ORIGINAL ARTICLE

Impacts of large mammals on movements of the pouched mouse (*Saccostomus mearnsi*) in central Kenya

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Abstract

Populations of large wild mammals are declining worldwide, while the abundance of livestock is increasing. The absence of large mammals frequently leads to increases in the abundance of small mammals such as rodents, but little is known about how the loss of large mammals affects the behaviour of small mammals. To investigate this question, we analysed long-term data collected at the Kenya Long-term Exclosure Experiment, which excludes different combinations of large mammals from a savannah ecosystem in central Kenya. We investigated the effects of excluding large mammals, both wild and domestic, on the movements of the pouched mouse (*Saccostomus mearnsi*), the most common species of small mammal in this habitat. Mice moved ~20% more in the presence of wildlife, but their movements were not significantly affected by the presence of cattle. An index of intraspecific contacts between mice was higher at higher mouse densities, and these high densities were more likely when wildlife and cattle were absent. The results suggest that the absence of large mammals led to higher densities of small mammals, which resulted in a greater probability of intraspecific contacts, despite lower average movement distances.

Abstrait

Les populations de grands mammifères sauvages déclinent partout dans le monde alors que la quantité de bétail est en augmentation. L'absence de grands mammifères entraîne souvent l'augmentation du nombre de petits mammifères tels que les rongeurs mais on connaît mal la façon dont la perte des grands mammifères affecte le comportement des petits. Pour étudier cette question, nous avons analysé les données récoltées depuis longtemps à la *Kenya Long-term Exclosure Experiment*, qui exclut différentes combinaisons de grands mammifères d'un écosystème de savane au centre du Kenya. Nous avons étudié les effets de l'exclusion de grands mammifères, tant sauvages que domestiques, sur les déplacements du « rat à poche » africain *Saccostomus mearnsi*, le petit mammifère le plus fréquent dans cet habitat. Cette espèce se déplaçait environ 20% de plus en présence d'animaux sauvages mais ses mouvements n'étaient pas significativement affectés par la présence de bétail. Un indice de contacts intra-spécifiques entre rats était plus élevé quand leur densité était plus grande, et une grande densité était plus probable lorsque grands animaux sauvages et domestiques étaient absents. Ces résultats suggèrent que l'absence de grands mammifères conduit à de plus grandes densités de petits

mammifères, qui entraînent une plus grande probabilité de contacts intra-spécifiques malgré des déplacements plus courts.

1 | INTRODUCTION

In Kenya, the abundance of large mammals has decreased by approximately 68% since 1977 (Ogutu et al., 2016). Ungulates that historically have been common, such as Thompson's gazelle (*Eudorcas thomsonii*), impala (*Aepyceros melampus*) and waterbuck (*Kobus ellipsiprymnus*), have suffered particularly large declines, with their populations plummeting by 72% or more (Ogutu et al., 2016). In contrast, livestock in Kenya have increased in number during the same time period, with a current biomass that is now more than eight times greater than the biomass of large wild mammals (Ogutu et al., 2016). These trends show no signs of abating, raising questions about what the consequences of declines in the abundance of Kenya's wildlife—and increases in the abundance of Kenya's livestock—will be.

The consequences of the decline in abundance of large wild mammals have been investigated in a large-scale, long-term experiment in Laikipia County in central Kenya. Established in 1995, the Kenya Long-term Exclosure Experiment (KLEE) was created to examine relationships between livestock and wildlife, particularly whether the two groups competed for resources (Young, Okello, Kinyua, & Palmer, 1998). Just a few months after the installation of the experimental plots, which exclude different combinations of large wildlife and livestock, the abundance of small mammals had increased dramatically on the plots from which all large mammals were excluded (Keesing, 1998b). The most common small mammal, the pouched mouse (*Saccostomus mearnsi*), had doubled in abundance, an increase that was sustained for more than a decade of monitoring (Keesing & Young, 2014; Keesing, 1998b).

These increases in mouse abundance ramify through the ecosystem. One key predator of the pouched mouse is the olive whip snake (*Psammophis mossambicus*). This snake, which is mildly venomous to humans, was twice as abundant in the absence of large mammals, correlated with the density of pouched mice (McCauley, Keesing, Young, Allan, & Pringle, 2006). Plots without large mammals had higher densities of mice and also higher densities of mouse-associated fleas (McCauley, Keesing, Young, & Dittmar, 2008). Fleas are common vectors for pathogens and could have negative effects on people living in areas with high densities of mice as the result of the absence of large mammals.

Pouched mice themselves could play a role in pathogen transmission. Over 10% of all rodents worldwide host at least one pathogen shared with humans, a so-called zoonotic pathogen (Han, Kramer, & Drake, 2016). Whether pouched mice are reservoirs for zoonotic pathogens is not clear. Indeed, even basic natural history information

on these mice is sparse, despite the fact that the geographic range of the species covers much of eastern Africa and that it is the most abundant small mammal in other habitats (Mikula et al., 2016). Further, almost nothing is known about its behaviour, particularly whether its behaviour changes as a result of declines in the abundance of large mammals (but see Keesing & Crawford, 2001). Impacts of large mammals on mouse behaviour could have effects on how mice interact with their predators, prey, and parasites.

We took advantage of a long-term data set of pouched mice on the KLEE plots to evaluate how large mammals affected the movement of pouched mice. We hypothesized that the absence of large mammals, wild or domestic, would affect the distances moved by pouched mice and the probabilities of intraspecific contacts among mice. By comparing movements of mice on plots with and without large wild mammals and with and without cattle, we were able to evaluate the effects of large mammalian herbivores both separately and together.

2 | METHODS

2.1 | Data collection

The fieldwork for this research was conducted within the Kenya Long-Term Exclosure Experiment (KLEE) at the Mpala Research Centre (0°17′N, 36°53′E) in Laikipia County of central Kenya. The KLEE habitat is characterized as a wooded grassland. Common large herbivores include elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), buffalo (*Syncerus caffer*), Grevy's zebra (*Equus grevyi*), common zebra (*E. quagga burchelli*) and domestic cattle (*Bos taurus*). Common predators include lion (*Panthera leo*), leopard (*P. pardus*) spotted hyaena (*Crocuta crocuta*) and black-backed jackal (*Canis mesomelas*). The pouched mouse, *Saccostomus mearnsi*, comprises 85% of the captures of small mammals (Keesing, 2000). Other small mammals include *Mus* spp., *Tatera robusta*, *Dendromus melanotis*, *Arvicanthis niloticus*, and *Crocidura* spp. The most common tree is *Acacia drepanolobium* Harms ex Y.Sjöstedt, which thrives on the heavy clay soil. The understory vegetation is dominated by five grasses—*Themeda triandra* Forssk., *Pennisetum stramineum* Peter, *P. mezianum* Leeke, *Lintonia nutans* Stapf and *Brachiaria lachnantha* (Hochst.) Stapf—and a variety of forbs including *Aspilia pluriseta*, *Solanum indicum*, *Monechma debile* and several *Commelina* spp. (Porensky, Wittman, Riginos, & Young, 2013). Rains are highly seasonal, usually occurring from about April or May to November, with a dry season in January–March.

The Kenya Long-term Exclosure Experiment consists of three blocks, each of which contains six treatments that exclude different combinations of large mammals (Figure 1). Wildlife presence is managed using two types of fencing. A high wire fence, with one electrified and one ground wire 2.4 m above the ground, excludes megaherbivores (giraffes and elephants) while allowing access by smaller animals. An 11-wire fence, 2.4 m tall, with every other strand electrified, excludes megaherbivores and also smaller mammals such as buffaloes and zebras. The duration and location of cattle grazing on specific treatments was managed by herders, who continually accompany cattle in this region.

Each of the 18 plots measures 200 × 200 m (4 ha). We focused our trapping on the three replicates of each of four treatments— those with and without all large wild mammals, and those with and without cattle (Figure 1). Within the inner hectare of each of the treatment plots, we placed one Sherman folding trap (~9 × 8 × 23 cm) on each point of a 10 × 10 grid with 10-m spacing (100 trapping stations per plot). This placement ensured that there were at least 50 m from a trap to the nearest plot (treatment) edge
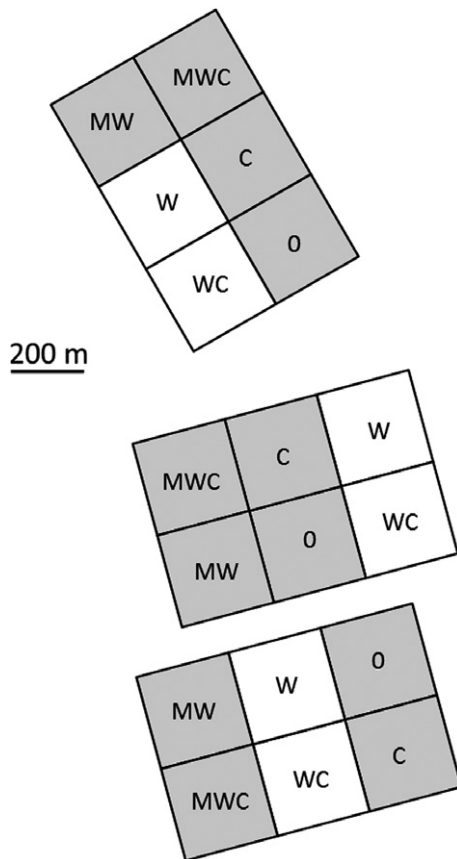
FIGURE 1 Diagram of the Kenya Long-term Exclusion Experiment (KLEE) in Laikipia County, Kenya. Animals were live-trapped in the treatments shaded with grey that allowed all wildlife (MW), cattle (C), neither (0), or both (MWC). Codes for the treatments are as follows: M = megaherbivores (giraffes, elephants) allowed; C = cattle allowed; W = other large wild mammals allowed; 0 = no large mammals allowed. There are three blocks, so that there are three replicates of each treatment. See Young et al. (1998) for further details of the KLEE design

and 100 m from the next nearest trapping grid. Traps were set in the evening, baited with a mixture of peanut butter and oatmeal, and checked before 10h00 the following morning for three consecutive days on each treatment. We identified all animals to species and recorded their sex, reproductive condition, weight and location of capture before releasing them at the point of capture. Upon first capture, we marked animals for individual identification.

For this study, we used data on captures of pouched mice from trapping sessions that took place approximately every 3 months from September 1999 to June 2006. In 1999–2001, there was an extended drought that reduced mouse density dramatically. On some trapping grids during this period, we captured too few mice to analyse movement; trapping grids with too few animals (<2) captured more than once were excluded from analysis.

2.2 | Data analysis

We performed all statistical analyses in R (R Core Team, 2017). To determine the movement distances of pouched mice captured during each of the trapping sessions, we determined the maximum distance travelled by each multiply trapped animal over each three-day trapping session, using Program CAPTURE (Rexstad & Burnham, 1991). An individual animal could be captured 0, 1, 2 or 3 times during any particular three-day trapping session. For our analyses, we included only individuals that were captured more than once in a trapping session because we could not calculate movement distance on the basis of fewer captures. We also excluded juveniles (weight <39 g; Keesing, 1998a). With the remaining animals in our sample, we calculated the mean of the maximum distances travelled by males and by females on each grid during each trapping session; we thus had two measures of mean distance travelled for each trapping session: one for females and one for males.

Because some trapping sessions had means for distance travelled that were zero, we first used binomial regression to ask whether density significantly affected the probability of a zero value for mean distance travelled. Next, we analysed the nonzero values using generalized additive mixed models, with trapping grid as a random effect, using function *gam* in package *mgcv* (Wood, 2011). Because the nonzero data on mean distance travelled did not meet assumptions of linear regression, we transformed these data using the formula $\ln(x + 1)$. Before including potential independent variables in our models, we assessed their possible collinearity using function *corvif* (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The variance inflation factors for all variables were <2, suggesting that collinearity among predictors was not a problem. With the transformed data, we compared a series of alternative, competing models using a likelihood ratio test (function *lrtest* in package *lmtest*). The models contained all versus only some of the predictor variables—wildlife (presence/absence), cattle (presence/absence), density of mice and sex (male/female) of mice—for each trapping session. For our analyses, we considered four of the six KLEE treatments: with and without all large mammals, and with and without cattle (treatments MW, MWC, 0, and C in Figure 1).

2.2.1 | Mouse density

We tested the hypothesis that wildlife (presence/absence) and cattle (presence/absence) affected mouse density using a generalized linear model (glm). First, to determine the appropriate distribution for our count data, we modelled abundance with the negative binomial glm (function *glm.nb*) from the MASS package (Venables & Ripley, 2002). We then compared the fit of a negative binomial model to the fit of a Poisson model using function *odTest* from package *pscl* (Jackman, 2015). The most appropriate model, based on an analysis of dispersion of the data, was then used to evaluate our hypothesis.

2.2.2 | Frequency of intraspecific contacts

To estimate the number of intraspecific contacts on each grid at each trapping session, we created a co-occurrence index by calculating the number of times two or more mice were captured at the same trap location during the same three-day trapping session. We then counted the number of trap stations for each grid and each trapping session at which there was at least one such co-occurrence. This frequency could vary from 0 (no such captures) to 100 (captures of conspecifics at every trap on a grid during a single three-day trapping session).

Because many of the grids had no co-occurrences for particular trapping sessions, there were frequent zero values in our data. Our data were also overdispersed, meaning that the variance of the frequencies was greater than the mean. To analyse these data, we evaluated the fit of zero-inflated negative binomial regression models. These analyses have two components: one that tests a model of the count data and one that tests a model of the zero-inflated data. We first conducted an analysis with mouse density as an estimator of both the count model and the zero-inflation model using the *zeroinfl* function in the *pscl* package in R. We compared this to a model with wildlife (presence/absence) and cattle (presence/absence) as predictors of the count model and density as a predictor of the zero-inflated model. We also built a standard negative binomial model that used density as a predictor of the count model without a separate model for zero inflation. We evaluated the fit of the two strongest of these models using a *vuong* test from package *pscl* (Jackman, 2015).

We created figures with the package *ggplot2* for R (Wickham, 2009), supplemented by the *cowplot* package (Wilke, 2017). We used packages *reshape2* (Wickham, 2007), *tidyr* (Wickham, 2017) and *plyr* (Wickham, 2011) for data manipulation.

3 | RESULTS

We analysed data from 6,109 captures of 3,567 individual pouched mice trapped during 23 three-day sessions over a period of 81 months. Seventy per cent of the 6,109 captures (*n* = 4,283) were from individuals that were trapped more than once in the same trapping session and 36% (*n* = 2,218) were from individuals captured three times during the same trapping session. The average pouched mouse moved 16.6 ± 2.2 m (mean ± *SE*) between captures during the same trapping session. Co-occurrences between two or more individuals at a single trapping station were not uncommon, occurring an average of 1.84 ± 0.14 times per grid during each trapping session, with a range from 0 to 14. Densities of pouched mice for the trapping sessions ranged from occasional lows of 0 mice/ha during the extended drought from 1999 to 2001, to a high of 65 mice/ha in September of 2003, with a mean density of 22.8 ± 0.8 mice/ha across all trapping sessions.

Based on binomial regression, the density of mice on the plots was a significant positive predictor of whether the mean maximum distance travelled on the plots was greater than zero ($p < 0.01$). For the nonzero values, we built a series of models that incorporated potential factors to explain the mean maximum distance travelled by mice in each trapping session. We evaluated these models using a likelihood ratio test. The model incorporating an interaction between the sex of the animals (female/male) and the overall density of mice on each plot, as well as the presence versus absence of wildlife, was a significantly better fit to the data than the other models (chi-square = 3.88, $p \ll 0.01$), and it explained 18% of the variation in the mean maximum distance travelled. The average male mouse moved 34% farther than the average female (males: 18.5 ± 0.3 m; females: 13.8 ± 0.3 m; Figure 2a). Overall, males showed a stronger reduction in distance travelled than females did as density of mice on the grids increased (Figure 2b). The presence of wildlife increased the mean distance moved by mice by 20%, from a mean of 16.3 ± 0.5 m on plots with no large wildlife to a mean of 19.9 ± 0.8 m on plots with large wildlife (Figure 2a).
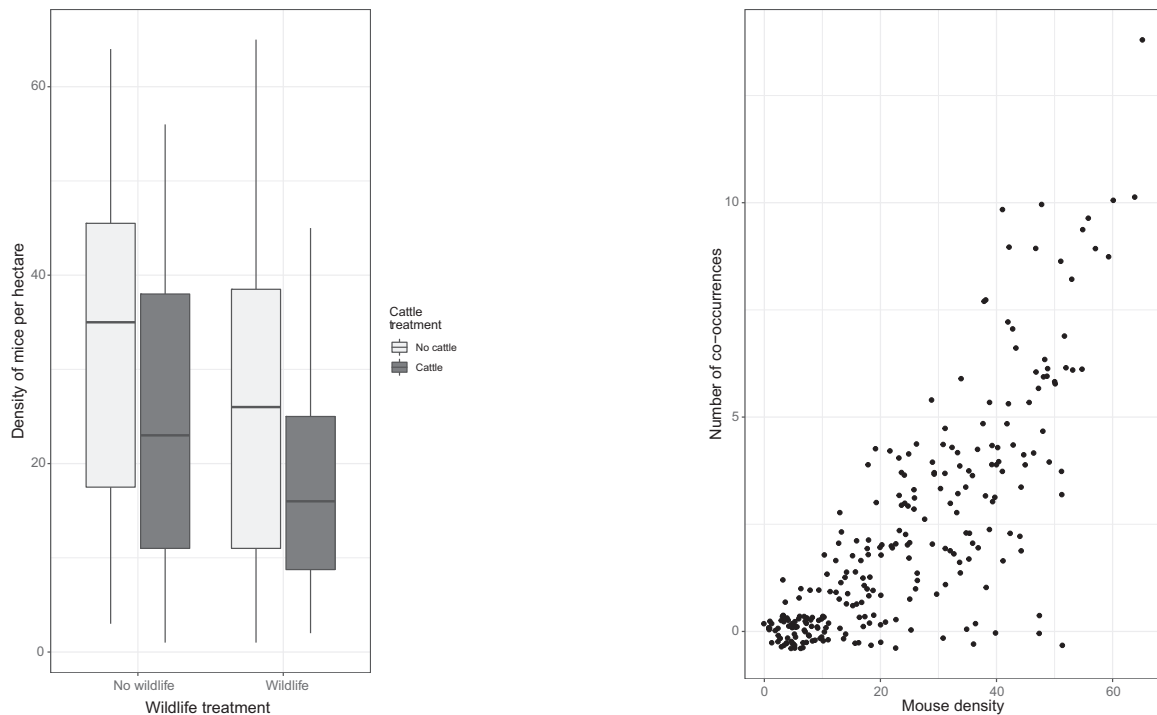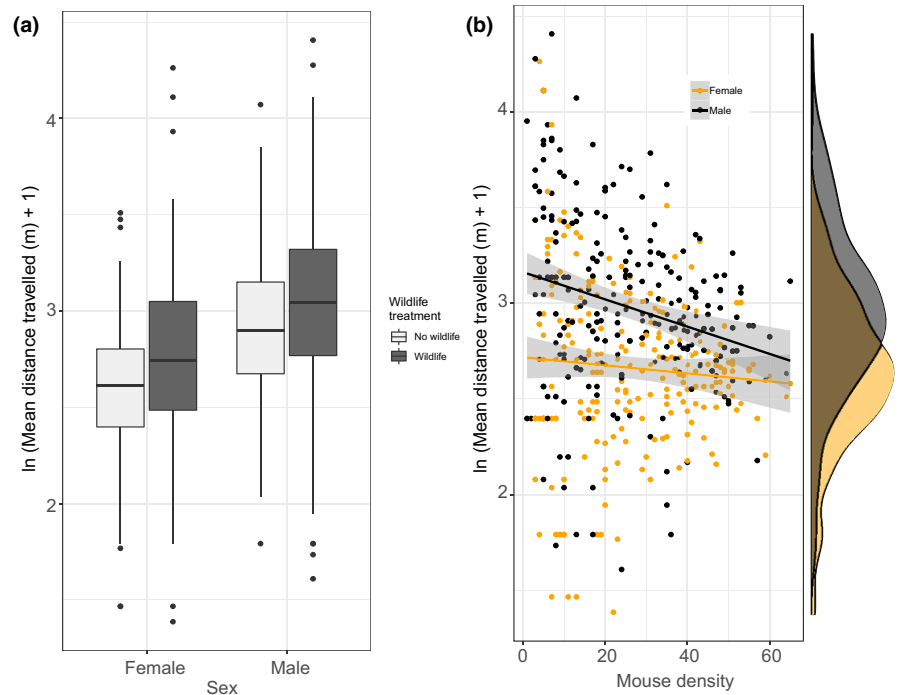
Across the 21 trapping sessions, the density of mice was almost 30% lower in the presence of either wildlife or cattle (negative binomial GLM; wildlife: $p \ll 0.01$; cattle: $p \ll 0.001$; Figure 3). On plots with both wildlife and cattle, mouse densities were approximately half what they were on plots with neither (Figure 3).

In evaluating potential factors affecting the frequency of intraspecific co-occurrence on each trapping grid, we found that the number of co-occurrences increased as mouse density increased (Figure 4). The model with the most support was a zero-inflated negative binomial glm with density explaining both the zero-inflated and the count data (Table 1; Figure 4). Based on a vuong test, this model was a significantly better fit for the data than a negative binomial model that did not incorporate a separate term to account for the frequency of zeros in the data (Vuong z-statistic = 3.55; $p \ll 0.01$).

4 | DISCUSSION

The average maximum distance moved by pouched mice was best explained by a model that incorporated the sex of the animal, the density of mice on the trapping grid and whether or not wildlife were allowed on the grid. Incorporating an interaction between sex and density improved the fit of the model, apparently because movements by males were more sensitive to changes in mouse density than movements by females were (Figure 2b).

FIGURE 2 (a) The natural log of the mean of the maximum distance travelled (m) + 1 by pouched mice (*Saccostomus mearnsi*) in Laikipia County, Kenya, across 21 trapping sessions on 12 treatment plots in the absence (*No wildlife*) versus the presence (*Wildlife*) of large wild mammals. Circles indicate statistical outliers. (b) Natural log of the mean maximum distance travelled (m) + 1 by females (orange circles) and males (black circles) as a function of total mouse density on each of the 12 trapping grids for each of the 21 trapping sessions. Density distributions of the ln (mean maximum distance travelled (m) + 1) by females (orange) and males (black) are shown at right.

FIGURE 3 Density of pouched mice (*Saccostomus mearnsi*) per hectare in Laikipia County, Kenya, on treatments with and without wildlife and with and without cattle, for the 12 treatment plots sampled at each of the 21 trapping sessions. Results of negative binomial generalized linear model; wildlife: $p \ll 0.01$, cattle: $p \ll 0.01$

FIGURE 4 Number of intraspecific co-occurrences (number of times two or more mice were captured at the same trap location on each trapping grid for each trapping session) as a function of total mouse density on the grid. Data points are jiggered vertically to allow visualization of the sample size

The number of potential intraspecific contacts—as measured by co-occurrences at the same trap station during a trapping session—was best predicted by overall mouse density, which positively

affected both the probability of having such co-occurrences and the number of co-occurrence events (Figure 3). We interpret this to mean that when mouse densities were below a certain value, co-occurrences were too rare to be detected with our methods. Above

TABLE 1 Model comparison statistics for independent variables potentially influencing the number of intraspecific co-occurrences of pouched mice (_Saccostomus mearnsi_) during each trapping session. "Means model" is the model based only on the intercept of the regression. Candidate models include a negative binomial model for frequency of co-occurrence, with or without a zero-inflated model for trapping sessions in which no co-occurrences were recorded. The model with the most support (lowest AIC value) is in bold; this model was a significantly better fit to the data than were the other models (see Section 2 for details)

Count model	Zero-inflated model	df	logLik	AICc	Delta
Density	**Density**	**5**	**−367.9**	**745.88**	**0.00**
Density	-	4	−391.8	789.53	43.65
Wildlife + cattle	Density	6	−427.1	866.20	120.32
Wildlife	Density	5	−430.1	870.22	124.34
Means model	-	5	−514.5	1,034.91	289.03

that threshold, co-occurrences became more common as density increased. Mouse densities were significantly reduced by the presence of large mammals, with cattle and large wild mammals having equally strong impacts. Taken together, our results suggest that the absence of large mammals leads to higher densities of small mammals, which results in a greater probability of potential contacts among conspecifics, despite lower average movement distances for each individual.

To answer our question about what affected mouse movements, we used a long-term data set that included over 6,000 captures of animals approximately every 3 months over a 7-year period during which mouse density varied dramatically. Previous studies have also used short-term (2–5 night) trapping data to make comparisons about relative movements of small mammals (Dickman, Greenville, Beh, Tamayo, & Wardle, 2010; Keesing & Crawford, 2001; Ostfeld, Lidicker, & Heske, 1985). Despite the size of our data set, however, for any given trapping session, we had a maximum of three captures per individual at traps spaced 10 m apart. This limited our ability to draw fine-scaled conclusions about movements of individual animals. Our approach relied on relatively coarse data for a large sample of individuals over a long period. An alternative would have been to conduct more intensive sampling of the movements of fewer individuals over a shorter period of time. A useful future study could utilize radiotelemetry to test the patterns generated by our analysis at a finer scale, which would be likely to reveal more details about the underlying mechanisms as well.

Our results suggested that the presence of large wild mammals directly affected movements of mice (Figure 2), but that the presence of cattle had little effect. In addition, both cattle and wildlife influenced mice indirectly by affecting the density of mice (Figure 3), which was an important predictor of mouse movements. We suspect that cattle did not strongly affect mouse movements because cattle are only brought onto the plots five to eight times per year, for only a few hours at a time and during daytime when pouched mice are

not active. In contrast, wildlife are present on the plots year-round and are active both during the day and at night when mice are foraging. Together, these direct and indirect impacts suggest to us that cattle and wildlife affect mouse density indirectly through their impacts on vegetation, which affects both food and cover for the mice. However, the presence of wildlife on the plots, year-round and at night when mice are active, affects the movement behaviours of the mice directly as well.

The effect of large mammals on the movements of pouched mice contradicts the results of an earlier study from the same system (Keesing & Crawford, 2001), which was based on data collected from KLEE during the first few years after the plots were established. Keesing and Crawford (2001) found that the activity of pouched mice was clumped at low density but more uniform at high density, suggesting that the animals spread out to fill in interstitial areas at high densities rather than grouping into high-density aggregations. They also found no direct effect of large mammals on the spatial distribution of the mice, though as in our study, there was an effect of large mammals indirectly through their effects on density. In our more extensive analysis, wildlife appear to have a direct effect on mouse movements. Both male and female mice moved about 20% farther, on average, on plots with wildlife compared to plots without. One possible explanation for this is that in the presence of wildlife, the mice maintain their burrows in microsites less likely to be damaged by large animals, such as the bases of thorny shrubs and trees. From these relatively safe burrows, the mice might then move longer distances for foraging. In contrast, in areas without large mammals, the mice might be able to establish burrows in more open areas and thus be able to move shorter distances for foraging, a pattern of burrow placement that we have observed in the field.

The absence of large grazing mammals is now known to increase the abundance of small mammals in habitats around the world (Foster, Barton, & Lindenmayer, 2014; Keesing, 1998b; Parsons, Maron, & Martin, 2013; Shelton, Henning, Schultz, & Clay, 2014; Torre et al., 2007). What is less well-documented, however, is the influence of large mammals on the behaviour of small mammals. Recently, Galetti, Bovendorp, and Guevara (2015) found that, in a tropical rain-forest ecosystem, the diets of small mammals changed when larger mammals were excluded, with small mammals eating a diet more similar to that of forest hogs after the hogs were removed. Studies have also shown that the distribution of small mammals within a habitat can be influenced by the presence of large mammals, a pattern that has been documented in both savannah and Mediterranean ecosystems (Keesing & Crawford, 2001; Muñoz, Bonal, & Díaz, 2009). However, we know of no other studies that have investigated how patterns of movement and spatial co-occurrence by small mammals are affected by the presence of large mammals.

Our re-analysis of the KLEE data on mouse density uses a new statistical approach but reaches the same basic conclusion as prior research—that large mammals reduce the abundance of small mammals and that the effects of wildlife and cattle are additive (Keesing & Young, 2014). Our analysis also suggests that small mammals are

more likely to have contacts with conspecifics when large mammals are absent because the high densities they achieve under these conditions increase the probability of contacts (Figure 4). Whether pouched mice are reservoirs for zoonotic pathogens is not known. If they are, increases in intraspecific contacts could directly affect human health by facilitating transmission in the reservoir population. Given global declines in the abundance of ungulates, and the now common finding that small mammals are likely to increase when large mammals decline, the patterns we observed in this study could be more widespread. Future work should investigate whether pathogen transmission among small mammals is more common when large mammals are absent.

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