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Relationships Between Cattle and Biodiversity in Multiuse Landscape Revealed by Kenya Long-Term Exclosure Experiment[☆]

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ABSTRACT

On rangelands worldwide, cattle interact with many forms of biodiversity, most obviously with vegetation and other large herbivores. Since 1995, we have been manipulating the presence of cattle, mesoherbivores, and megaherbivores (elephants and giraffes) in a series of eighteen 4-ha (10-acre) plots at the Kenya Long-term Exclosure Experiment. We recently (2013) crossed these treatments with small-scale controlled burns. These replicated experimental treatments simulate different land management practices. We seek to disentangle the complex relationships between livestock and biodiversity in a biome where worldwide, uneasy coexistence is the norm. Here, we synthesize more than 20 yr of data to address three central questions about the potentially unique role of cattle in savanna ecology: 1) To what extent do cattle and wild herbivores compete with or facilitate each other? 2) Are the effects of cattle on vegetation similar to those of wildlife, or do cattle have unique effects? 3) What effects do cattle and commercial cattle management have on other savanna organisms? We found that 1) Cattle compete at least as strongly with browsers as grazers, and wildlife compete with cattle, although these negative effects are mitigated by cryptic herbivores (rodents), rainfall, fire, and elephants. 2) Cattle effects on herbaceous vegetation (composition, productivity) are similar to those of the rich mixture of ungulates they replace, differing mainly due to the greater densities of cattle. In contrast, cattle, wild mesoherbivores, and megaherbivores have strongly guild-specific effects on woody vegetation. 3) Both cattle and wild ungulates regulate cascades to other consumers, notably termites, rodents, and disease vectors (ticks and fleas) and pathogens. Overall, cattle management, at moderate stocking densities, can be compatible with the maintenance of considerable native biodiversity, although reducing livestock to these densities in African rangelands is a major challenge.

Introduction

Worldwide, rangelands that support domestic livestock production are playing an increasingly important role in biodiversity conservation (du Toit et al., 2017). In particular, shrinking wildlife habitats and declining livestock revenues underpin changing management of rangelands toward mixed uses, especially promoting coexistence between livestock and wildlife (Niamir-Fuller et al., 2012; Reid, 2012; Chaminuka, 2013; Vetter, 2013; Western et al., 2015; Fynn et al., 2016; Ranglack and du Toit, 2016; Allan et al., 2017; Holechek and Valdez, 2018). It is clear that livestock-wildlife coexistence is problematic when livestock are inappropriately managed to the point of range degradation (du Toit and Cumming, 1999; Asner et al., 2004; Fynn et al., 2016; Coppock et al., 2017). However, less clear is the compatibility between wildlife and moderately stocked, well-managed livestock (du Toit et al., 2010, 2017; Butt and Turner, 2012; Reid, 2012; Allan et al., 2017; Cromsigt et al., 2017).

Competitive relationships between livestock and large ungulate wildlife are often assumed despite the fact that wild ungulate diets

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and habitat use often differ substantially from those of livestock. Conversely, it is unclear to what extent dietary overlap can be relied upon as a measure of competition (Scasta et al., 2016; Kimuyu et al., 2017b). Indeed, dietary overlap may be strongest when forage species are not limiting (Kilonzo et al., 2005). The more common forage species may not be the species for which ungulates compete most strongly. For example, there may be sufficient grass for all (and overlap in diet), but limiting amounts of N-rich forage (Odadi et al., 2013). We also need to better understand how livestock and wild ungulates, within a given study system, differ in their effects on habitat quality (forage and visibility) or interactively (e.g., nonadditively) influence their habitat. These effects of livestock and wildlife on habitat also can have cascading effects on multiple components of diversity, such as predators, rodents, birds, insects, and pathogens (e.g., Georgiadis et al., 2007; Pryke et al., 2016; Schieltz and Rubenstein, 2016). Yet nearly all studies of the effects of grazing herbivores on communities do not separate the effects of livestock and wildlife. Indeed, in many cases the removal of only one group is studied (typically livestock) and the potential for compensatory effects by the other group (here wildlife, which often can access livestock-exclosure plots) on the response variables is not explored and is often ignored. Alternatively, in the conservation literature, the effects of wildlife loss are often explored in either protected areas without livestock or via exclosures that remove all large ungulates, including livestock. This is problematic because outside of experimental systems the removal of large wild ungulates is not typically isolated, but rather accompanied by the addition of domestic stock. This can lead to mismatches between effects predicted via exclosures and those associated with realistic patterns of wildlife loss (e.g., Young et al., 2013, 2017). Few studies have separated the effects of livestock and wildlife on ecosystems (e.g., Jones, 1965; Veblen et al., 2016), and no fully replicated experimental manipulations of both livestock and wildlife have occurred. Here we synthesize > 22 yr of research from one such experiment, the Kenya Long-term Exclosure Experiment (KLEE), that was designed to examine interactions between cattle and wild ungulates, as well as the separate and combined effects of cattle and wildlife on their habitat. We have also crossed this design with burning treatments, although not as richly (or at as large a scale) as at Konza (Manning et al., 2017) or Kruger (Staver et al., 2017).

In a previous synthesis, we addressed the ways in which the KLEE project illuminated the effects of traditional pastoralism on savanna ecology (Riginos et al., 2012). The current review 1) explores the lessons we have learned about the role of cattle as large herbivores that differ from native wild ungulates, with which they coexist in savanna ecosystems and in many places have functionally replaced, and 2) expands our consideration of pastoral activities to review effects of modern commercial ranching practices (e.g., cattle dipping). We do not cover again here the effects of pastoral practices that dominated the previous review (e.g., bomas/corrals, tree clearing, or fire research outside of KLEE) (see Riginos et al., 2012 for a review of those topics, as well as Pringle et al., 2011; Porensky and Veblen, 2012, 2015; Veblen, 2012, 2013; Porensky and Young, 2013, 2016; Porensky et al., 2013b; Kimuyu et al., 2017a). Instead we focus here on updating and expanding our understanding of the relationships between cattle (and commercial cattle management) and biodiversity. We use KLEE's unique study design to ask three questions about the potentially unique role of cattle in savanna rangelands: 1) To what extent do cattle and wild herbivores compete with or facilitate each other in rangelands where both guilds are present? 2) Are the effects of cattle on vegetation similar to those of wildlife, or do cattle have unique effects? and 3) What effects do cattle and commercial cattle management have on other aspects of savanna ecology, and do these differ from the effects of wildlife?

Study Site and Exclosure Design

This research was carried out at Mpala Conservancy, located on the Laikipia plateau in central Kenya (0°17′N, 36°52′E; 1 800 m asl). The study site is located within *Acacia drepanolobium* wooded grassland at an elevation of 1 800 m, on heavy clay ("black cotton") soils. The understory is dominated by several species of perennial grasses, with a rich community of ~100 species of additional forbs and grasses (see Supplement 1 in Porensky et al., 2013a). Mean annual rainfall during the study period (1995 − 2017) was 600 mm/yr (range 364 − 1003 mm/yr), which on average falls in a weakly trimodal seasonal pattern, with a distinct dry season December − March. The area has been under various forms of cattle management for > 3 000 yr (Marshall, 1990; Marshall and Hildebrand, 2002; Prendergast, 2011; Marchant and Lane, 2014; Marchant et al., 2018), most recently (past 100 yr) as a commercial ranching operation increasingly tolerant of wildlife (i.e., active wildlife patrols, less wildlife removal and control, maintaining water sources).

The Mpala Conservancy is managed for both wildlife conservation and livestock production. Cattle are stocked at moderate densities ($0.10 - 0.15$ cattle ha^{-1}). Wild ungulates commonly found in the black cotton system include plains zebra (*Equus quagga* Gray), Grant's gazelle (*Gazella [Nanger] granti* Brooke), elephant (*Loxodonta africana* Blumenbach), steinbuck (*Raphicerus campestris* Thunberg), Grevy's zebra (*Equus grevyi* Oustalet), cape buffalo (*Syncerus caffer* Sparrman), eland (*Taurotragus oryx* Pallas), giraffe (*Giraffa camelopardalis* L.), hartebeest (*Alcelaphus buselaphus* Pallas), oryx (*Oryx gazella beisa* L.), and warthog (*Phacochoerus africanus* Gmelin) (Veblen et al., 2016). Wildlife densities in Laikipia are the second highest in Kenya, after the Maasai Mara National Reserve.

In 1995, we established the KLEE, designed to tease apart the separate and combined effects of cattle and wildlife on each other and on the savanna ecosystem that they share. The KLEE experiment uses a series of semipermeable barriers to allow access by different combinations of cattle ("C"), native mesoherbivore ungulates 15 − 1 000 kg ("W": zebras, gazelles, eland, hartebeest, oryx, buffalo) and megaherbivores ("M": elephants and giraffes). Below, we call these three classes of herbivores "guilds," in recognition of the unique ecological positions occupied by livestock and megaherbivores (Owen-Smith, 1988), relative to mesowildlife. The experiment consists of three replicate blocks separated from one another by 70 − 200 m. In each block, there are six random-stratified 200 × 200 m (4-ha) treatment plots (18 total plots; 24 ha). The six treatments are 1) MWC—accessible to megaherbivores, mesoherbivore wildlife and cattle; 2) MW—accessible to megaherbivores and mesoherbivore wildlife; 3) WC—accessible to mesoherbivore wildlife and cattle; 4) W—accessible to mesoherbivore wildlife; 5) C—accessible to cattle; and 6) O—no large herbivore access (Fig. 1). One small antelope, steinbuck (< 15 kg), is able to access all experimental treatment plots (Young et al., 2005), as are rodents and hares, and most carnivores. (see Tables 1 and 2).

Herds of 100 − 120 mature cows (sometimes with calves) are grazed in each cattle-treatment plot for 2 hr on each of 2 − 3 consecutive days, typically 3 − 4 times per year. These grazing and herding practices reflect typical cattle management on most private and some communal properties in the region. The cattle are in an individual plot for only a few hours per year, greatly reducing the possibility that wildlife responses are due to direct avoidance of cattle. For cattle performance trials (Odadi et al., 2007, 2009, 2011b, 2013, 2017) smaller groups (5 − 6) comprising individuals of 2- to 3-yr-old heifers and steers were used. For full details of the basic experimental design, see Young et al. (1998) and Porensky et al., (2013a, Supplement 1). For survey methods of individual response variables, see the relevant references cited later.

In addition, we later embedded both heavy grazing and fire treatments within the KLEE design. In 2008, we assigned one 50 × 50 m subplot in each cattle treatment (C, WC, and MWC) to be grazed at a much higher level than the basic plots (which are grazed at normal ranch densities). At the end of each cattle run, we held the herd within the designated subplot for an additional 20 − 30 minutes. This resulted in substantially reduced residual forage and an altered community structure (see later). In Feb − Mar 2013, we burned one 30 × 30 m subplot in each of the 18 KLEE treatment plots and monitored these and paired