Can integrating wildlife and livestock enhance ecosystem services in central Kenya?

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Because wildlife and livestock compete for grazing resources, biodiversity conservation and livestock ranching typically have been portrayed as conflicting uses of African savannas. Here, we offer an alternative perspective by describing a savanna ecosystem in central Kenya where wildlife and livestock exhibit a suite of potential positive interactions. For example, treating livestock with an acaricide offers the unintended benefit of removing ticks from the landscape, a result that has now been shown to occur at both large and small scales. When humans derive financial benefits both from wildlife (through tourism) and from livestock (through food production), they may achieve greater economic stability than when income is derived solely from one source. The integrated management of wildlife and livestock can simultaneously improve human health and wildlife conservation. Optimization of human and wildlife benefits will require the management of ecological and socioeconomic trade-offs when conflicts occur between stakeholders.

Covering more than half of continental Africa, savannas are highly productive habitats, important for both livestock and wildlife (Scholes and Archer 1997) and as such are a frequent source of human–wildlife conflict (Thirgood et al. 2005). The most obvious forms of conflict are predation of livestock by wild carnivores and competition for access to forage and to water sources. Wildlife and livestock may also exchange parasites and pathogens (Woodroffe et al. 2005a).

Livestock husbandry is not only a critical source of food, income and financial stability for many people in Africa (Minjauw and McLeod 2003) but is also a source of cultural identity. Conflicts between wildlife and livestock therefore essentially represent a clash between the well-being of wildlife and that of humans. Historically, the most common method for minimizing these conflicts was to reduce contact between livestock and wildlife in order to avoid perceived competition for forage and water (Woodroffe et al. 2005b). However, this approach failed to account for more complex interactions between livestock and wildlife. For example, during the wet season in central Kenya, grazing by wildlife actually improved forage quality for cattle through selective consumption of competing grass species (Odadi et al. 2011a), which can potentially raise their market value, though there was competition during the dry season. In return, cattle can serve as ecological traps (ie hosts that are perceived to be high quality, but actually are low quality) for the tick parasites they share with wildlife (Keesing et al. 2013), reducing total tick abundance and potentially the prevalence of tick-borne diseases.

Rapid human population growth in East Africa is escalating conflicts between the needs of livestock and wildlife, and these tensions are exacerbated by increasing aridity (Fields 2005). These circumstances create a timely opportunity for investigating whether the needs of humans and their livestock must inevitably diverge from those of...
wildlife. Here we explore wildlife–livestock interactions that may affect human health and well-being through multiple pathways. The historical approach to management may have failed to take advantage of benefits that could be derived from a more integrated approach to livestock production and wildlife conservation. In particular, we highlight published and new data on how the control of tick and tick-borne diseases associated with the integration of livestock and wildlife populations may have beneficial outcomes for human health in Kenya. However, we also acknowledge that there are costs to wildlife–livestock integration, the net outcomes of which are poorly understood. We therefore advocate that considering multiple ecosystem properties— including infectious disease dynamics and potential trade-offs in income from tourism versus livestock production—is necessary to determine the consequences of such integration for health and well-being in African savanna ecosystems.

Livestock and wildlife management on Kenyan savannas

The livestock industry accounts for nearly 50% of Kenya’s gross agricultural product and over 12% of the national gross domestic product (FAO 2005; ICPALD 2013). Traditionally, cattle have been herded by nomadic ranchers, sometimes in mixed herds with indigenous breeds of sheep, goats, and camels, and grazed on natural pasture. However, across much of Kenya in recent years, land use has shifted from traditional nomadism to sedentary pastoralism, and increasingly to cultivation in wetter regions that can support it (Nyariki et al. 2009). Tensions over access to adequate forage are particularly acute during droughts.

Some land managers attempt to reduce the presence of wildlife on their properties in order to maximize the delivery of livestock-related benefits such as income and nutrition from cattle, employment through husbandry, and reduced exposure to diseases (Figure 1a; Figure 2a, purple shading). An alternative approach on the same savannas, practiced primarily by privately owned conservancies and national parks and reserves, has been to emphasize the benefits derived from high wildlife abundance and diversity, such as tourism income and tourism-related employment (Figure 1b). In so doing, these conservancies, parks, and reserves have chosen to enhance wildlife populations through various means and to develop benefits associated with tourism (Figure 2a, blue shading). Land managers who focus on wildlife-related benefits may exclude or minimize livestock on their properties, and so do not gain any livestock-related benefits.

The rationale for pursuing one management system over another is based on the assumption that livestock and wildlife—and the benefits associated with each—are incompatible on savanna landscapes, resulting in the greatest benefits to humans being derived from either one source or the other (Figure 2a). If, on the other hand, any loss of benefits due to a reduction in livestock (or wildlife) is directly compensated by a gain of benefits due to an increase in wildlife (or livestock), the outcome for humans is neutral (Figure 2b). Finally, if there are positive interactions
between livestock and wildlife, the greatest net benefit would be derived from a combination of both (Figure 2c).

**Laikipia County – a natural laboratory**

Laikipia County in central Kenya presents an ideal natural laboratory for exploring relationships between humans, livestock, and wildlife. Covering 9666 km², the county ranges from the foothills of Mount Kenya in the east to high plains overlooking the Great Rift Valley to the west. Home to pastoralists for thousands of years, the region is also a hotspot for wildlife diversity, with higher densities of several rare species than in other portions of their geographic distributions. These include white and black rhinoceroses (*Ceratotherium simum* and *Diceros bicornis*), African wild dogs (*Lycaon pictus*), Grevy’s zebras (*Equus grevyi*), Laikipia hartebeests (hybrid of *Alcelaphus buselaphus cokii* and *Alcelaphus buselaphus lelwel*), and less-common antelope species such as gerenuks (*Litocranius walleri*).

Most of the land in Laikipia is privately owned or managed by a wide range of stakeholders, including livestock ranchers, conservancy managers, and members of indigenous communities, who manage their lands for many purposes. Historically, priorities such as wildlife conservation and livestock production have been directly at odds. However, over the previous several decades, an increasing number of property managers have adopted an integrated management approach (Figure 1c) due to a growing perception of the potential net benefits derived from multiple revenue sources and management strategies (Figure 3).

Laikipia is also home to the Mpala Research Centre (MRC), where long-term studies provide some of the best evidence that integrating livestock and wildlife offers potential benefits for human well-being. MRC supports a large 24-ha replicated wildlife exclosure experiment called the “Kenya Long-term Exclusion Experiment” (KLEE), which uses a combination of electrified fences and cattle-herding treatments to investigate the effects of wildlife and cattle, and their interactions, on the ecology of African savannas (Keesing et al. 2013). Results from KLEE have revealed many important aspects of the ecology of this ecosystem, including the conditions that cause cattle and native grazers to either compete with or facilitate one another (Odadi et al. 2011a and b).

**Potential benefits of integrated management**

Data from KLEE demonstrate that there are circumstances in which livestock and wildlife can not only coexist, but can even benefit from sharing habitat. For example, Odadi et al. (2011a) found that in the wet season, cattle grazed in treatment plots that were shared with wildlife gained more weight than those grazed in plots from which wildlife were excluded. This may have been due in part to a higher overall density of herbivores that stimulated growth and improved forage quality (Odadi et al. 2011a). In the dry season, however, cattle gained less weight in the presence of wildlife than in their absence. Net benefits for livestock production of such co-management will therefore need to be carefully weighed, and the balance point may vary across space (eg drier versus wetter regions) and time (eg effects of climate change on precipitation). Additionally, when cattle and donkeys (used as a surrogate for zebras) grazed together, both species gained more weight, had higher bite rates (bites per minute), and selected more favorable diets (ie more digestible organic matter and higher crude protein content) than when grazed separately, suggesting that the presence of cattle may also benefit wildlife (Odadi et al. 2011b). Together, these interactions may raise the value of cattle and increase the abundance of wildlife, but the importance of these findings has not been established outside of this tightly controlled experimental setting.

Landowners and community members in Laikipia are increasingly recognizing that an additional potential benefit – improved and diversified income from dual revenue streams (Figure 3) – may arise from integrating livestock and wildlife on private lands. In the traditional model of management, tourists – 1.3 million of whom travel to Kenya each year (KNBS 2015) – visit areas that do not allow livestock within their borders. Though most spend their time in national parks and preserves, others visit private conservancies, which typically offer luxury
wildlife, which would diminish the economic benefit of wildlife–livestock integration. However, widespread engagement in cultural tourism (Okello 2005) suggests that many tourists may appreciate viewing traditional pastoralists and their livestock.

If wildlife and livestock compete with each other, as assumed in traditional management models (Woodroffe et al. 2005b), then gains from tourism should be offset by losses from livestock production (Figure 2b). However, long-term research in Laikipia has shown that where wildlife is favored by land managers, both livestock and wildlife can thrive, even at moderately high stocking densities of livestock (10–20 total livestock units per square kilometer; Kinnaird and O’Brien 2012). The biggest source of competition between livestock and wildlife may in fact be for water, rather than for food (Ogutu et al. 2014). In this case, coexistence may be promoted through spatial partitioning of permanent and seasonal water bodies (Sitters et al. 2009).

Finally, the loss of livestock to predation by wild carnivores continues to be perceived as a major source of wildlife–livestock conflict and motivation for spatial separation of wild and domestic animals. Interestingly, in some regions, current costs of livestock losses to predators may be small as compared to the costs of losses to theft and disease, and surveyed ranchers indicate a higher tolerance for abundant predator populations in the presence of revenue from wildlife-oriented tourism (Frank et al. 2005). Regardless, managers on many commercial ranches have developed a technological solution to protect cattle from large predators: herds are housed at night in mobile metal corrals (called “bomas” because of their similarity to traditional thorn enclosures) close to grazing areas, greatly reducing livestock losses to predation (G Prettejohn, pers comm).

Integrated management for disease control

Elements of both the positive and negative interactions between livestock and wildlife have been observed at multiple scales in Laikipia, but one major interaction has been largely overlooked. In East Africa, infectious diseases inflict a heavy toll on humans, livestock, and wildlife, perhaps more than anywhere else on Earth (Kuris 2012). This region serves as a global hotspot for tick diversity, with over 40 species present in some areas

Figure 3. Potential linkages among contributors to human well-being for (a) ranches that focus only on benefits from livestock production, (b) conservancies that focus only on benefits from wildlife tourism, and (c) integrated ranch/conservancies that derive benefits from both livestock production and tourism. Blue and red lines indicate increases and decreases, respectively.
These ticks can inflict morbidity and mortality on wildlife and livestock directly through parasitism (Van Der Merwe et al. 2005), and also indirectly by serving as the vectors for a diversity of infectious agents, including protozoal, bacterial, and viral pathogens (Berggoetz et al. 2014). Economic analyses suggest that the impact of tick-borne diseases on livestock production represents the greatest barrier to economic development in East Africa (Perry and Young 1995; Minjauw and McLeod 2003). Ticks and tick-borne pathogens impose such a burden on livestock production that ranchers in the region have depended upon the use of synthetic, tick-specific pesticides (ie acaricides) for decades (Young et al. 1988). Historical (arsenic-based) acaricide formulations were associated with adverse environmental consequences, including region-wide declines in oxpeckers in South Africa (Stutterheim 1981). No substantial negative environmental consequences of formulations currently in use (eg amitraz) have been reported. Data on the prevalence of tick-borne disease in humans in East Africa are rare because these diseases are often difficult to diagnose. Because herders on both commercial and community ranches live in close proximity to cattle, their exposure to tick-borne diseases is likely to be particularly high.

The KLEE in Laikipia has provided valuable insights into how ticks affect cattle–wildlife dynamics. Monthly tick surveys maintained for over 7 years within KLEE indicate that for two of the most common species of tick in the region, *Rhipicephalus pulchellus* and *Rhipicephalus praetextatus*, the presence of cattle significantly reduces the density of ticks as compared to plots with only wildlife (Figure 4; Keesing et al. 2013). Cattle markedly reduce the abundance of host-seeking nymphal and adult ticks, the two stages responsible for transmitting a multitude of tick-borne pathogens. This reduction in tick abundance apparently occurs because of the widespread application of acaricides (eg amitraz) to cattle that are grazed commercially in this region (Mugambi et al. 2012). Ticks on treated animals are killed during their attempt to feed, rather than being repelled prior to feeding. As a result, treated livestock remove ticks from the landscapes in which they graze, thus functioning as ecological traps for ticks (Keesing et al. 2009).

Despite the comparatively small scale of KLEE relative to the size of wildlife and livestock movements, it appears that the tick results continue to hold true outside a strictly experimental context, and at an even larger spatial scale. At Ol Pejeta Conservancy, a 36,000 ha conservancy in southern Laikipia, both livestock production and wildlife conservation occur, and the land is divided into large management blocks that experience different levels of cattle grazing intensity. Wildlife movements within the conservancy are unrestricted. In December 2012, we conducted additional tick surveys at the large scale of nine grazing blocks (each approximately 1000–2500 ha) spanning a range representative of how recently grazing by acaricide-treated cattle had occurred. The grazing blocks had experienced: (1) high-intensity grazing by cattle (ie grazing by between two and four herds of 100–200 head of cattle each until vegetation biomass was greatly reduced) at the time that sampling took place, (2) high-intensity grazing 3–6 months prior to sampling, or (3) no grazing for 3–4 years prior to sampling. There were three replicates of each treatment, and we sampled each of the nine grazing blocks using the drag-sampling method, where observers drag a 1-m$^2$ white cloth along randomly placed transects, stopping every 30 m to remove attached ticks. In each grazing block, we sampled six 150-m transects, or 900 m$^2$, for host-seeking ticks.

![Figure 4. Abundance of adult (a) Rhipicephalus pulchellus and (b) Rhipicephalus praetextatus ticks per 400-m transect on plots that allow different levels of wildlife, crossed with the presence (red bars) versus the absence (black bars) of cattle. Error bars represent ± 1 standard error of the mean. Lowercase letters represent statistically significant differences. Redrawn from Keesing et al. (2013).](image)
application of acaricide to free-ranging cattle at the large scale of the Ol Pejeta Conservancy appears to create herds that act as ecological traps, attracting and killing host-seeking ticks. Given that the spatial effects of tick-killing are temporary, cattle movements appear to create a shifting mosaic of relatively tick-free zones that might attract native herbivores because of increases in forage quality (Odadi et al. 2011b) and decreases in the risk of parasitism and disease. Although these interactions on Ol Pejeta are important, their potential to influence wildlife health and human well-being will be realized only if the same relationships hold at an even larger scale, and in climatically and socially variable systems. We are now investigating these relationships across the Laikipia region to determine whether wildlife conservation, livestock production, and human health are indeed coupled across the ecosystem.

Despite the high abundance of ticks and the prevalence of tick-borne diseases in the region, and their well-documented impact on livestock production, the consequences of ticks for human and wildlife health are poorly understood. However, wildlife in the region experience substantial tick burdens (Walker et al. 2000), and there are reports of mortality caused by tick-borne pathogens for species of conservation concern, including critically endangered species such as the black rhinoceros (Diceros bicornis) (Nijhof et al. 2003, 2005). These losses could, in theory, be offset by population-level benefits from parasites; these benefits could include enhanced stability of food webs (Lafferty et al. 2006) and increased species diversity (Hatcher et al. 2012), though these outcomes have not been specifically tested for African wildlife.

While the integration of livestock and wildlife may ultimately serve to control ticks and tick-borne pathogens, it may facilitate the exchange of other economically problematic infections. Spillover of pathogens such as foot-and-mouth disease (Sutmoller et al. 2000) and brucellosis (Godfroid 2002) from wildlife sources could substantially reduce the economic benefits derived from wildlife–livestock integration. Conversely, the successful eradication of rinderpest exclusively via the vaccination of cattle suggests that livestock were the primary source of pathogen spillover to wildlife (Dobson 1995). On working ranches in Laikipia, exchange of pathogens is an important economic consideration in the decision to integrate (G Prettejohn, pers. comm.), and costs associated with vaccinations and treatment of infected animals should be included in valuations of the net costs or benefits of wildlife–livestock integration.

**Measuring trade-offs through ecosystem service models**

Different economic scenarios emerge from lands managed for wildlife tourism, livestock production, or both. Of these scenarios, integrated management may offer the greatest net benefits to landowner income through increased income diversity, and to landowner health through nutrition from livestock and reduced exposure to tick-borne diseases (Figures 2c and 3c). If these positive interactions occur consistently at relevant spatial scales, this integrated management approach could provide a rare win–win for human development and conservation (Tallis et al. 2008). However, most ranches have only recently begun to formally integrate livestock and wildlife. At the moment, it is unclear what the impacts will be if more properties adopt this strategy, and if it is maintained for long periods of time. Fortunately, these questions can be explored with models of ecosystem services that link ecological change to human well-being, parameterized by data gathered at relevant spatial scales and over relevant time periods.

In our study system in Laikipia, no models currently capture multi-species interactions in systems with different management practices, but empirical data suggest that feedbacks between species are important. Traditional approaches to livestock and wildlife management would separately model these two components under the assumption that they are decoupled (Figure 3, a and b). In contrast, we are currently assessing the hypothesis that the provisioning of ecosystem services in this system, and the outcomes for human income, nutrition, and disease risk, will vary based upon whether livestock production and wildlife conservation are decoupled (Figure 3, a and b) or integrated (Figure 3c).

Models that incorporate ecological production functions are one of the best ways to estimate how management options will affect multiple outcomes (Tallis and Polasky 2011). These models are designed to display variation – across time and space – in the ability of ecosystems to produce services and in the ability of people to access and benefit from those services. But there are few exam-
ples of this approach for some of the most important services linked to development and poverty alleviation, such as disease regulation, wildlife-based tourism, livestock production (Ericksen et al. 2012), and the interplay between the three. In part, these limitations exist because models have thus far focused mainly on services with clearly understood mechanisms (Kareiva et al. 2011). For some key services, the functional relationships between the environment and human well-being have not been defined well enough to allow models to be broadly applied.

In Kenya, production–function models are needed for a core set of ecosystem services that contribute strongly to the well-being of humans living in rural areas. Specifically, simple production–function models of this system must capture (1) forage–livestock–wildlife interactions, (2) contributions of wildlife to tourism visitation rates and income, (3) contributions of livestock to income and human nutrition, and (4) wildlife–livestock–tick interactions that determine tick-borne disease risk for livestock and people. These simple models would not only provide the first opportunity to clarify interactions among these services but would also offer an ideal system for expanding the set of metrics measuring human well-being. Rural people in developing countries are particularly dependent on the local provisioning of ecosystem services (Narain et al. 2008), but many of the services most critical to rural well-being, such as those that contribute to health, agriculture, and livestock production, are missing from existing metrics of ecosystem services (Tallis and Polasky 2011). The models we propose would expand from relying solely on metrics dealing with monetary benefits to include those reflecting disease risk and nutrition as well.

Conclusions

We have described a system in which a simple management tool for increasing livestock production – treating cattle with acaricides – has the unintended but potentially desirable consequence of removing vast numbers of host-seeking ticks from the environment. This result shows that the net costs and benefits of wildlife–livestock integration require further consideration, and raises the question of whether cattle can be used as a management tool to improve the delivery of ecosystem services under certain circumstances. Because ticks are parasites and can transmit pathogens to both wildlife and humans, treating cattle may positively affect wildlife and human health, although the overall consequences of ticks and tick-borne diseases for wildlife health are largely overlooked. Under particular environmental conditions, cattle can also benefit wildlife – and vice versa – by enhancing forage quality. However, in other circumstances, the interaction remains competitive, suggesting that these outcomes remain condition-specific. The presence of a diverse assemblage of wildlife populations can increase local income from tourism, which may be enhanced rather than hindered by simultaneous management for livestock production. Whether tourists prefer to experience wildlife in the absence of domestic livestock, appreciate the role of livestock as an ecological management tool for African savannas, or are indifferent to the practice of integration remains unknown. Human health benefits may accrue from the production of meat, milk, and other cattle products, from reduced exposure to tick-borne pathogens, and from local economic gains from wildlife-related tourism. Conversely, increased wildlife–livestock interaction could facilitate the spillover of pathogens from wildlife and even select for wider host ranges. Our proposition that wildlife conservation, livestock production, and human health are coupled in this system suggests the need for a new framework for understanding interactions among different ecosystem services, derived from a single management intervention. Simultaneous consideration of multiple ecosystem services, with a focus on the ecological, financial, and social trade-offs of different management practices, will allow for an improved understanding of the net costs and benefits of wildlife–livestock integration. If it is shown to offer a net benefit, even if only under a specific set of conditions, both anthropocentric and ecocentric goals may be achievable, potentially resulting in a win–win scenario for humans and for the environment.

Note added in proof: Since the preparation of this paper, an outbreak of violence triggered by drought and exacerbated by political conflicts has resulted in mass incursions of livestock and pastoralists onto a number of private ranches and conservancies in Laikipia, leading to deaths of people, livestock, and wildlife. The present conditions deviate substantially from the previous 15–20 years of livestock–wildlife integration in Laikipia, as described above, and show that long-term integration depends on maintaining cooperation and security, particularly when resources are scarce.

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