

Effects of the removal of large herbivores on fleas of small mammals

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ABSTRACT: The removal of large herbivorous mammals can cause dramatic increases in the densities of small mammals. These small mammals are hosts for a variety of ectoparasites, many of which are important pathogens of human diseases such as plague and murine typhus. It is thus valuable from a human health perspective to understand if large herbivore removals can indirectly affect ectoparasite numbers and thus potentially alter disease risk. To make this determination, we experimentally excluded large herbivores and measured the number of fleas present on the numerically dominant small mammal, the pouched mouse, *Saccostomus mearnsi*. Removing large herbivores nearly doubled *S. mearnsi* density, while the percentage of mice infested with fleas (prevalence) and the average number of fleas per sampled mouse (intensity) remained constant. The net effect of doubling the number of mice via the removal of large herbivores was a near doubling in the number of fleas present in the study habitat. Because these fleas also parasitize humans and can serve as disease vectors, this work empirically demonstrates a potential mechanism by which ecosystem alterations could affect human risk for zoonotic diseases. *Journal of Vector Ecology* 33 (2): 263-268. 2008.

Keyword Index: Siphonaptera, mammal, host density, disease, epidemiology.

INTRODUCTION

Recent experiments have demonstrated that removing large herbivorous mammals can increase the density of small mammal species (Keesing 1998, 2000, Caro 2001, 2002, Steen et al. 2005, McCauley et al. 2006, Saetnan and Skarpe 2006). However, it remains largely unknown how such increases affect ectoparasites associated with these small mammals, despite the fact this information could have important implications for disease transmission to humans living in and around areas with high densities of small mammals. Parasite infestation is a composite of two parameters: "prevalence" (the percentage of infested hosts) and "intensity" (the mean number of parasites/ individual sampled host). The relationship between prevalence and/or intensity of parasites and host density is complex. Theoretical models and empirical data illustrate that the host/parasite relationship can be positive in certain contexts (Anderson and May 1978, Dobson 1990, Arneberg et al. 1998, Krasnov et al. 2002) and negative or absent in others (Haukissalmi and Henttonen 1990, Decker et al. 2001, Stanko et al. 2002, Fichet-Calvet et al. 2003, Stanko et al. 2006). A positive relationship between numbers of hosts and parasites is typically thought to be the result of increased contact between individual hosts which facilitates the spread of parasites throughout the host population. Deviations from this trend have been explained by myriad factors including behavior, physiology, and natural history of hosts/parasites as well as the influence of local abiotic conditions (Stanko et al. 2006).

Using a large-scale, replicated experiment that excluded

large herbivorous mammals, we monitored the density of a common small mammal, the pouched mouse (*Saccostomus mearnsi*), in plots with and without large herbivores. We then determined the prevalence and intensity of fleas (Order Siphonaptera) on these hosts in response to changes in host density to test whether prevalence or intensity or both was higher in areas of higher host density.

MATERIALS AND METHODS

Study site

We conducted this research from September 2003 to October 2004 at the Mpala Research Centre (MRC) in the Laikipia District of Kenya (0°20' N, 36°53' E). The experiment was conducted within the Kenya Long-Term Exclusion Experiment (KLEE), established in 1995 (for details see Young et al. 1998). KLEE consists of three 400 X 600 m (24 ha) blocks. Each block consists of six 200 X 200 m (4 ha) treatments which excludes a particular combination of large mammals. For our experiments we used only plots that excluded all large herbivores >15kg (n = 3) and unfenced control plots (n = 3) where all animals had free access.

KLEE is located within an *Acacia drepanolobium* savanna-woodland on "black cotton" soil. Rainfall is weakly trimodal with peaks in April-May, July-August, and October-November, and a distinct dry season in January-February. There is considerable year-to-year variation in total rainfall. Total precipitation at MRC was 740 mm in 2003, and 826 mm in 2004 (T.P. Young, unpublished data).

Woody vegetation at KLEE is dominated by *A.*

drepanolobium, with trees of this species accounting for >98% of the overstory vegetation (Young et al. 1998). The herbaceous understory is dominated by five grasses and six forbs (for a more detailed description, see Young et al. 1998). Large mammalian herbivores recorded at the site include domestic cattle, Burchell's zebras (*Equus burchelli*), Grant's gazelles (*Gazella granti*), African elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), elands (*Taurotragus oryx*), Jackson's hartebeests (*Alcelaphus buselaphus jacksoni*), cape buffalos (*Syncerus caffer*), Beisa oryx (*Oryx beisa*), Grevy's zebras (*E. grevyi*), and steinbucks (*Raphicerus campestris*). Regular dung count data (Young et al. 2005) indicate both that all of these ungulates are resident in the study area (with Plains zebras being the most common), and that the large herbivore barriers are 90-100% effective in excluding the targeted species.

Small mammal sampling

The small mammal community of KLEE is dominated by the northern pouched mouse (*Saccostomus mearnsi*); six other species are also present in lower numbers (Keesing 2000). Populations of small mammals in the KLEE plots have been monitored continuously since 1995 (Keesing 1998, 2000). In conjunction with this research, we trapped plots with and without large herbivores four times: Sep. 2003, Jan. 2004, Jun. 2004, and Oct. 2004. One large folding Sherman trap was placed at each point on a permanent 10x10 grid with 10 m spacing. Trapping grids were located in the inner hectare of each 4-ha plot with and without large herbivores so that no trap was closer than 50 m to the edge of the KLEE plot. Traps were baited with a mixture of oats and peanut butter. Trapping was conducted for three consecutive nights in each plot during each session. Captured individuals were marked, weighed, and sexed (Keesing 1998). Abundances of *S. mearnsi* were calculated with the program CAPTURE (Rexstad and Burnham 1992) using the model of homogeneity of captures. We used a repeated measures ANOVA to compare densities in different treatments through time and to test for differences in mass (only males were analyzed to avoid the confounding effects of undetected female pregnancy) and sex of pouched mice.

Flea sampling

Two species of fleas were identified from *S. mearnsi* in KLEE: *Xenopsylla aequisetosa* (Enderlein 1901) and *Xenopsylla sarodes sarodes* (Jordan 1937); total rodent flea diversity in KLEE may include additional species. All *S. mearnsi* captured for the first time in any given trapping session were sampled for fleas. One technician would restrain captured mice by the nape of the neck and tail and hold them over a white plastic tub containing a small amount of ethanol. Another technician collected fleas by passing a fine-toothed metal flea comb sprayed with ethanol ten times over the right flank of the animal from the base of the neck to the base of the tail (Krasnov et al. 2003, Seery et al. 2003). Only fleas that fell into the tub and fleas lodged in the comb were counted. Mice were released unharmed after flea collection. Lethally and more comprehensively

sampling pouched mice for ectoparasites was not feasible given the context of this experiment. Patch sampling for ectoparasites has, however, been shown to accurately predict total ectoparasite loads (Mooring and McKenzie 1995). Similarly, sampling infestation of fleas on the bodies of hosts has been demonstrated to be a reliable indicator of flea population size (Krasnov et al. 2004).

We evaluated flea infestation using two metrics: *prevalence* – the percentage of *S. mearnsi* in each treatment that were infested with fleas (an infested mouse was defined as a mouse from which ≥ 1 fleas were collected during a combing); and *intensity* – the mean number of fleas combed from the *S. mearnsi* sampled in each treatment. Because both of these metrics are based on data obtained by patch sampling *S. mearnsi* for fleas, they provide an underestimate of actual prevalence and intensity values. Prevalence and mean intensity of fleas were compared between plots with and without large mammals using a repeated measure ANOVA. Values for prevalence were power transformed ($\wedge 2$) prior to analysis to maximize normality.

Statistics were computed using program R Version 2.1.1 (R Foundation for Statistical Computing, Vienna, Austria) and JMP IN 5.1.

RESULTS

Small mammal sampling

Seven species of small mammals were captured during the course of this study. The most abundant small mammal at the site, representing 75% of all captures, was the pouched mouse, *Saccostomus mearnsi*. A total of 883 *S. mearnsi* was sampled for fleas during the course of this experiment (595 in plots without large mammals, 288 in plots with large mammals). Pouched mice were almost twice as abundant in the plots without large herbivores as in plots with large herbivores (Figure 1, $F_{1,4}=15.1$, $P=0.02$). There were no significant differences between the sex ratios and mass of pouched mice between treatments.

Flea sampling

Both flea prevalence and flea intensity were similar in plots with and without large herbivores (prevalence: $F_{1,4}=0.08$, $P=0.78$; intensity: $F_{1,4}=0.11$, $P=0.75$). There was a significant effect of time on both prevalence and intensity (prevalence: $F_{3,2}=218.4$, $P<0.01$; intensity: $F_{3,2}=105.9$, $P<0.01$); values for prevalence and intensity were both lowest in June 2004.

Neither mean flea prevalence nor mean flea intensity in each replicate was significantly correlated with the mean density of *S. mearnsi* (prevalence: $R^2=0.08$, $P=0.30$; intensity: $R^2=0.06$, $P=0.31$). To generate a proxy for the actual density of fleas present in experimental treatments, we calculated the mean total number of fleas collected from *S. mearnsi* (number of infested mice X intensity; averaged across time for the three replicates of enclosure and control treatments). Plotting mean total number of fleas against mean density of *S. mearnsi* in each replicate yielded a significant positive correlation (Figure 2; $R^2=0.88$, $P<0.01$).

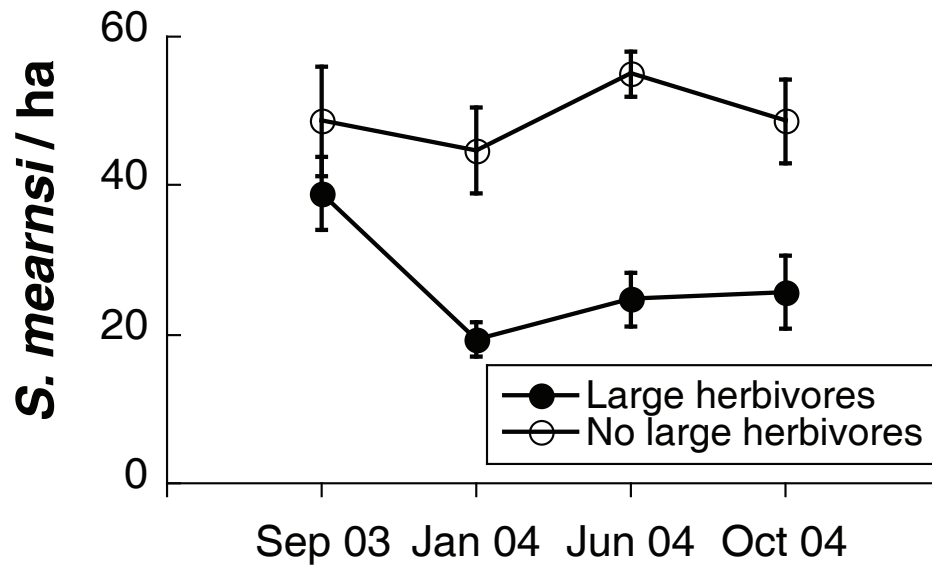


Figure 1. Mean density of the most abundant small mammal, the pouched mouse, *Saccostomus mearnsi*, in experimental plots with (solid circles) and without (open circles) large herbivores (pooled over three replicates at each time; \pm SE). *Saccostomus mearnsi* were found at significantly higher densities in plots where large herbivores had been removed ($F_{1,4}=15.1$, $P=0.02$).

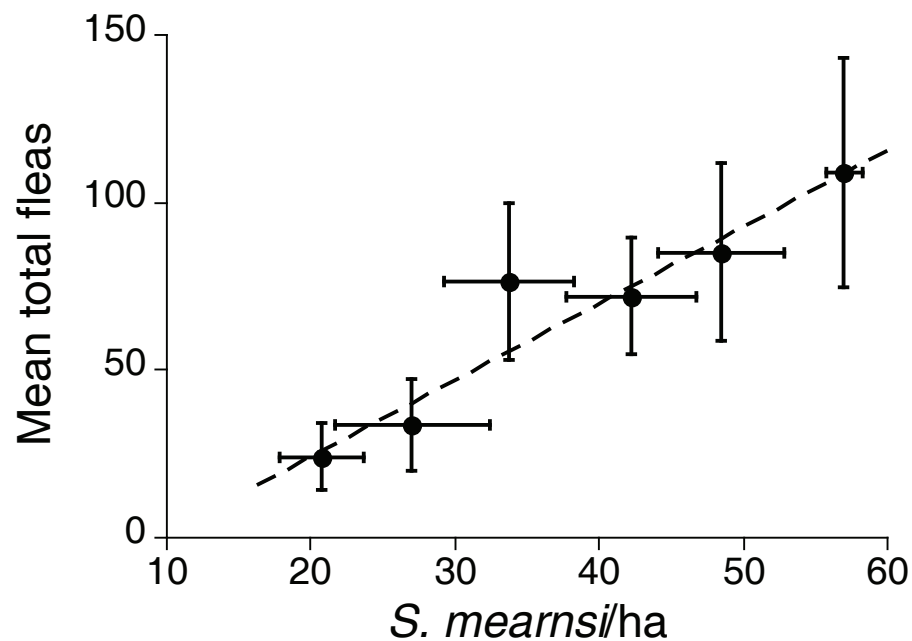


Figure 2. Relationship between the mean total number of fleas collected from the mouse *Saccostomus mearnsi* in each plot and the density of *Saccostomus mearnsi* (pooled across four sampling sessions; $R^2 = 0.88$, $P < 0.01$; \pm SE).

DISCUSSION

There were no significant differences between either prevalence or intensity of fleas on *S. mearnsi* between plots with and without large herbivores, despite the fact that pouched mice were nearly twice as dense in plots without large herbivores (Figure 1). These findings parallel results from other research that found no relationship between small mammal density and flea prevalence and intensity (Stanko et al. 2002, Stanko et al. 2006). A variety of mechanisms have been offered to explain how host density and parasite intensity and prevalence may become decoupled. These include characteristics of the host, such as host grooming behavior, age structure, sex ratios, sociality, immune response, and burrowing behavior (Hart 1994, Levin and Fish 1998, Soliman et al. 2001, Krasnov et al. 2002, Stanko et al. 2002, Fichet-Calvert et al. 2003, Whiteman and Parker 2004, Krasnov et al. 2006); characteristics of the parasite, including transmissibility, life history, and exposure to intra/inter-specific competition (Day and Benton 1980, Krasnov et al. 2005, Stanko et al. 2006); as well as differential rates of host/parasite reproductive capacity, parasite-induced host mortality, and the influence of microhabitat and climate/seasonality (Haukisalmi and Henttonen 1990, Oguge et al. 1997, Krasnov et al. 1997, Krasnov et al. 2001, Fichet-Calvert et al. 2003, Stanko et al. 2006). Not enough is yet known about the ecology of the relationship between *S. mearnsi* and its flea ectoparasites to determine what combination of these or other mechanisms may have produced the results we observed. Because fleas rarely use ungulate hosts (Wall and Shearer 1977), we do not believe that the removal of large herbivores contributed directly to producing the trends we observed for small mammal fleas.

There was an interesting effect of seasonality on both metrics of flea abundance. Prevalence and intensity of flea infection were each at their lowest during sampling in June 2004, the period immediately following the prolonged rainy season in KLEE. Other work in East Africa has demonstrated a strong effect of seasonality on the success of fleas in the genus *Xenopsylla* (Traub 1972, Schwan 1986, Makundi and Kilonzo 1994). Differences in temperature, rainfall, and humidity were cited as causes of the seasonality observed in these studies, although the nature and degree of seasonal response differed between *Xenopsylla* species and varied by study location.

Because prevalence and intensity of fleas on *S. mearnsi* did not differ between treatments, the net effect of the removal of large herbivores was an increase in the total number of fleas in enclosure plots. This increase was driven simply by increases in rodent density. Increases in rodent host and flea density have previously been linked to human disease outbreaks primarily because of increased opportunity for fleas to switch from rodent to human hosts (Shepherd et al. 1983, Parmenter et al. 1999, Keeling and Gilligan 2000a, 2000b, Ensore et al. 2002, Duplantier et al. 2005). The relationships between host, vector, and pathogen in zoonotic disease ecology are highly complex and in most cases still poorly understood. However, based on the results from

this experiment, we suggest that natural (e.g., drought) and anthropogenic (e.g., hunting) reductions in large mammals might facilitate outbreaks of rodent-borne diseases. Future work can test this hypothesis by sampling in hotspots for rodent diseases, by testing how flea communities respond immediately following a large herbivore extirpation event, and by replicating these experiments in systems where the rodent species/flea assemblages more classically implicated in disease spread are dominant.

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