praetextatus, Rhipicephalus parvus, Rhipicephalus simpsoni, Rhipicephalus sp.*

Mean infestation intensity (mean per infested host) for all hosts that had at least one tick, and infestation range (or a single number if there was no range). Zeros from uninfected hosts excluded. (M) denotes tick species known to vector pathogens of human medical importance, and (V) denotes ticks known to vector pathogens of veterinary importance.

[a] Total number of hosts examined for all ectoparasites and number of hosts examined parasitized by ticks (in parentheses).

[b] New host association

species parasitized between two and four mammalian host taxa (Table 4). The rarefaction analysis and extrapolation results indicate that mite species richness would increase with increased sampling of six mammalian host species: *Acomys kempi*, *Acomys percivali*, *Arvicanthis nairobae*, *Mastomys natalensis*, *Saccostomus mearnsi*, and *Taterillus harringtoni* (Table 6).

Eleven species of sucking lice were identified from 110 louse individuals collected from 10 mammalian host taxa (Table 5). Two of the identified species, referred to as *Hoplopleura* n. sp. 1 and *Polyplax* n. sp. 1 in this paper, represent new species which were morphologically and genetically distinct from other sampled taxa. Mean infestation intensity (± SE) of all host taxa parasitized by lice was 3.93 ± 1.51 lice per host individual. From the collected lice species, *Polyplax brachyrrhyncha*, *Polyplax oxyrrhyncha*, and *Polyplax* n. sp. 1 each parasitized two different host species. The remaining louse species each parasitized only one host taxon. Most of the host taxa were only parasitized by a single species of louse, with the exception of *A. kempi* (three louse spp.), *A. percivali* (two louse spp.), and *Mus* sp. (two louse spp.; Table 5). Results from the rarefaction analysis and extrapolation indicate that sampled louse richness was saturated for all host species (Table 6).

Nestedness Analysis

Community structure varied across the four different ectoparasite groups. Flea community structure was significantly nested (weighted nestedness [WIN]) = 0.244, *z*-score [standardized effect size] = 1.80, $P = 0.04$). Flea species such as *X. brasiliensis* and *X. robertsi* parasitized a wider range of both common and less common hosts such as *G. dolichurus* (Fig. 1). *Saccostomus mearnsi* and *G. robustus*, the species best represented in our trapping data, were parasitized by the most flea species, including species such as *Ctenocephalides felis strongylus* and *Echidnophaga gallinacea*, which parasitized fewer host species (Fig. 1). Results from the nestedness analysis for tick, louse, and mite community structures are presented in Suppl. Material 2 [online only].

Discussion

Host–Parasite Associations

Most of the flea species collected in this study had been previously documented in Kenya (Roberts 1936, Heisch et al. 1953, Zimba et al. 2012), with the exception of *Ctenophthalmus ansorgei*, which has been previously reported in southern Africa (Isaäcson 1975). We also found new host associations for 13 of our 14 documented flea species, including all host associations documented here for *D. kempi* and *Parapulex echinatus* (Table 2). Of medical relevance, five of the identified flea species are associated with the transmission of human pathogens. Two of these flea species, *D. lypusus* and *X. brasiliensis*, are generalists with regard to the number of hosts they parasitize and are known vectors of *Y. pestis*, the causative agent of plague (Roberts 1939, Heisch et al. 1953). Other recorded flea species parasitized a less diverse suite of hosts in this study, but are also of medical importance, as they are also known vectors of *Y. pestis* and of *Rickettsia* spp. bacteria that cause murine typhus and other rickettsial illnesses in humans. These other flea vectors include *C. calceatus cabirus* (*Y. pestis*), *X. cheopis* (*Y. pestis*; *Rickettsia* spp.), and *E. gallinacea* (*Rickettsia* spp.; Pearse 1929, Heisch et al. 1953, Loftis et al. 2006, Zimba et al. 2012).

All of the tick species we collected had been previously documented in Kenya (Dick and Lewis 1947, Clifford et al. 1976, Lwande et al. 2013). However, we found new host associations for three of the nine collected tick species (Table 3). Three of the collected tick species, which include two of the species with generalist host associations (*H. leachi* and *R. parvus*), are associated with human and livestock pathogens. *Haemaphysalis leachi* and *H. truncatum* are both vectors of *Rickettsia* spp., the causative agents of febrile illnesses in humans, and *R. parvus* is a vector of *T. parva*, the cause of East Coast Fever in livestock (Dick and Lewis 1947, Norval et al. 1992, Walker et al. 2000, Mediannikov et al. 2010). *Hyalomma truncatum* is a vector of Crimean-Congo hemorrhagic fever virus, which causes a zoonotic disease that manifests as inapparent short-term infections in ungulates but can be fatal in humans (Sang et al. 2011).

Four of the 25 reported mite species are new to science (one *Laelaps*, one *Echinolaelaps*, and two *Androlaelaps*) and several other mites are tentatively identified to species, "nr." being used to indicate uncertainty. When "nr." is used, it is because the mite keys out to the named species but is exhibiting some morphological variability that separates it from the species named. Whether these differences represent morphological variability within the species or whether these represent new species is impossible to determine based on the information available. Of the 25 species, only eight

Table 4. Mite infestations of small mammals in Kenya, 2009–2013

Host species	*A. centrocarpus*	*A.* nr. *dasymys*	*A.* n. *ghanensis*	*A.* nr. *longipes*	*A.* n. *marshalli*	*A.* nr. *tateronis* sp. 1	*A.* nr. *tateronis* sp. 2	*A.* nr. *villosissimus*
Acomys kempi	–	–	–	–	1,1[a]	–	–	1,1[a]
Acomys percivali	–	–	–	–	–	–	–	–
Aethomys hindei	–	–	–	–	–	–	–	–
Arvicanthis nairobae	1,1[a]	1,1[a]	–	–	–	–	–	–
Arvicanthis niloticus	1,1[a]	–	–	1,1[a]	–	–	–	–
Elephantulus rufescens	–	–	–	–	–	1,1[a]	–	–
Gerbilliscus robustus	–	–	–	–	1,1	1,1[a]	–	–
Grammomys dolichurus	–	–	–	–	–	–	–	–
Lemniscomys striatus	–	–	–	–	–	–	–	–
Mastomys natalensis	–	–	–	–	–	–	–	–
Mus spp.	–	–	–	–	–	–	–	–
Myomyscus brockmani	–	–	–	–	–	–	–	–
Rattus rattus	–	–	–	–	1,1	–	–	–
Saccostomus mearnsi	–	–	–	–	1,1[a]	1,1[a]	–	–
Taterillus harringtoni	1,1[a]	–	–	2,1–4[a]	1,1[a]	–	–	–
Zelotomys hildegardeae	–	–	1,1[a]	–	–	–	1,1[a]	–

Host species	*A.* nr. *zumpti*	*A. oliffi*	*A. theseus*	*E. muricola*	*E.* n. *giganteus*	*E.* nr. *grandis*	*E.* n. *sedlaceki*	*E.* n. sp.1	*E.* n. sp.2	*L. keegani*
Acomys kempi	–	–	–	1,1[a]	–	–	–	–	–	–
Acomys percivali	–	–	–	–	–	–	–	–	–	–
Aethomys hindei	–	–	1,1[a]	–	–	–	–	2,1–4[a]	–	–
Arvicanthis nairobae	–	–	–	–	3.5,2–5[a]	–	–	1,1[a]	–	1,1[a]
Arvicanthis niloticus	–	1,1[a]	–	–	1.14,1–2	–	–	–	–	–
Elephantulus rufescens	–	2,2[a]	–	–	–	–	–	–	–	–
Gerbilliscus robustus	–	1,1[a]	1.84,1–6[a]	–	–	–	–	–	–	–
Grammomys dolichurus	–	–	–	–	–	–	–	–	–	–
Lemniscomys striatus	–	–	–	–	–	–	–	–	1.5,1–2[a]	–
Mastomys natalensis	–	–	–	2.2,1–4	1,1	–	–	–	–	–
Mus spp.	–	–	–	–	–	–	–	1,1[a]	–	–
Myomyscus brockmani	–	–	–	–	–	–	1,1[a]	–	–	–
Rattus rattus	–	–	1.5,1–2[a]	–	–	–	–	–	–	–
Saccostomus mearnsi	1.67,1–4[a]	–	1,1[a]	–	–	–	–	–	–	–
Taterillus harringtoni	–	1,1[a]	1.2,1–2[a]	–	–	–	–	–	–	–
Zelotomys hildegardeae	–	–	–	–	–	2.75,1–5[a]	–	–	–	–

Host species	*L.* nr. *aethiopicus*	*L.* nr. *benoiti*	*L.* nr. *brandbergensis*	*L.* n. *kampalensis*	*L.* n. *liberiensis*	*L. vansomereni*	*L.* n. sp.	Number of hosts[b]
Acomys kempi	–	–	–	–	–	–	–	21 (4)
Acomys percivali	–	–	–	–	–	–	1,1[a]	14 (2)
Aethomys hindei	–	–	–	–	–	1,1[a]	–	51 (16)
Arvicanthis nairobae	–	1,1[a]	–	–	–	1,1[a]	–	22 (6)
Arvicanthis niloticus	–	–	–	–	–	–	–	38 (10)
Elephantulus rufescens	–	1,1[a]	–	–	–	–	–	12 (4)
Gerbilliscus robustus	–	–	–	–	–	–	–	132 (34)
Grammomys dolichurus	–	2,1–5[a]	1,1	–	–	1,1[a]	–	11 (7)
Lemniscomys striatus	–	—	–	1,1	1,1	–	–	9 (4)
Mastomys natalensis	–	–	–	–	1.33,1–2	–	–	77 (8)
Mus spp.	–	–	–	–	–	–	–	5 (1)
Myomyscus brockmani	–	2.83,1–7[a]	–	–	–	–	–	9 (7)
Rattus rattus	–	–	–	–	–	–	–	4 (2)
Saccostomus mearnsi	1,1[a]	–	–	–	–	–	–	458 (9)
Taterillus harringtoni	–	–	–	–	–	–	–	38 (13)
Zelotomys hildegardeae	–	–	–	–	–	–	–	8 (6)

Mite species: *Androlaelaps centrocarpus*, *Androlaelaps* nr. *dasmys*, *Androlaelaps* nr. *ghanensis*, *Androlaelaps* nr. *longipes*, *Androlaelaps* nr. *marshalli*, *Androlaelaps* nr. *tateronis* sp. 1, *Androlaelaps* nr. *tateronis* sp. 2, *Androlaelaps* nr. *villosissimus*, *Androlaelaps* nr. *zumpti*, *Androlaelaps oliffi*, *Androlaelaps theseus*, *Echinolaelaps muricola*, *Echinolaelaps* nr. *giganteus*, *Echinolaelaps* nr. *grandis*, *Echinolaelaps* nr. *sedlaceki*, *Echinolaelaps* n. sp. 1, *Echinolaelaps* n. sp. 2, *Laelaps keegani*, *Laelaps* nr. *aethiopicus*, *Laelaps* nr. *benoitii*, *Laelaps* nr. *brandbergensis*, *Laelaps* nr. *kampalensis*, *Laelaps* nr. *liberiensis*, *Laelaps vansomereni*, *Laelaps* n. sp.

Mean infestation intensity (mean per infested host) for all hosts that had at least one mite, and infestation range (or a single number if there was no range). Zeros from uninfected hosts excluded.

[a] New host association.

[b] Total number of hosts examined for all ectoparasites and number of hosts examined parasitized by mites (in parentheses).

Table 5. Sucking louse infestations of small mammals in Kenya, 2009–2013

Host species	*H.* n. sp. 1	*H. rukenyae*	*H. setzeri*	*H. zelotomydis*	*P. abyssinica*	*P. brachyrrhyncha*
Acomys kempi	–	–	–	–	–	2.5,1–6
Acomys percivali	–	–	–	–	–	1.5,1–2
Aethomys hindei	–	–	–	–	–	–
Arvicanthis nairobae	–	–	–	–	2,2[b]	–
Grammomys dolichurus	–	–	3,3	–	–	–
Lemniscomys striatus	–	–	–	–	–	–
Mus spp.	2,2[b]	1,1	–	–	–	–
Myomyscus brockmani	–	–	–	–	–	–
Saccostomus mearnsi	–	–	–	–	–	–
Zelotomys hildegardeae	–	–	–	4,4	–	–

Host species	*P. jonesi*	*P.* n. sp. 1	*P. oxyrrhyncha*	*P. phthisica*	*P. solivaga*	Number of hosts[a]
Acomys kempi	–	3,3[b]	1,1	–	–	21 (9)
Acomys percivali	–	–	3,1–5	–	–	14 (3)
Aethomys hindei	–	–	–	–	2,1–3[b]	51 (2)
Arvicanthis nairobae	–	–	–	–	–	22 (1)
Grammomys dolichurus	–	–	–	–	–	11 (1)
Lemniscomys striatus	–	–	–	1,1[b]	–	9 (1)
Mus spp.	–	–	–	–	–	5 (2)
Myomyscus brockmani	–	1.5,1–2[b]	–	–	–	9 (2)
Saccostomus mearnsi	9.5,1–44[b]	–	–	–	–	458 (6)
Zelotomys hildegardeae	–	–	–	–	–	8 (1)

Lice species: *Hoplopleura* n. sp. 1, *Hoplopleura rukenyae, Hoplopleura setzeri, Hoplopleura zelotomydis, Polyplax abyssinica, Polyplax jonesi, Polyplax n.* sp. 1, *Polyplax oxyrrhyncha, Polyplax phthisica, Polyplax solivaga*

Mean infestation intensity (mean per infested host) for all hosts that had at least one louse, and infestation range (or a single number if there was no range). Zeros from uninfected hosts excluded.

[a] Total number of hosts examined for all ectoparasites and number of hosts examined parasitized by lice (in parentheses).

[b] New host association.

Table 6. Results of rarefaction analysis (S_{est} and SD) with tripled sample size Bernoulli product model extrapolation

Host species	Fleas	Ticks	Mites	Lice
Acomys kempi	4.93 (1.55)	1.00 (0.00)[a]	**7.20 (3.88)**	3.93 (1.54)
Acomys percivali	2.00 (0.00)	–	**3.21 (0.64)**	2.00 (0.00)
Aethomys hindei	**8.65 (1.27)**	**10 (4.92)**	3.96 (1.58)	1.00 (0.00)
Arvicanthis nairobae	**8.66 (2.67)**	–	**15.58 (6.47)**	1.00 (0.00)[a]
Arvicanthis niloticus	8.95 (1.60)	1.00 (.000)[a]	4.24 (0.7)	–
Elephantulus rufescens	2.00 (0.00)	3.00 (0.00)	**8.16 (3.98)**	–
Gerbillus pusillus	1.00 (0.00)	–	–	–
Gerbilliscus robustus	10.24 (0.72)	4.48 (1.25)	4.48 (1.25)	–
Grammomys dolichurus	**5.39 (2.83)**	–	3.44 (1.15)	1.00 (0.00)[a]
Lemniscomys striatus	3.87 (1.46)	–	3.22 (0.66)	1.00 (0.00)
Mastomys natalensis	8.00 (0.00)	1.00 (0.00)	**5.71 (2.74)**	–
Mus spp.	2.78 (1.33)	–	1.00 (0.00)	2.78 (1.33)
Myomyscus brockmani	1.00 (0.00)	–	2.00 (0.00)	1.00 (0.00)
Rattus rattus	4.73 (1.38)	1.00 (0.00)[a]	2.36 (0.97)	–
Saccostomus mearnsi	**13.30 (3.97)**	2.00 (0.00)	**8.30 (3.97)**	1.00 (0.00)
Taterillus harringtoni	**6.69 (2.71)**	3.24 (0.71)	**6.68 (2.70)**	–
Xerus erythropus	2.00 (0.00)	–	–	–
Zelotomys hildegardeae	**6.31 (2.77)**	–	3.42 (1.11)	1.00 (0.00)[a]

Values indicate expected ectoparasite species richness had all host species been sampled to a greater degree.

Bolded values indicate S_{est} was more than one species greater than found number of species, suggesting host was inadequately sampled.

[a] Only one host individual had an ectoparasite (flea, tick, louse, or mite).

(*Androlaelaps centrocarpus*, *A. marshalli*, *Echinolaelaps muricola*, *Echinolaelaps giganteus*, *Echinolaelaps grandis*, *Laelaps aethiopicus*, *Laelaps liberiensis*, and *Laelaps vansomereni*) had been previously documented on Kenyan mammals (Keegan 1956, Zumpt and Till 1961, Till 1963, Herrin and Tipton 1976). Most of the species not known from Kenya had been previously reported in South Africa, Ethiopia, Uganda, Tanzania, or the Democratic Republic of Congo. We also found new host associations for 23 of our 25 recorded mite species (Table 4). None of the mites identified in this study are known to be associated with human pathogens, although very little pathogen survey work has been done with these mites. Reeves et al. (2006) did find pathogens in genera such as *Rickettsia*

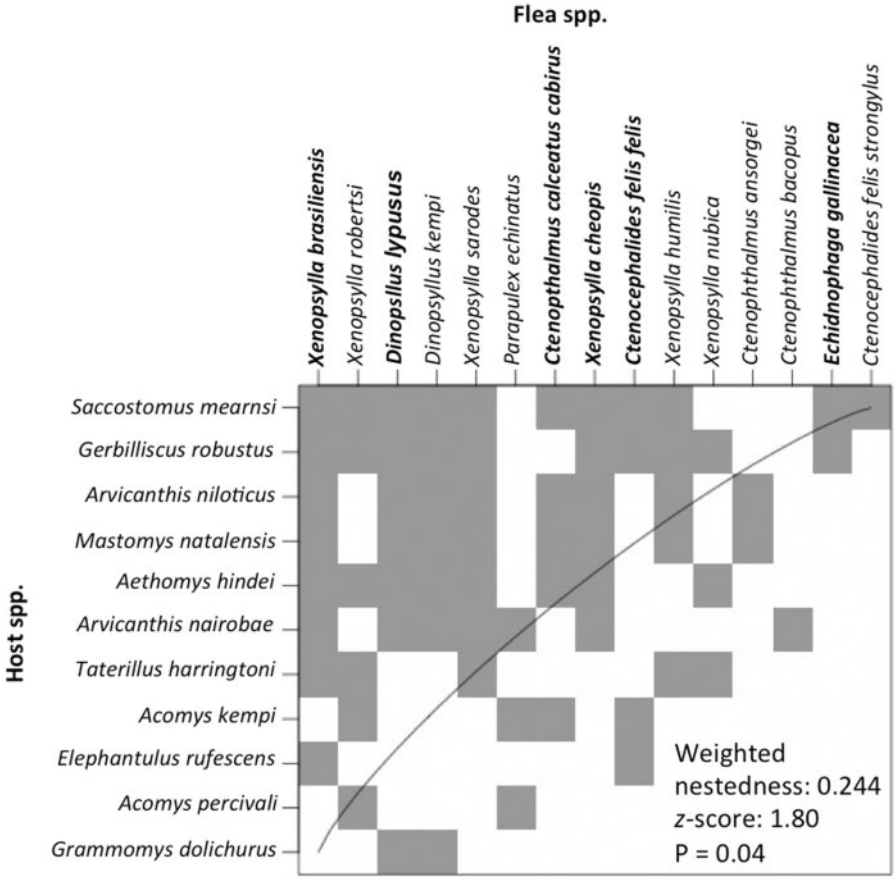

Fig 1: Nestedness plot of ectoparasite community structure for fleas showing a nested community structure. Host species are shown on the Y-axis and flea species on the X-axis, gray blocks indicate incidence of host–parasite association, and bolded ectoparasite species names indicate species of human health or veterinary importance.

and *Anaplasma* in related mite species, which may indicate that further pathogen research should be conducted.

Of the nine collected species of sucking lice, two (*Hoplopleura* n. sp. 1 and *Polyplax* n. sp. 1) are undescribed (Table 5). Of the remaining species, only two had not been previously documented in Kenya (Johnson 1960, Kim and Emerson 1968, Durden 1991, Durden and Musser 1994): *Polyplax jonesi*, which has been previously documented in Botswana, Mozambique, Namibia, South Africa, Democratic Republic of Congo, and Saudi Arabia (Lyal 1980, Durden and Musser 1994), and *Polyplax solivaga*, which has only been documented in South Africa (Kleynhans 1969). New host associations were found for four louse species: *Polyplax abyssinica*, *P. jonesi*, *Polyplax phthisica*, and *P. solivaga* (Table 5). Largely because of the relatively high level of host specificity that they exhibit, none of the louse species identified are known vectors of medically relevant viruses or bacteria. However, some species of sucking lice are known to be enzootic vectors of zoonotic pathogens between small mammals and can be important in maintaining these pathogens in nature. Pathogens in this category include *Rickettsia typhi* (the causative agent of murine typhus), *Francisella tularensis* (the causative agent of tularemia), *Bartonella* spp. (causative agents of bartonellosis and associated clinical manifestations), and *Rickettsia* spp. (causative agents of rickettsioses; Traub and Wisseman 1978, Durden and Lloyd 2009). Bridge vectors could transmit these pathogens to humans.

It is important to reiterate that because our sampling technique was primarily designed for fleas and not all host taxa were equally sampled, infestation intensity data may not be as representative of tick, sucking louse, and mite infestations as for flea infestations.

Nestedness Analysis

Results from the nestedness analysis suggest that specialist tick and flea species tend to parasitize host species with high parasite richness, whereas generalist tick and flea species tend to parasitize host species with low tick and flea species richness (Fig. 1, Supp. 1A [online only]).

Of medical relevance, *S. mearnsi* and *G. robustus*, the most highly connected host species within the nested flea community, were parasitized by various flea species that harbor human pathogens. Among these is the flea species *D. lypusus*, which in addition to being a vector for the causative agent of plague is also connected to a high number of host species (Fig. 1). Similarly, the tick species with the most host connections, *H. leachi* and *R. parvus*, are vectors for causative agents of human and livestock disease and interact with the most connected hosts, *A. hindei* and *G. robustus* (Supp. Fig. 1A [online only]). The high connectedness of medically relevant ectoparasites in these flea and tick communities suggests that diseases such as plague, rickettsioses, and theileriosis could have the potential to spread widely among vertebrate hosts. This highlights the potential medical importance hosts could have for the spread of pathogens in a system.

Overall, our study provides important information on ectoparasite–host associations in the semiarid savanna region of Kenya and

underscores the need for additional information on the prevalence of pathogens in highly connected parasite species, such as *D. lypusus*, *H. leachi*, and *R. parvus*, to further refine predictions on disease transmission and spread in this area.

Supplementary Data

Supplementary data are available at *Journal of Medical Entomology* online.

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