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DRIVERS OF INTENSITY AND PREVALENCE OF FLEA PARASITISM ON SMALL MAMMALS IN EAST AFRICAN SAVANNA ECOSYSTEMS

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ABSTRACT: The relative importance of environmental factors and host factors in explaining variation in prevalence and intensity of flea parasitism in small mammal communities is poorly established. We examined these relationships in an East African savanna landscape, considering multiple host levels: across individuals within a local population, across populations within species, and across species within a landscape. We sampled fleas from 2,672 small mammals of 27 species. This included a total of 8,283 fleas, with 5 genera and 12 species identified. Across individual hosts within a site, both rodent body mass and season affected total intensity of flea infestation, although the explanatory power of these factors was generally modest (<10%). Across host populations in the landscape, we found consistently positive effects of host density and negative effects of vegetation cover on the intensity of flea infestation. Other factors explored (host diversity, annual rainfall, anthropogenic disturbance, and soil properties) tended to have lower and less consistent explanatory power. Across host species in the landscape, we found that host body mass was strongly positively correlated with both prevalence and intensity of flea parasitism, while average robustness of a host species to disturbance was not correlated with flea parasitism. Cumulatively, these results provide insight into the intricate roles of both host and environmental factors in explaining complex patterns of flea parasitism across landscape mosaics.

Patterns of prevalence and intensity of flea infestations in small mammals remain poorly understood. This knowledge gap has important implications both for the fitness of animals directly impacted by fleas (Khokhlova et al., 2002; Devevey and Christe, 2009; Kam et al., 2010), and also for the health of wildlife and humans in communities that are affected by fleas and flea-borne diseases. The density of fleas is considered to strongly impact the likelihood of disease transmission among hosts and critically drive the emergence of flea-borne epizootics among humans (Gage, 1998; Keeling and Gilligan, 2000; Samia et al., 2011). This study was conducted in East Africa, where small mammal ectoparasites, and particularly fleas, are known vectors for a variety of pathogens important to both human and wildlife health, including plague, murine typhus, cat flea typhus, and bartonellosis (Richards et al., 2010; Parola, 2011; Eisen and Gage, 2012). In particular, we seek to understand the factors that drive the variation in intensity and prevalence of ectoparasitism by fleas across multiple levels of organization.

Many factors have been postulated to affect prevalence and intensity of flea parasitism among and within host species (Krasnov et al., 2002c; Whiteman and Parker, 2004; Hawlena et al., 2005; Krasnov et al., 2005; Kiffner et al., 2013). Most factors fall broadly into 2 categories: host factors and environmental factors. Host factors encompass a range of attributes, including individual-level properties (such as sex, age, body condition, and health), species-level properties such as taxonomy and life history (e.g., body size, longevity, sociality), and community-level properties such as host density and host composition and diversity (Krasnov et al., 2002c; Stanko et al., 2002; Linardi and Krasnov, 2013).

In addition to host factors, because ectoparasites tend to be more exposed to the environment than most other parasites, environmental factors may be particularly critical in determining prevalence, intensity, and richness of ectoparasitism (Cumming and Van Vuuren, 2006; Oorebeek and Kleindorfer, 2008; Merino and Møller, 2010; Malenke et al., 2011). Such factors influence fleas both indirectly, via their effects on many host characteristics, and directly, as many fleas spend much of their lives detached from the host and, even when attached to the host, generally remain in direct contact with the external environment (Krasnov et al., 2002b). Examples of direct impacts of environment on fleas include effects of rainfall and substrate texture on success and development rates of flea larvae (Krasnov et al., 2001a, 2001b). Examples of indirect effects of environment on flea parasitism include instances where environment may change host behavior (e.g., social contact, grooming rates, or burrowing behavior [Shenbrot et al., 2002]), physiology (e.g., via immune investment [Khokhlova et al., 2004]), or community composition and density (Young et al., 2015).

The relative importance of host versus environmental factors in driving prevalence and intensity of flea parasitism may vary based on spatial scale, while effects operating at different scales may in turn interact (Linardi and Krasnov, 2013). In this study, we examine the relative importance of a suite of both environmental and host factors in explaining variation in the intensity and prevalence of flea parasitism across small mammal communities in central Kenya. This work is conducted at multiple scales. We first look locally at the individual level, within a species and population of hosts, and specifically ask: (1) To what extent do host body size, host sex, and seasonality affect the prevalence and intensity of total flea infestation? Then, scaling up to the

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landscape level, we ask, (2) To what extent do variation in host density and diversity, and environmental factors including soil, rainfall, vegetation cover, and anthropogenic disturbance explain variation in flea parasitism across host populations within a host species? Finally, we look across host species, within a single landscape and ask, (3) To what extent do variations across host species in body mass and robustness to anthropogenic disturbance explain patterns of flea abundance and prevalence?

While other studies have examined drivers of abundance or intensity of flea infestations, this study's unique multiscale approach within a large landscape provides new insight on the importance of these factors across scale. Moreover, while previous studies have tended to focus on effects on 1 or several species of fleas, this study expands instead to intensity and prevalence of total flea parasitism. While this focus on total flea burden overlooks nuanced dynamics of specific host–parasite relationships, it is nevertheless critical from the perspective of impacts on host fitness and disease transmission, because, in this system, there are multiple generalist flea species that can transmit many locally relevant pathogens.

MATERIALS AND METHODS

Study site

From 2009 to 2013, small mammals were sampled from 98 localities across an ~3,000 km^2 area in a semiarid savanna region of Laikipia and Isiolo Counties, Kenya. The sites sampled spanned a productivity gradient and also a range of land uses, including conserved landscapes with abundant large wildlife, and anthropogenically disturbed landscapes. The productivity gradient was driven by a large regional rainfall range (~400–900 mm/yr) and by strong local variation in soil properties, as there are 2 major soil types in the area: black cotton soil, a high-productivity, high-clay soil type; and red soil, a low-productivity, low-clay soil type.

Small mammal sampling

Small mammal trapping was conducted with 3 different approaches in order to answer questions about flea burdens at different scales (Fig. 1): (1) To assess variation across individuals (within a population), we conducted intensive grid-based trapping in 1 locality across multiple seasons; (2) To assess variation across populations (within a species), we extended the same grid-based trapping across a range of localities within a single sampling period; (3) To assess variation across all small mammal species in the landscape, we supplemented grid-based sampling with additional "diversity" trapping in the same landscape to allow comparison of flea communities across a wider range of host species.

First, for comparison of individual variation in flea infestation intensity, we trapped small mammals in 1 area across 5 different seasons spanning from November 2009 to March 2012. In this 3 km^2 area, we placed 6 trapping grids. Each grid was 100×100 m in dimension with 10×10 m spacing between each trapping point ($n = 600$ traps). One $7.6 \times 8.9 \times 22.3$ cm Sherman trap was placed on the ground at each grid point. Traps were baited with peanut butter and oats; they were opened in the evening and shut in the morning to avoid heat stress to animals. Small mammal abundance from this trapping effort is reported as catch per unit effort, calculated as the minimum number of animals known alive per gridded trap night (3,000 trap nights total). After capture, host species were identified using morphological features, and their ectoparasites were sampled (details below). Blood samples were taken to confirm host species identifications genetically. Body mass, sex, and reproductive condition of host were recorded, and the host was marked (using numbered ear tags) in order to avoid resampling. Animals were then released at point of capture; however, on the final day of trapping at each site, a subset of the hosts was lethally sampled for morphological voucher specimens to verify species identifications. Ultimately, all individual hosts were identified to species, except for *Crocidura*, which were lumped at the genus level, as well as some individuals from the genus *Mus* (both these species groups are morphologically cryptic, and we were unable to get CO1 barcodes from all individuals). Animals captured a second time were not resampled but were simply recorded and released.

Between January and July of 2011, we extended these same trapping grid protocols to a total of 98 localities selected to represent a range of habitats in the counties. Trapping was again conducted for 3 nights at each site. Grid size was typically 10×10 m (with 10 m spacing between traps), but in some sites of small available area ($n = 12$), it was 7×7 m (again with 10 m spacing between traps), yielding 147–300 trap nights per site.

Finally, we conducted additional diversity trapping to compare flea communities across a broader range of host species. While the standardized grid-based trapping effort allowed us to characterize density of small mammal hosts at each site, it was suboptimal for catching many mammal species. Thus, we conducted additional trapping off grids in order to target those species and habitats that were not well sampled in initial grid-based trapping. This type of strategic trapping included trees, buildings, rocky outcroppings, and riparian systems, and extended from November 2009 to December 2013. For this trapping type, we also used supplementary forms of bait, including dried fish, fresh fruit, and canned meat, and we conducted additional diurnal trapping.

Flea sampling

Immediately after removal from the trap, the small mammal was held stretched over a container of ethanol and thoroughly combed for fleas on all parts of the body using a standard flea comb, with a standardized number of passes over the animal. All fleas were then collected by hand from the ethanol container and counted to calculate an index of infestation intensity. Previous work has shown that this index of flea infestation intensity can be used as an index of absolute abundance across species of fleas and hosts (Krasnov et al., 2004).

A subset of all fleas was then identified to species using morphological features and currently available taxonomic keys. Given difficulties of identification for some of these species, multiple research groups independently assessed the identities and then mutually confirmed the identities of all species. For a large subset of the morphologically identified animals, we also used barcodes of the mitochondrial CO1 gene to identify potentially cryptic species and confirm morphological clusters (Ratnasingham and Hebert, 2007). The sequences obtained from both fleas and hosts are now posted online with the Barcode of Life Project (boldsystems.org). Slide-mounted fleas used for identification are deposited in the National Museum of Natural History, Smithsonian Institution.

In all analyses for infestation intensity, we used the total number of individual fleas per host (either absolute number when individual was the unit of replication, or mean number per individual when site or species was the unit of replication). For prevalence, we calculated the percentage of hosts parasitized within a species or site.

Environmental characteristics

At each of the 98 density trapping sites, we took detailed measurements of multiple abiotic and biotic environmental characteristics. At each site, 3–5 soil samples were taken, integrating soil sampling units from 0 to 20 cm depth. Soils were dried and sieved, and sand:silt content was subsequently analyzed (Brookside Laboratories, New Knoxville, Ohio). Among biotic factors, vegetation was surveyed using 50 sampling points (on a 20×20 m grid) per site. Sampling details are provided in Young et al. (2013b). Essentially, at each sampling point, we dropped a 50 cm sampling pin 5 times (each drop was 1 m apart) and recorded the identity and height of every plant species that contacted the pin as well as the presence or absence of vegetation above that height. For this analysis, we used only the metric of vegetation cover, calculated as the total number of contacts of vegetation with the survey pin at each sampling location, as this metric will likely be the most relevant to both small mammal and ectoparasite communities. Annual rainfall levels for each site were interpolated using an extensive set of long-term rainfall data in the area (Franz et al., 2010). In this dry savanna, seasonality was assumed to be driven primarily by rainfall rather than temperature, and seasonality was thus quantified as the average amount of rainfall in the month prior to the sampling date. Thirty days was chosen as an index of seasonality from the perspective of a flea, as it is roughly the time of development from egg to adult for several species in the dominant genus *Xenopsylla* (Krasnov et al., 2002b). Land use was a categorical classification determined via discussion with landowners as well as by visual inspection, with all sites classified

simply as either disturbed (heavy livestock use or any level of agricultural use) or undisturbed. Additional work using camera traps and dung cover (per m^2) has confirmed our a priori classifications of land use (Young et al., 2013b, 2015).

Statistical analyses

First, to examine drivers of variation across individuals (within a population in a single general locality), we used generalized linear models (GLMs) with a Poisson distribution and a log link (for count data); intensity of flea infestation per individual was the response variable. As factors in the model, we included sex and body mass (a proxy for both maturity and health) of the animal, and the interaction between these, as well as the amount (mm) of rainfall in the 30 days prior to capture (index of seasonality). Adult versus juvenile state was not included as it was collinear with body mass. These analyses were performed on just 1 species (*Saccostomus mearnsi*), which dominated captures at our focal sites (59% of all captures in the locality used for individual level analyses, and 94% of all captures of animals with at least 1 flea at this locality). All models were then compared using Akaike information criterion (AIC) weights. Since there were multiple models that received strong empirical support ($AIC_c < 2$), we compared models using a model averaging approach, which calculated each model's contribution to a parameter estimate being proportionately adjusted using its Akaike weights (including only those models with $\Delta AIC_c < 2$). For prevalence analyses, we used an identical approach, except that, since the data were presence or absence of fleas, we used a binomial distribution with a logit link. All analyses were conducted using R v. 2.14.2 (R Core Development Team, 2012).

Next, to examine effects of variation in environmental factors on intensity and average prevalence of flea infestation across populations (within species), we used similar GLMs, here using Gaussian distributions and identity link functions. In these analyses, we used only sites that had at least 3 animals of the focal host species per site, and only those species which were both widespread (present in at least 20 sites with at least 3 individuals per site) and commonly carried fleas (the rodents *Gerbilliscus robustus*, *Taterillus harringtoni*, *S. mearnsi*, and *Aethomys hindei*). As a response variable for infestation intensity, we used the log-transformed mean abundance of fleas per site ($\log[n + 1]$) in order to meet model assumptions. For prevalence, we used an arcsin transformation of the proportion of animals in which fleas were present. For each species and response variable, we first constructed sets of candidate regression models with the following factors as explanatory variables: abundance of small mammal hosts, diversity of hosts, vegetation cover, mean annual rainfall, soil sand:silt ratio (which is effective for discriminating between the dominant soil types in the area), and land use type. For host abundance, we used total abundance of host species rather than abundance of conspecifics because most of the fleas can infest multiple species and because host density effects on host parasite richness have been previously demonstrated to operate interspecifically (Stanko et al., 2002). Prior to analyses, we tested all of the environmental factors and found no substantial collinearity using a variance inflation factor test ($VIF < 2$). Model averaging was conducted as detailed above. For these analyses, we used only data gathered from the standardized grid-based trapping conducted between January and July 2011.

Finally, to examine drivers of intensity and prevalence of flea infestation across species in the landscape, we used GLMs, again with Gaussian distributions and identity link functions, now with average flea abundance per host individual (square root transformed to meet model assumptions) and prevalence of infestation (proportion of individuals of a host species having any fleas, arcsin transformed) as response variables. As predictor variables, we used host body mass (log transformed) and a calculated host robustness metric. This host robustness metric was intended to estimate how robust each species is to human disturbance and was calculated as the proportion of total captures of that species that occurred in anthropogenically disturbed (rather than conserved) landscapes. These analyses were performed both with and without poorly sampled species (those with less than 20 individuals sampled). In order to account for non-independence among species due to variation in the extent of shared ancestry among hosts, we also conducted the analysis using phylogenetic generalized least squares models (PGLS; Pagel, 1999). These models account for non-independence among species by including an error term in the variance–covariance matrix. We then estimated λ, a multiplier of the off-diagonal elements of the covariance matrix, in order to assess the extent of phylogenetic signal in the model residuals. Values of λ range from 0 to 1, with 0 implying phylogenetic independence and 1 implying a Brownian motion model of evolution based on the tree and branch lengths. We ran all these analyses using the R package caper (Orme et al., 2012). The tree used for PGLS was generated from CO1 sequences generated from individuals collected for this project and submitted to the Barcode of Life Database (BOLD). A representative sequence from each species was used (total = 31; BOLD reference numbers are given in Supplementary Data Table S1). Sequences were aligned using MUSCLE implemented in MEGA5 and included 658 bp of the 5′ end of CO1 (Tamura et al., 2011). A maximum likelihood analysis was run using RaxML implemented through the CIPRES Gateway (Stamatakis, 2006). CO1 has been shown to offer informative phylogenetic trees in the tribe Praomyini of African rodents, being more informative than cytochrome b (Nicolas et al., 2012).

RESULTS

In total, 2,672 small mammals, including 27 species, were sampled for fleas (Supplementary Data Table S2). One species, *Saccostomus mearnsi*, dominated captures (40% of all captures). In total, 8,283 fleas were sampled. Given these large numbers, only a subset of these fleas was identified (n = 1,690). Identification was prioritized to include all fleas from at least 20 individuals of each host species, except for a group of 6 small mammal species, for which fewer than 20 individuals were captured and flea combed (*Dasymys incomtus*, *Dendromus mystacalis*, *Dendromus melanotis*, *Mus sorella*, *Mus tenellus*, *Steatomys parvus*). For those 6 species, all individual fleas collected were identified. From within the remaining 21 host species, the individuals selected for flea identification were randomly selected, and 5 genera and 12 species were identified (*Ctenocephalides felis felis*, *C. felis strongylus*, *Ctenophthalmus calceatus cabirus*, *Dinopsyllus lypusus*, *D. kempi*, *Parapulex echinatus*, *P. chephrensis*, *Xenopsylla cheopis*, *X. humilis*, *X. nubica*, *X. robertsi*, *X. sarodes*, *X. brasiliensis*). For many of the species of fleas identified, little is known about the ecology, biology, and disease transmission potential; however, several of the species identified are known vectors of zoonotic diseases to humans. These include 2 of the more frequently identified species: *Xenopsylla cheopis* and *X. brasiliensis*. Although many of the factors discussed here may also affect flea species richness and community composition, as the purpose of this study is to understand predictors of total flea burden, all fleas are considered together in subsequent analyses.

Across individuals

With a total sample of 635 individuals of *S. mearnsi* sampled within our 1 focal area, we found that both body mass and seasonality were highly significant in our models (Table I). Flea abundance was higher on larger individuals and in drier seasons. Sex and sex by mass interactions had no significant effects, although they did appear in some supported models. Overall, the power of our models to explain individual variation in intensity of flea parasitism was not high. The best-fit model (rainfall and body mass) explained 9% of the total variance in intensity of flea parasitism among individuals.

Results for prevalence of flea infestation showed rainfall to be the most important factor in explaining flea prevalence (higher prevalence in drier sites), with no other factor showing up as significant in stepwise regressions. The best-fit model, however, was again rainfall and mass; for prevalence, it explained only 6% of the total variance in flea abundance across individuals.

TABLE I. Factors explaining variation in flea parasitism across individual *Saccostomus mearnsi* mice based on model averaging using GLMs. RI = relative importance of the factor across models. *P* values are determined using backwards stepwise regression.

	Intensity			Prevalence		
	Coefficient ± SE	RI	*P*	Coefficient ± SE	RI	*P*
Rainfall	$-6.19 \times 10^{-4} \pm 0.47 \times 10^{-4}$	1	0.0001	−0.01 ± 0.01	1	<0.0001
Mass	0.01 ± 0.00	1	<0.001	0.01 ± 0.01	0.81	0.15
Sex	−0.07 ± 0.14	0.52	0.61	−0.14 ± 0.72	0.39	0.84
Sex × mass	0.02 ± 0.01	0.27	0.14	0.02 ± 0.01	0.13	0.28

Across populations

Four species (*Aethomys hindei*, *Gerbilliscus robustus*, *Saccostomus mearnsi*, and *Taterillus harringtoni*) met our criteria (minimum 20 sites with at least 3 individuals with fleas per site) for across-population analysis. The ability of models to explain variation in flea abundance ranged substantially across these 4 species. Best-fit models explained 51% of variation in intensity for *A. hindei*, 10% for *G. robustus*, 14% for *S. mearnsi*, and 33% for *T. harringtoni*. Models for prevalence of fleas explained similar, but slightly lower amounts of variation for all species (48%, 5%, 14%, and 24%, respectively).

Host density had a positive relationship with intensity of flea infestation for all 4 species (Table II), with a relative importance greater than 0.5 in all cases. (Relative importance is calculated as an AIC_c weighted proportion of the models with $\Delta AIC_c < 2$ in which the term was utilized.) Vegetation cover also had negative relationships with flea abundance (more fleas in habitats with less cover) for all species, and this relationship was significant and important (relative importance > 0.69) for all species. The importance and significance of other factors were much more variable with species. When sand:silt relationships occurred, they were negative, with sandier sites having higher flea prevalence. Annual rainfall had the most variable effect as a predictive factor, appearing as a strong driver in intensity of flea abundance for *S. mearnsi* and limited or no effect on flea abundance for other species. Host diversity and land-use status had relatively limited explanatory power across species. Drivers of flea prevalence were very similar to those observed for intensity of flea infestation within a species, although there were some subtle variations (Table II).

Across species

Body size explained most of the variation across species in intensity and prevalence of flea parasitism, with larger species harboring more fleas more frequently (Table III; Fig. 2). In contrast, host robustness to human disturbance was not important in predicting either intensity or prevalence of flea parasitism. The best-fit model (body mass only) explained 35% of variation in intensity of infestation and 55% of variation in prevalence of infestation. The largest species studied, the ground squirrel *Xerus erythropus*, was a major outlier in both prevalence and intensity analyses. If this species is removed from analyses, the relationships become stronger (Table III), explaining 54% and 69% of variation in intensity and prevalence of infestation, respectively. In this analysis, there is some slight support for a positive relationship between flea parasitism and robustness (more robust species have higher levels of flea parasitism). When we removed species with fewer than 20 individual hosts sampled, the results are qualitatively very similar, although proportion of variance explained was lower with the smaller sample size β. Estimates of λ were high in our phylogenetic least squares analysis of intensity of parasitism, with a maximum likelihood of 0.960 (range 0.25–1), suggesting a strong role of evolutionary history in driving levels of parasitism. However, after accounting for this variation, the overarching patterns remain, with body mass playing a significant role (explaining 39% of variance in intensity, $P = 0.03$) and host robustness playing no significant role ($P = 0.83$). For prevalence, estimates of λ were again high (maximum likelihood 0.87). Again, host mass remained important in predicting prevalence (35% variance explained, $P < 0.01$), while robustness was not important ($P = 0.91$).

DISCUSSION

Our results suggest highly variable power of the independent variables for explaining the drivers of total flea parasitism, depending on the scale examined.

Across individuals

Of the factors that may explain variation in intensity of flea infestation among individuals in a population, we examined 3 of the best supported in the literature: body size, sex, and season. Larger individuals are generally predicted to host higher abundances of fleas because they present a larger food resource for ectoparasites; they also tend to live longer, thus representing a more predictable food source (Peters, 1983; Krasnov et al., 2006). Larger "well-fed hosts" may also provide better nutritional resources for parasites if they are in better body condition (Christe et al., 2003; Hawlena et al., 2005, 2007). However, juveniles, and smaller "poorly fed" hosts may spend less time grooming or otherwise defending against parasitism, thus providing a safe escape for parasites (Buxton, 1948; Christe et al., 1998). Very heavily parasitized hosts may also be in poorer body condition as a result of high levels of parasitism (Khokhlova et al., 2002; Neuhaus, 2003). Here, we found evidence for slightly higher intensity of flea infestation on larger individuals.

Many studies have found sex-biased differences in levels of parasitism, with a tendency towards male-biased parasitism (Matthee et al., 2010). This may be due in part to body size differences, with larger males providing a larger food resource, but it has also been attributed to differences in immune function (caused by androgen immune suppression), grooming patterns, movement, and social contact patterns (Perez-Orella and Schulte-Hostedde, 2005; Krasnov et al., 2012). Yet, many other studies have failed to find sex-biased parasitism, or they have found that sex-biased parasitism varies based on parasite examined (Krasnov

TABLE II. Factors explaining variation in flea parasitism across populations for 4 rodent species based on model averaging using GLMs. Sample size (n) = the number of populations; RI = the relative importance of the factor across models. *P* values are determined using backwards stepwise regression approaches. Significant values are shown in bold.

	Aethomys hindei (n = 20)			*Saccostomus mearnsi* (n = 41)			*Gerbilliscus robustus* (n = 40)			*Tatera illus harringtoni* (n = 28)		
	Coefficient ± SE	RI	*P*	Coefficient ± SE	RI	*P*	Coefficient ± SE	RI	*P*	Coefficient ± SE	RI	*P*
Intensity												
Host abundance	0.02 ± 0.01	0.5	0.11	0.02 ± 0.01	0.52	0.06	0.02 ± 0.01	0.71	0.08	0.04 ± 0.01	1	**0.01**
Host diversity							−0.41 ± 0.38	0.14	0.28	–	–	–
Soil	−0.11 ± 0.11	0.59	0.07	–	–	–	−0.11 ± 0.11	0.13	0.3	−0.16 ± 0.12	0.37	0.21
Veg. cover	−0.16 ± 0.01	1	**<0.001**	$-2.7 \times 10^{-3} \pm 1.6 \times 10^{-3}$	0.69	**0.06**	−0.16 ± 0.01	1	**0.02**	−0.16 ± 0.07	1	**0.04**
Rainfall	–	–	–	−0.09 ± 0.05	0.61	0.1	0.00 ± 0.00	0.32	0.17	–	–	–
Prevalence												
Host abundance	$9.6 \times 10^{-4} \pm 4.7 \times 10^{-4}$	0.76	0.06	$1.7 \times 10^{-4} \pm 1.9 \times 10^{-4}$	0.31	38	$5.49 \times 10^{-4} \pm 4.68 \times 10^{-4}$	0.27	0.27	$1.55 \times 10^{-3} \pm 0.73 \times 10^{-3}$	1	0.04
Host diversity							$-7.81 \times 10^{-4} \pm 1.28 \times 10^{-4}$	0.09	0.55	–	–	–
Soil	$-1.1 \times 10^{-2} \pm 0.6 \times 10^{-2}$	0.53	0.07	–	–	–	$-2.95 \times 10^{-4} \pm 4.32 \times 10^{-4}$	0.10	0.51	–	–	–
Veg. cover	$-7.8 \times 10^{-3} \pm 2.7 \times 10^{-3}$	1	**0.02**	–	–	–	$-3.93 \times 10^{-4} \pm 2.60 \times 10^{-4}$	0.36	0.14	$-6.7 \times 10^{-3} \pm 3.5 \times 10^{-3}$	0.72	0.07
Rainfall	$1.7 \times 10^{-4} \pm 1.0 \times 10^{-4}$	0.2	0.13	$1.8 \times 10^{-4} \pm 1.9 \times 10^{-4}$	1	**0.02**	$5.12 \times 10^{-4} \pm 8.40 \times 10^{-4}$	0.09	0.55	$-1.4 \times 10^{-4} \pm 1.4 \times 10^{-4}$	0.20	0.35

et al., 2012; Kiffner et al., 2013; Waterman et al., 2013). No evidence of sex-biased parasitism across all flea species was found in this study, even when we included size and sex interaction. There may well have been undetected sex biases within a flea species as these effects have been shown to vary by flea species (Krasnov et al., 2005); however, there was no net effect when pooled across flea species.

As most fleas spend much of their larval periods and parts of their adult life detached from hosts (in burrows or nests), they are likely to be strongly influenced by environmental factors, including seasonality (Krasnov et al., 2004). Several studies have shown pronounced variation in abundance in areas with high seasonality (Lindsay and Galloway, 1997; Krasnov et al., 2002a). However, other studies have shown little or highly variable responses of flea abundance in response to seasonality (Krasnov et al., 2002a; Laudisoit et al., 2009). In this region, the predominant seasonal climatic variation is in rainfall. We thus included in our analyses a measure of seasonal rainfall (accumulated rainfall over the 30 days prior to trapping). We found a small but significant negative effect of recent rainfall on intensity of flea infestation, such that drier sites had more fleas. This is in some ways unexpected, as more precipitation should lead to higher relative humidity, which, up to a point, increases flea development and survival. However, this may be due to the fact that flooding can kill developing fleas (especially in areas where drainage is poor, as in many of these sites), and that drier periods tend to also be warmer, and fleas develop better in sites with warmer temperatures (Krasnov et al., 2001b).

Across populations

In the second part of the study, we examined the effects of annual rainfall, soil properties, vegetation cover, human disturbance, host density, and host diversity on flea parasitism across populations of 4 species of rodents: *S. mearnsi*, *T. harringtoni*, *G. robustus*, and *A. hindei*.

The most consistent and important variables identified in predicting intensity and prevalence of flea parasitism across populations of host species in our analyses were host abundance (positive) and vegetation cover (negative). Host density was one of the earliest factors hypothesized to be correlated to prevalence and intensity of parasitism (May and Anderson, 1978; Dobson, 1990). Increased likelihood of contact between individuals should favor both increased intensity and prevalence of parasitism. This relationship should plateau at some point, particularly when parasites induce host mortality (May and Anderson, 1978; Grenfell and Dobson, 1995). However, there are many factors that may undermine this relationship, notably host behavior (grooming), and variation in environmental factors related to host density. Empirical studies to date have not found consistent relationships between host density and ectoparasite prevalence and intensity (Li and Zhang, 1997; Sorci et al., 1997; Krasnov et al., 2002c; Stanko et al., 2002; McCauley et al., 2008). In this study, at the population level, we find host density to be a widespread and important explanatory variable of flea parasitism.

The pattern of negative effects of vegetation cover on flea prevalence and intensity may be driven by direct effects of vegetation in changing environmental conditions faced by fleas. For example, by creating cooler air temperatures and high relative humidity, vegetation cover may decrease survival and develop-

TABLE III. Factors explaining variation in intensity of flea parasitism for 4 rodent species based on model averaging using GLM. Relationships in bold are significant explanatory factors, using a backwards stepwise regression analysis.

	Intensity			Prevalence		
	Coefficient ± SE	RI	$P(>z)$	Coefficient ± SE	RI	$P(>z)$
All species						
Log(mass)	**0.36 ± 0.10**	**1**	$\boldsymbol{P < 0.0001}$	**0.02 ± 0.00**	**1**	**<0.0001**
Vulnerability	–	–		–	–	
X. erythropus removed						
Log(mass)	**0.50 ± 0.10**	**1**	$\boldsymbol{P < 0.0001}$	**0.03 ± 0.00**	**1**	**<0.0001**
Vulnerability	−0.37 ± 0.33	0.34	0.27	−0.01 ± 0.01	0.27	0.41

ment of fleas (Krasnov et al., 2001a, 2002b). While no significant collinearity was detected with other variables, vegetation cover may also provide a good integrated index of many environmental and anthropogenic factors that may both directly and indirectly (via changes in host abundance) impact flea growth and survivorship (e.g., presence of other potential host species, abundance of other ectoparasites, type of anthropogenic land use).

Two factors that consistently had low impact on flea intensity or prevalence in our among-populations analyses were site-level host diversity and disturbance status. This is of particular interest in light of increasing interest in the effects of human disturbance and host diversity on levels of parasitism and particularly on disease transmission. Multiple studies have argued that high host diversity and low levels of anthropogenic disturbance tend to lead to lower intensities and prevalence of parasitism and disease in a wide range of systems (Keesing et al., 2010; Haas et al., 2011; Lacroix et al., 2014; Venesky et al., 2014), with vector-borne diseases in rodents being one important study system (LoGiudice et al., 2003; Friggens and Beier, 2010). However, other studies have failed to find a causal relationship (Giraudoux et al., 2013; Oda et al., 2014), or they have found idiosyncratic relationships across hosts, parasites, and environmental conditions (Froeschke et al., 2013; Salkeld et al., 2013; Young et al., 2013a; Kedem et al., 2014). Here, in contrast to other studies on fleas and flea-borne disease (Thamm et al., 2009; Friggens and Beier, 2010), we find no substantial support for a general effect of either disturbance or host diversity on frequency or levels of flea parasitism. Of course, disease risk may still increase via changes in host abundance (Keesing et al., 2006; Young et al., 2014) or competence of hosts or flea species for carrying and transmitting the disease (Johnson et al., 2013), but there was no evidence for a systematic effect of host diversity or anthropogenic disturbance on intensity or prevalence of vectors on hosts in this system.

Other factors, such as rainfall and soil characteristics, had intermediate and variable effects on prevalence and intensity among populations, depending on the host species examined. The relative power of environmental and host factors in predicting patterns of flea parasitism across populations also varied widely among host species. This may be due to variation in life history or

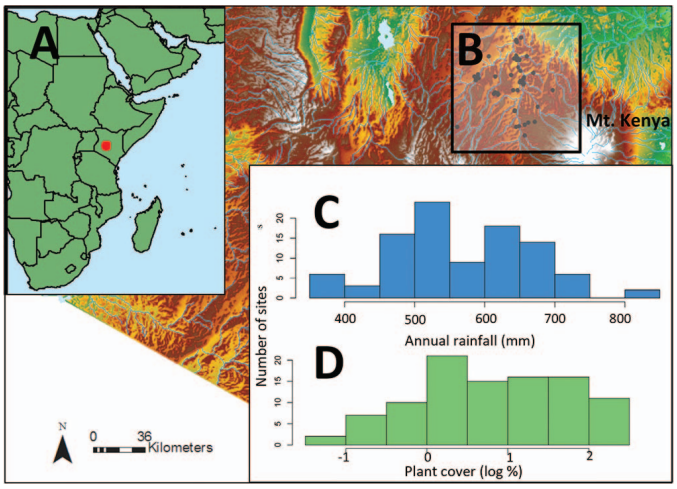

FIGURE 1. Study area in (**A**) central Kenya, including (**B**) 98 sites (dots) distributed across Laikipia and Isiolo Counties. The sites experience a wide range of (**C**) annual rainfall, which, combined with variation in human use patterns, drives strong variation in (**D**) plant cover.

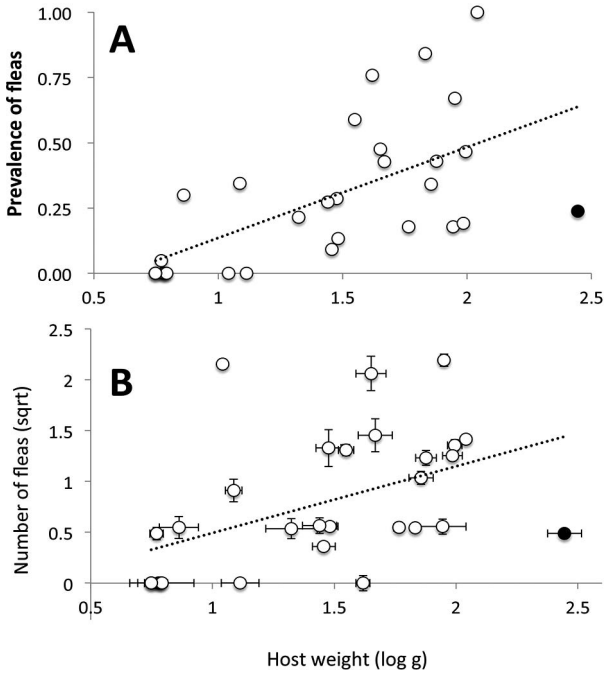

FIGURE 2. Host body mass was the most important factor in predicting (**A**) prevalence and (**B**) intensity of flea parasitism. The ground squirrel we sampled (*Xerus erythropus*) is depicted in black. Relationships are significant; full model values are provided in Table III.

physiology of hosts or differences in ecology of flea communities that typically infect these hosts. Variation in host body size (Froeschke et al., 2013; Van der Mescht et al., 2013), extent of sexual dimorphism (Morand et al., 2004; Krasnov et al., 2005), longevity (Rozsa, 1997), sociality (Hart, 1994; Loehle, 1995), and immune parameters (De Coster et al., 2010) are examples of host life-history factors that may interact with environmental factors in explaining flea parasitism at the population level among species.

Across species

Finally, we examined 2 potential drivers of variation in intensity and prevalence of flea parasitism across species in the landscape. As previously discussed, body size in particular has been suggested to be important in affecting each of these ectoparasite response metrics, both across and within species (Peters and Wassenberg, 1983; Krasnov et al., 2006). We found very strong support for the hypothesis that larger species of animals will support more total fleas and higher prevalence of fleas. However, as many life-history traits (e.g., life span) covary with body size, it is possible that other life-history factors not considered here may be the causal factor. The ground squirrel *Xerus erythropus*, however, was an interesting outlier in both diversity and prevalence analyses, as individuals had many fewer fleas than would be anticipated based on their (larger) body mass. Many life-history factors of hosts can affect flea abundance, including movement and contact patterns, structure of burrows, and density of hosts. *Xerus erythropus* typically lives alone, or in pairs, is somewhat territorial, and is known to engage in frequent grooming behavior (Herron and Waterman, 2004). These factors may explain relatively low levels of parasitism compared to other species, many of which are less territorial and live in higher densities (Jones et al., 2009). This outlier aside, the large amount of variation in flea burden explained by body mass alone was surprising. While we would certainly expect to see a relationship between body mass and flea burden, given the diverse group of species and considerable variation in life histories of the small mammals studied here (including not only rodents, but also shrews and elephant shrews), it was surprising to see body mass account for so much of variation in prevalence and intensity of infestation.

In contrast to strong support for body mass and parasitism relationships across species, we found very little support for the hypothesis that host vulnerability to disturbance is related to the prevalence or intensity of parasitism. A range of studies have suggested that "weedy" species—those tending to persist in disturbed environments—may be more highly parasitized (higher competence) than those species more sensitive to human disturbance (Keesing et al., 2010; Huang et al., 2013; Johnson et al., 2013; Joseph et al., 2013). However, other studies have failed to find such relationships (Young et al., 2013a). Here we found little to no support for a relationship between vulnerability (the inverse of "weediness") and levels of parasitism.

SYNTHESIS

Consistent with current knowledge of flea ecology and life histories, our results indicate strong effects of both host and environmental factors in controlling prevalence and intensity of flea infestation. The power of environmental and host factors to predict characteristics of total flea parasitism became increasingly strong at larger scales, with high predictive power across species, moderate predictive power across populations, and relatively low predictive power among individuals in a population. This likely reflects high stochasticity involved in flea burdens at the individual level; probably, the high level of pooling at population and species levels eliminates much of this variation. As in other studies, we find that the importance of environmental factors varies among host species, likely due to significant variation in life history among the host species and the fleas that dominate these communities. Given that many studies have found strong variation in the effect of both host and environmental factors based on the species of flea studied, it is not surprising that we detected some, but not all, effects observed in other studies in total number of fleas.

Interestingly, we found very little support for any effect of disturbance on flea parasitism. Across populations, neither the diversity of host species nor the presence of anthropogenic disturbance in a landscape impacted intensity or prevalence of flea parasitism. Similarly, across species, there was no relationship between a host's robustness to disturbance and its level of flea parasitism. This is at odds with suggestions that disturbance and diversity loss will drive general increases in prevalence of parasites (Keesing et al., 2010). However, it may well be that such relationships exist for individual flea species. Several studies have shown that the importance of dilution effects on parasites and pathogens varies, depending on the pathogen and system studied (Krasnov et al., 2007; Salkeld et al., 2013; Young et al., 2013a; Wood et al., 2014). Moreover, given that rodent community composition and abundance change systematically across disturbance gradients (Young et al., 2015), flea communities will likely change as well, as observed in other systems (Laudisoit et al., 2009). Since vector efficiency of fleas for diseases endemic in this region varies across species (Burroughs, 1947; Gage and Kosoy, 2005), there may well still be an effect of disturbance and host diversity loss on disease; however, at least in this system, it is not likely mediated by increases in total flea burdens. Further research on relative vector competence of these species of fleas will be critical in understanding and predicting patterns of disturbance on flea-borne diseases.

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