Cascading Consequences of the Loss of Large Mammals in an African Savanna

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*African savannas are home to an abundant and diverse assemblage of wild herbivores, but the very grasses that sustain these wild herds also make savannas attractive to humans and their livestock. We used the Kenya Long-term Exclosure Experiment to investigate the ecological effects of different combinations of native and domestic grazers. The experimental removal of large grazing mammals set into motion a cascade of consequences, beginning with the doubling in abundance of a small grazing mammal, the pouched mouse (*Saccostomus mearnsi*). The presence of abundant mice attracted venomous snakes such as the olive hissing snake (*Psammophis mossambicus*); devastated seedlings of the dominant tree (*Acacia drepanolobium*); and doubled the abundance of fleas, which potentially increased the risk of transmission of flea-borne pathogens. Together, these results show the potential for the loss of large mammals to have cryptic consequences for African savannas, with important and often undesirable repercussions for humans.*

Keywords: conservation, ecology, land-use management, plant–animal interactions, tropical ecosystems

The savannas of Africa are renowned for their spectacular wildlife. Vast herds of large grazing mammals, such as zebras and buffalos, and their predators, such as lions and leopards, roam through grasslands that are among the most productive on Earth. But, in recent decades, wildlife populations have declined dramatically both inside and outside of protected areas (Western et al. 2009, Georgiadis 2011). In Kenya, for example, large grazing mammals are at one-third of what their abundance was in the 1970s (Ogutu et al. 2011). Part of the reason for these declines is that the very productivity that harbors such a diversity and abundance of wildlife has made these lands desirable places for people to live and raise their own grazing animals. As human populations increase in savanna habitats, the needs of wildlife are increasingly in conflict with the needs of people and the cattle, sheep, and goats that they tend.

To many who live on African savannas, wildlife is a threat. Zebras (*Equus quagga*), for example, have been thought to compete with cattle (*Bos taurus*), and lions (*Panthera leo*) and leopards (*Panthera pardus*) kill livestock and, occasionally, people (Woodroffe et al. 2005, Reid 2012). Elephants (*Loxodonta africana*), too, can harm human interests by raiding crops and even killing people and their animals (Gadd 2005, Woodroffe et al. 2005). For others, wildlife is a source of income from tourism (Woodroffe et al. 2005, Reid 2012), and wildlife tourists prefer more abundant and diverse fauna (Fredline and Faulkner 2001).

In most studies in which conflicts between humans and African wildlife have been investigated, wildlife communities have been compared in areas that differ in land use (e.g., intensity of grazing or human population density) or protection status (e.g., inside versus outside parks; Gadd 2005, Western et al. 2009, Ogutu et al. 2011, Kiffner et al. 2013). Although these comparative studies have contributed enormously to our understanding of human–wildlife dynamics in African savannas, they are often limited by the quality of their controls and by limited replication. Using a different approach, a large-scale experiment has been under way for over 15 years in the Laikipia District of central Kenya, an area with both abundant wildlife and plentiful livestock. Its purpose is to understand how humans and their cattle interact with large wild mammals and to explore the consequences of those interactions using a replicated, factorial experimental design. The experiment, called the Kenya Long-term Exclosure Experiment (KLEE) is set on the Laikipia plateau at the Mpala Research Centre.

In this area, cattle are closely supervised by herders by day and enclosed inside thorn-walled compounds at night to protect them from predators. Sharing the landscape is a full complement of native savanna wildlife, including giraffes, elephants, antelopes, zebras, and lions. But the savanna habitats also harbor less-charismatic species such as mice, snakes, ticks, and fleas. One of the surprises of KLEE has been the degree to which these lesser-known animals interact with

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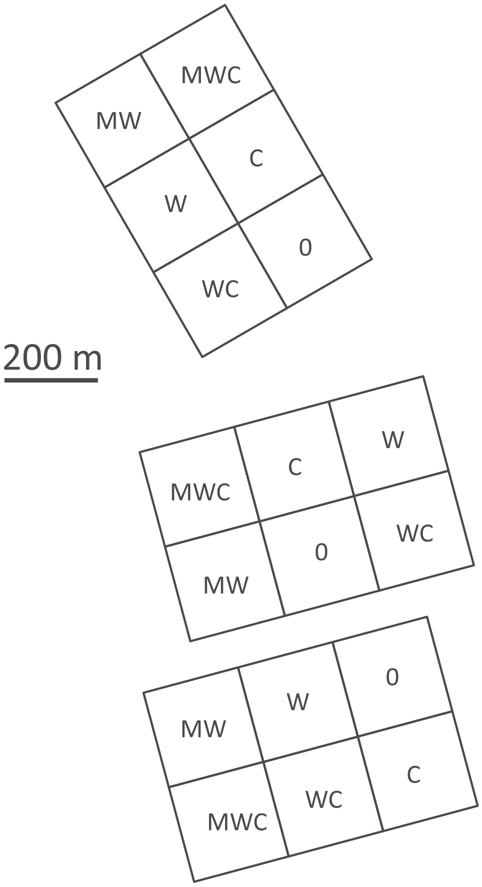

Figure 1. The layout of the Kenya Long-term Exclosure Experiment (KLEE). Each of the three blocks contains six treatments, each of which allows a particular combination of large mammals. There are three replicates of each of the treatments, and each treatment area is 4 hectares, with 200 meters (m) on each side. Details about the treatments are provided in the text. Abbreviations: C, cattle; M, megaherbivores; W, other wild mammals; 0, no large mammals.

their larger counterparts, with potentially crucial consequences for humans and their livestock.

The Kenya Long-term Exclosure Experiment

KLEE was established in 1995 with an extensive system of wire fences (Young et al. 2005). This part of the Laikipia plateau is a large flat lava flow 1800 meters (m) above sea level where poor drainage has resulted in the generation of soils with a high clay content. Their odd appearance and structure have led these to be called *black cotton* soils. These soils, common throughout eastern and southern Africa, support a dense grassland interspersed, in Laikipia, with a single species of tree: the whistling thorn tree (*Acacia drepanolobium*). Rainfall follows a weakly trimodal seasonal pattern, with a pronounced dry season in January–March and averages of 550–600 millimeters per year, although this is highly variable across years.

KLEE is equipped with two types of fences (figure 1) to keep out different combinations of large mammals. The first consists of 11 strands of wire, with every other strand electrified at 3000–7000 volts. These fences effectively keep out all the large mammals, including the biggest ones—giraffes and elephants, which are collectively called *megaherbivores*. The second type of fencing keeps out only the megaherbivores while allowing all of the smaller species to enter. This is accomplished with two high, horizontal strands of wire, along which electrified wires hang down to a height of 2 m above the ground.

Because we were interested in how cattle interact with wildlife, we took advantage of the fact that the Mpala Research Centre is encompassed by a ranch that harbors 2000–2800 head of cattle. Herders move the cattle through the landscape, giving them access to grass and water while also protecting them from predators. For KLEE, we taught the herders which treatment plots cattle could access and which they could not, and we coordinated grazing frequency and intensity on those plots so that they mimic the patterns of the surrounding ranch. On average, a herd of approximately 120 cattle is herded into each treatment area four to eight times each year for 2 hours each time.

Combining the closely monitored grazing of cattle with the two types of fences, we were able to establish six types of experimental plots (figure 1), each of which excludes a particular combination of large mammals. There are three levels of wildlife treatment—no wildlife, all wildlife, and all wildlife except megaherbivores. Each of these wildlife treatments has a version with cattle and a version without. Each plot is large, 200 m on each side, or four hectares in area, and there are three replicates of each treatment type laid out along the plateau (figure 1).

Effects of large mammals on small mammals

As the fences were being completed in 1995, we set out to survey both the vegetation and the wildlife. The large mammals and birds were fairly well documented, but the small mammals were virtually unknown. To capture them, we used small aluminum Sherman box traps baited with oats and peanut butter. The captured animals were sexed, weighed, and marked with an individually numbered ear tag. The most common small mammal that we found was a poorly known and almost entirely unstudied rodent called the pouched mouse (*Saccostomus mearnsi*; figure 2), which accounted for about 85% of the animals that we caught in our traps. We also captured an assortment of other rodents, including *Mus* spp., *Arvicanthis niloticus*, *Mastomys natalensis*, *Dendromus melanotis*, *Aethomys hindei*, several gerbil species, and several species of shrews of the genus *Crocidura*.

In September 1995, when the KLEE fences had just been completed, we found equal numbers of pouched mice on the plots with and without large mammals (figure 3). Within a few months, however, the plots without large mammals had significantly more mice than those with a full complement of larger species (figure 3). Over time, this difference became even more pronounced, with mice on plots without

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*Figure 2. The northern pouched mouse (*__Saccostomus mearnsi__*), which is the dominant small mammal in the savanna habitat of central Kenya, where the Kenya Long-term Exclosure Experiment is located. These mice represented 85% of the small mammals captured over 11 years. Photograph: Felicia Keesing.*

large mammals being twice as abundant on average. During over 10 years of monitoring, the only time the two types of plots had similar densities of mice was toward the end of a prolonged drought in 2000, when mice virtually disappeared from all of the plots (figure 3).

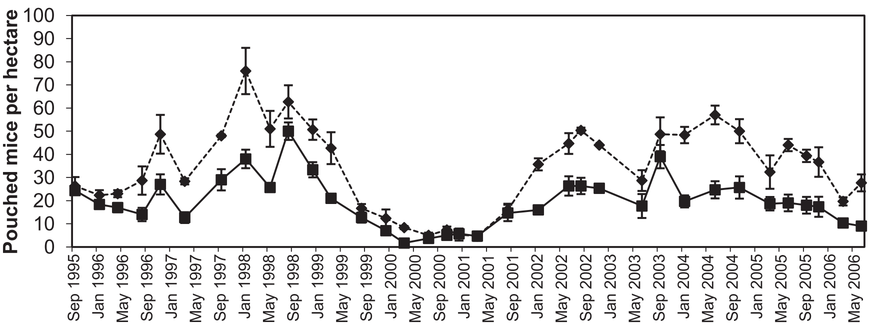

*Figure 3. The density of pouched mice (*__Saccostomus mearnsi__*) per hectare through time on plots with (solid lines) and without (dashed lines) large mammals. The Kenya Long-term Exclosure Experiment was established in September 1995 and plots without large mammals quickly developed significantly higher densities of pouched mice (repeated measures analysis of variance; treatment, *$p < .01$*; time, *$p < .01$*; treatment × time interaction, *$p < .02$*). These differences were maintained for years, except at the end of a prolonged drought in 2000. The error bars represent standard errors.*

On the plots that allowed large wildlife, we observed fewer mice than on the plots that did not, and this was true regardless of whether cattle were also allowed on those plots (figure 4). Similarly, on the plots that allowed cattle, there were fewer mice regardless of whether large animals were present (figure 4). Together, these observations suggest that both cattle and large wildlife reduce the abundance of mice and that they do so in an additive way. In other words, large wildlife species suppress mouse populations by about 25%, and cattle suppress them by an additional 25%.

Although the presence of cattle on the plots is tightly monitored and controlled by the herders, wildlife can move freely, at least on the treatments to which they have access. For example, if zebras or elephants prefer to avoid plots where cattle have grazed, they can spend their time elsewhere. To evaluate how much this occurred, Duncan Kimuyu and the KLEE team identified and counted the dung of eight species of large mammals on the treatment plots for 5 years beginning in 2006 (Riginos et al. 2012). On the basis of these dung surveys, they determined that the wildlife avoided areas where cattle had been grazing, spending 44% more time on plots to which cattle did not have access. So the effects of large mammals on mice that we described above are the effects of cattle plus the cascading effects of large wildlife, incorporating the degree to which wildlife avoid cattle.

We do not know for certain how large grazing mammals reduce the abundance of mice, but we pose two possibilities. First, if mice compete with larger mammals for food, the absence of large mammals should make it easier for mice to find food. Plots should then support larger populations of mice. We conducted feeding trials to ask whether pouched mice might compete with other grazers (Metz and Keesing 2001). Previous work suggested that they were primarily granivorous, but we determined that these mice are also herbivorous, consuming the same grasses and forbs preferred by larger grazers (Metz and Keesing 2001). Therefore, it is possible that the mice thrived because they were released from competition.

Another possible reason for the increase in mouse populations is that the mice on plots without large mammals were better able to avoid their predators. For example, if vegetation were more abundant on plots without large mammals, mice might have more plant cover under which to hide. In the early years of KLEE, the cover was fairly similar on all of the types of plots (Keesing 2000), which suggests that, at least at first, differences in exposure to predators could not explain higher abundances of mice on plots without large mammals. Over time, plots from which large herbivores have been excluded have tended to have

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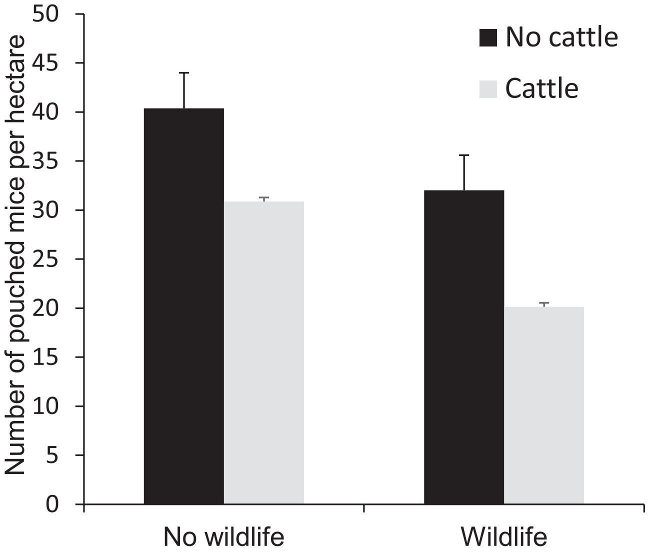

*Figure 4. Abundance of pouched mice (***Saccostomus mearnsi***) per hectare on plots with and without large wild mammals and with and without cattle. The mouse abundance for each treatment type was averaged across years and then analyzed using a two-factor analysis of variance with wildlife (present, absent) and cattle (present, absent) as factors (wildlife,* $p = .001$*; cattle,* $p < .001$*; wildlife × cattle interaction,* $p = .67$*).* **Wildlife** *here means large wild mammals. The error bars represent positive standard errors.*

more cover (Young et al. 2005). If the mice on plots without large mammals were better able to hide from predators, we would expect mice to survive better on those plots. After analyzing data from thousands of individual mice over tens of thousands of trap nights, however, we found that there are no differences in the survival of mice on the two types of plots ($p = .93$). Taken together, the evidence suggests that differences in density are probably due to mice experiencing less intense competition for food and, consequently, higher reproductive rates on the plots without large mammals; the mice survived just as well as they did on plots with half the density, because they had more food and possibly food of better quality, as well.

Studies in other parts of Africa have since shown similar patterns. In Botswana, for example, Saetnan and Skarpe (2006) found higher densities of rodents in experimental areas from which large mammals had been excluded. In a comparative study in Tanzania, Caro (2001, 2002) found lower densities of small mammals inside a national park than in an area outside of the park that sustained agriculture and pastoralism and had lower densities of large mammals. Taken together, these studies suggest that large mammals can regulate the abundance of small mammals and that the effect seems to be largely through the effects of large mammals on food quality or quantity, rather than through their effects on protective cover.

Small mammals are not the only herbivores that change in abundance when large mammals are absent. Ogada and colleagues (2008) found that arthropods—primarily, insects—caught in pitfall traps were more abundant on KLEE plots without large mammals. This increase was correlated with an increase in the diversity of passerine birds, which feed on the insects (Ogada et al. 2008). Similarly, *Colotis* butterflies, which are the most common butterflies on the plots, were more common in the treatments without native large mammals (Wilkerson et al. 2013). These plots, which were missing large browsers, had more of the shrub (*Cadaba farinosa*) on whose flowers *Colotis* feed, and the shrubs produced more flowers. Surprisingly, the butterflies were also more abundant on the plots with cattle than without, and the shrubs on these plots produced more flowers. The underlying mechanisms for this pattern remain unclear, although it may be due to reduced competition from grasses (Wilkerson et al. 2013). Clearly, the shift in vegetation that accompanies the absence of large mammals affects consumers, often but not always increasing their abundance. And, although cattle and wildlife have many similar effects, grazing by cattle leads to some different outcomes from those of browsing by some of the native large mammals.

Effects of large and small mammals on snakes

Our first results demonstrated that, when large mammals are absent, there is a shift from a savanna dominated by large mammals to one dominated by small mammals. What are the consequences of such a change? We were particularly interested in how the predator community might respond to a shift to smaller prey. Small mammals have many predators, including raptors, snakes, and smaller mammalian carnivores such as jackals. We focused our efforts on a particularly common venomous snake, the olive hissing snake (*Psammophis mossambicus*). We asked whether these snakes were more abundant on plots that had switched from dominance by large mammals to dominance by small mammals (McCauley et al. 2006). We placed snake boards—1-square-meter pieces of plywood—at several locations in each plot. These boards are useful tools for estimating snake abundance, because snakes tend to use them as refuges. Most (94%) of the snakes under the boards were olive hissing snakes; the rest were puff adders, which are even more venomous. Over a 3-year period, the pattern was clear. On plots with abundant small mammals, there were twice as many snakes (figure 5a), and the abundance of snakes on each plot tracked the abundance of mice (figure 5b). In summary, when large mammals are absent from these savannas, there are twice as many venomous snakes. This ecological shift could have dramatic consequences for human health; people in East Africa suffer from among the highest levels of venomous snakebites and fatalities worldwide, with estimated annual rates of 13–23 bites and 0.4–3.0 deaths per 100,000 people (Kasturiratne et al. 2008).

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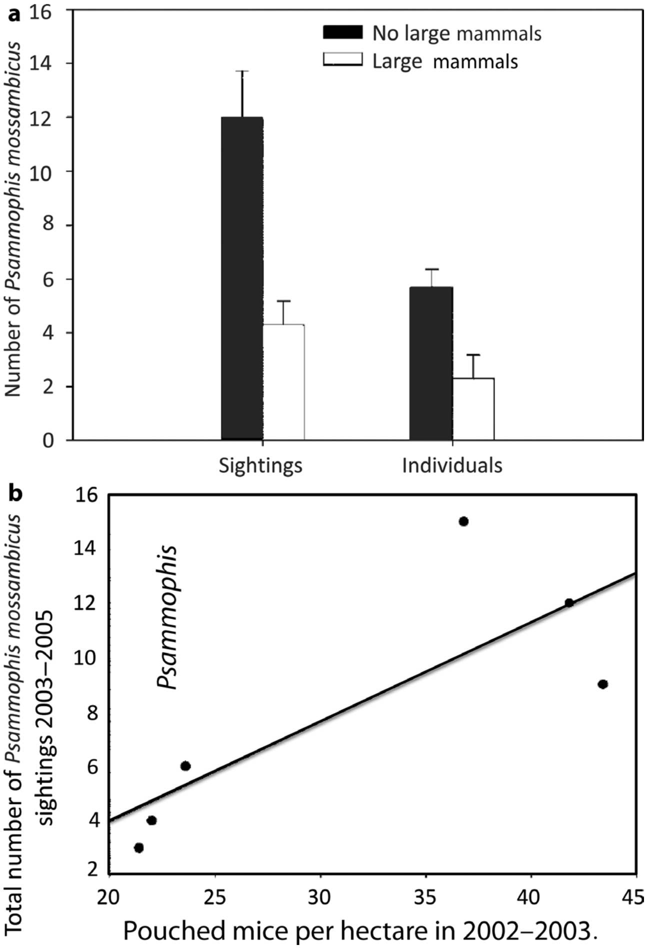

*Figure 5. (a) Number of sightings and individual olive hissing snakes (*Psammophis mossambicus*) per hectare on plots with (white bars) and without (black bars) large wild mammals (sightings, p < .01; individuals, p = .06). The error bars represent positive standard errors. (b) Abundance of pouched mice (*Saccostomus mearnsi*) as a function of the total number of sightings of olive hissing snakes in 2002–2003 ($R^2 = .65$, p = .05). Source: Adapted from McCauley and colleagues (2008).*

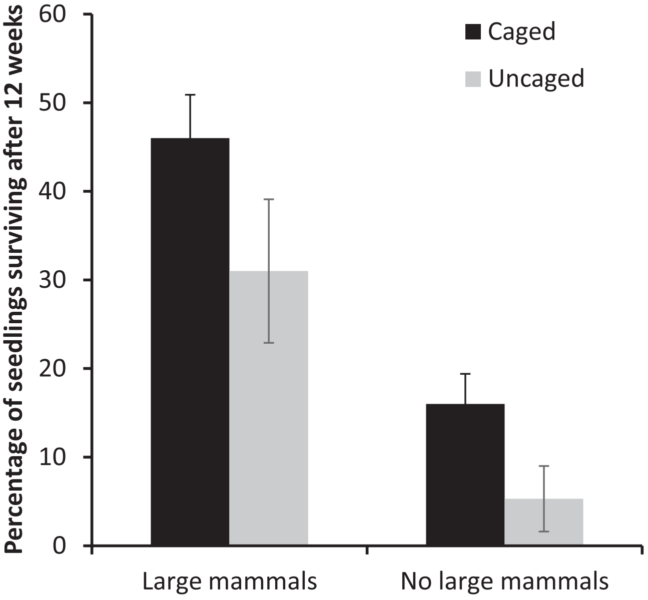

Figure 6. Survival of **Acacia drepanolobium** *seedlings after 12 weeks as a function of the presence of large mammals (p = .0001), depending on whether the seedlings were caged to exclude small mammals (dark gray bars) or uncaged (light gray bars), allowing access by small mammals. Uncaged seedlings exposed to smaller consumers such as mice suffered the greatest predation, particularly when these consumers were at high abundance because of the removal of large mammals. Source: Adapted from Goheen and colleagues (2004).*

Effects of large and small mammals on *Acacia* trees

Another potential consequence of abundant small mammals is that they might affect their own food. Small mammals were known to be important predators on tree seeds and seedlings in many parts of the world, but no one had asked whether the same were true in African savannas. Shortly after KLEE was established, we showed that rodents consumed large numbers of the seeds of acacias in this area (Keesing 1997). Later, we planted seeds of *Acacia drepanolobium* and grew them to the seedling stage (Shaw et al. 2002, Goheen et al. 2004). The seedlings were planted in plots with and without large mammals, and we protected some of them further by covering them with cages that kept out small mammals and large invertebrates. Then we monitored the seedlings closely for several months.

Until these experiments, people had assumed that the death of acacia trees was usually the result of damage by large mammals. The results of our studies suggested otherwise. We found that young acacias were primarily killed by rodents and large invertebrates and that three times as many uncaged seedlings survived when large mammals were present (Shaw et al. 2002, Goheen et al. 2004). Contrary to our expectations, large mammals protected seedlings by suppressing their major predators, such as rodents and insects (figure 6).

Perhaps not surprising, native large mammals affect the survival of young trees somewhat differently from how cattle do (Goheen et al. 2010). As was predicted from our earlier work on small mammals, both groups of large mammals reduced predation on tree seeds by reducing the abundance of small mammals, but the roles of the large mammals diverge from there. Some native large mammal species, such as giraffes and elephants, browse acacia trees, reducing the number of seeds that they produce. Cattle, which do not browse trees, do not have this effect. As a result, cattle have a greater positive effect on net seed survival than native large mammals do (Goheen et al. 2010). This effect increased further at the seedling stage, because cattle consumed more grass than did the native grazers, thus reducing shade and

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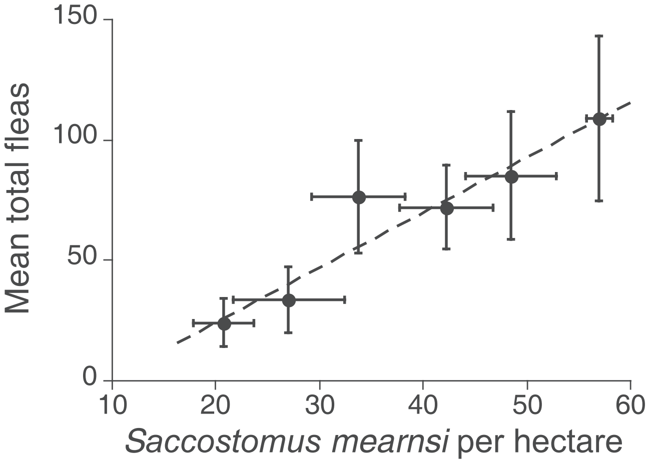

Figure 7. Average total abundance of fleas on pouched mice (*Saccostomus mearnsi*) as a function of the abundance of pouched mice per hectare (*$R^2 = .88$, $p < .01$*). The error bars represent standard errors. Source: Adapted from McCauley and colleagues (2008).

Figure 8. A cow passing through a chamber where it is being sprayed with an acaricide that kills ticks as they attempt to feed. Photograph: Becky Chaplin-Kramer.

competition for young plants (Riginos and Young 2007, Goheen et al. 2010).

Acacia trees serve crucial functions in savannas. On one hand, trees attract large herbivores with shade and enhanced forage beneath their canopies (Riginos et al. 2009, Treydte et al. 2010). On the other hand, higher densities of trees reduce visibility, which aids predators, and are avoided by herbivores (Riginos and Grace 2008). The trees matter for people, as well. In Kenya, up to 75% of people use wood or charcoal for fuel, and acacias are a major potentially sustainable source (Okello and Young 2000). Our findings suggest that areas that lose large mammals might see long-term declines in the availability of fuelwood and charcoal.

Effects of large and small mammals on parasites

Pouched mice abound with fleas, so one likely outcome of an increase in mice is an increase in these parasites. This has potentially great consequences for humans, because fleas can serve as vectors of pathogens, including the bacterium that causes plague. After catching each pouched mouse during dozens of regular censuses, McCauley and colleagues (2008) carefully combed each mouse to remove its fleas. Two species were common: *Xenopsylla aequisetosa* and *Xenopsylla sarodes*. There was no difference in the number of fleas on each mouse whether they were in plots with or without large mammals (McCauley et al. 2008). However, because there were more mice in plots without large mammals, there was also a greater total abundance of fleas on these plots (McCauley et al. 2008). In fact, the total abundance of fleas tracked the total abundance of mice on each plot (figure 7). From other studies, we know that increases in rodent density and flea abundance are linked to human exposure to flea-borne illnesses (Keeling and Gilligan 2000, Enscore et al. 2002, Duplantier et al. 2005). It would not be surprising, then, if declines in large mammals led to an increased risk of flea-borne pathogens such as *Yersinia pestis*, which causes bubonic plague.

Fleas are not the only common ectoparasites in African savannas. It is not uncommon for savanna visitors to find as many as several hundred ticks on their pant legs. If these ticks are not quickly removed, they will embed themselves in one's skin, feed on blood, and then drop off again into the grass. In the course of feeding, they can transmit blood-borne bacteria and viruses, including pathogens that cause Nairobi sheep disease and Q fever in livestock and tick typhus and Crimean–Congo hemorrhagic fever in people.

In savannas, ticks are costly. The ticks themselves can do considerable damage to their hosts through parasitism (Norval 1990), but the infections they transmit can also harm and even kill humans, livestock, and wildlife, and they are expensive to treat (Bock et al. 2004, Parola et al. 2005, Fyumagwa et al. 2011). Because of the risks, people in East Africa who raise cattle almost always treat them with a chemical that kills ticks (figure 8). The cattle are treated as seldom as once every few months or as often as twice per week, depending on the abundance of ticks, the risk of disease, and the resources of the livestock owner. When cattle that have been treated encounter ticks, the ticks attempt to feed and die in the process. We suspected that cattle might affect the number of ticks to which wildlife were exposed, because the cattle moved through the landscape, collecting ticks, which then died from exposure to chemical treatments. The KLEE plots were the ideal place to test our hypothesis.

For 7 years, we counted ticks in each of the KLEE plots, both those with and those without cattle. Each month, two researchers walked the perimeter of the central hectare of each plot. Over 81 months of sampling, this added up to more than 500 kilometers of savanna surveyed and more than 40,000 ticks counted (Keesing et al. 2013). Two tick species are common in KLEE: *Rhipicephalus praetextatus* and *Rhipicephalus pulchellus*. In the field, we cannot tell the two

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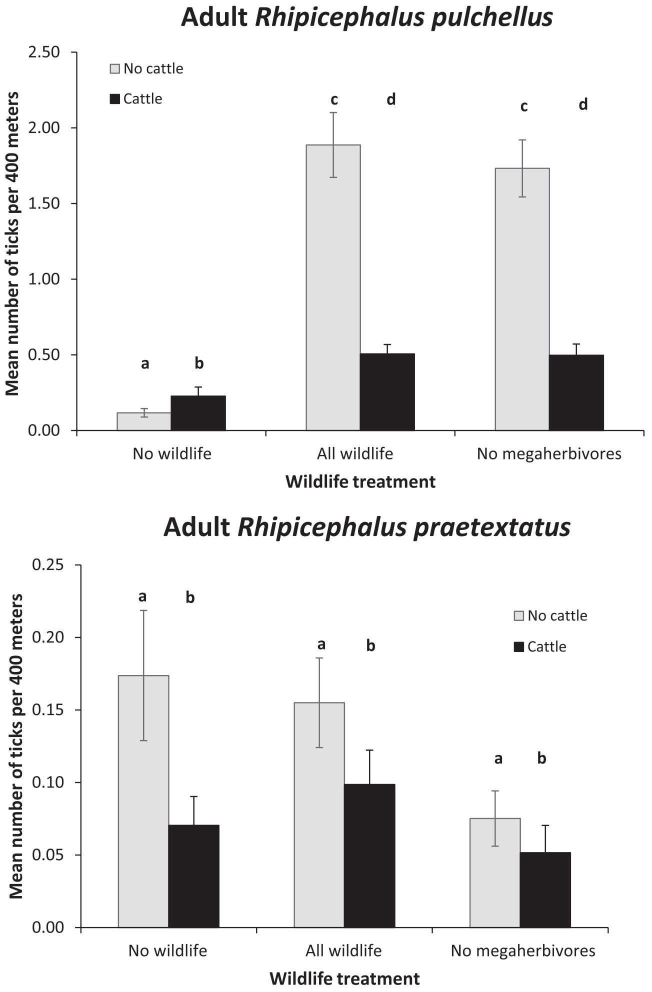

Figure 9. Abundance of adult ticks per 400-meter transect on plots that allow different levels of wildlife as a function of the presence (dark gray bars) or the absence (light gray bars) of cattle. The error bars represent standard errors. The lowercase letters represent statistically significant differences. Source: Adapted from Keesing and colleagues (2013).

species apart when they hatch out of eggs as larvae nor after they take their first blood meal and molt into the nymphal stage, but they are easily distinguishable as adults, a stage they reach if they successfully feed and molt as nymphs.

On plots with wildlife but no cattle, adult *R. pulchellus* ticks were abundant, averaging about two ticks collected per 400 m of transect, through wet seasons and dry (figure 9). When cattle were also present, however, tick abundance plummeted to a quarter of that level. As we predicted, when neither wild nor domestic large mammals were allowed, the abundance of *R. pulchellus* declined even further (figure 9). In this situation, without large wildlife, the presence of cattle actually increased tick abundance, although not by very much. We suspect that this modest increase captures the failure rate of the cattle spraying, perhaps late in the dipping cycle. In other words, cattle are infested by a few ticks—the ticks not killed by the spray—and they appear to import those ticks into the cattle-only plots, where ticks have little else on which to feed.

The pattern for the less common tick, *R. praetextatus*, was different. Unlike their more abundant relatives, these ticks feed on small- and medium-size mammals, including rodents, in addition to large ones. Perhaps not surprising then, they were abundant even on plots without wildlife or cattle (figure 9). Cattle still reduced their numbers, but not to the degree that we observed for *R. pulchellus*, and the presence of wildlife did not significantly alter their abundance (figure 9).

From our results, it appears that the judicious use of cattle treated with acaricide can reduce the abundance of ticks for wildlife and humans across entire landscapes, but there are reasons to be cautious. One possibility is that the ticks will evolve a resistance to the sprays, a problem that has already begun to develop in some species of ticks treated with amitraz (Foil et al. 2004). This could potentially be combated through integrated pest management, including deliberate, occasional switching from one type of spray to another, but determining the optimal frequency of switching will take time. Another potential problem is that the use of chemicals to kill ticks could adversely affect some wildlife. In South Africa, a previous generation of acaricides was made of arsenic compounds that were thought to be responsible for the death of some animals, including oxpeckers (Bezuidenhout and Stutterheim 1980), a charismatic bird that eat ticks infesting wildlife. The current acaricides do not appear to have these toxic effects, but further studies are warranted, as is monitoring of how declines in tick abundance affect populations of animals such as oxpeckers that depend on ticks for their food.

Conclusions

Together, the results of investigations at KLEE demonstrate that the loss of large mammals from African savannas can have a suite of unexpected consequences. Many of these arise from the replacement of large herbivores by smaller ones such as small mammals and arthropods, and many have important consequences for humans. If the loss of large mammals leads to an increased abundance of venomous snakes and flea vectors of pathogens and a reduced abundance of trees, savanna ecosystems may become less hospitable to people and their livestock. However, the potential of the integration of cattle and wildlife to reduce tick abundance reveals that careful coordination between the needs of humans and those of wildlife could have benefits for both, at least in some cases. Other studies at KLEE provide reason for further optimism. For example, several land management practices used by traditional pastoralists in this ecosystem have been shown at KLEE to have benefits for wildlife. Fire, for instance, which has been used by pastoralists in the past but is now often suppressed, increases grass quality, with benefits for wildlife, and areas that pastoralists have cleared of woody vegetation are preferred by wildlife, because they offer greater visibility, which aids in predator

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avoidance (Riginos et al. 2012). In addition, recent work at KLEE has shown that the magnitude of competition for food between cattle and wild large herbivores, which has long been assumed, is more complex than was previously thought (Odadi et al. 2011). For example, wildlife compete with cattle during the dry season but facilitate cattle performance during the wet season (Odadi et al. 2011). These and other manipulative experiments reveal important possibilities and potential pitfalls for the sustainability of African savannas (Pringle et al. 2011).

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