

Pathways for Positive Cattle–Wildlife Interactions in Semiarid Rangelands

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ABSTRACT. Livestock-wildlife interactions in rangelands are often viewed in terms of competition, but livestock and native ungulates can also benefit each other through long-term modifications of rangeland habitats. Here we synthesize research on rangelands in central Laikipia focusing on two types of cattle-wildlife interactions that have implications for their long-term coexistence. The first interaction occurs via redistribution of soil nutrients within the ecosystem, which is a consequence of the use of bomas (temporary corrals) to manage livestock. Our studies on two different soil types show that rotational boma management creates hectare-scale patches in the landscape that are enriched in soil and plant nutrients and persist for decades to centuries. In both of the predominant soil types in Laikipia, forage phosphorus content is low relative to ungulate demands during peak lactation. Nutrient-rich boma sites (hereafter referred to as glades) provide a key wet-season forage resource of nutritional sufficiency for lactation. Our studies further show that a wide range of native ungulates selectively use glades relative to surrounding nutrient-poor habitats. Impala (*Aepyceros melampus*) in particular show intensive use of glades on sandy soils and are rare in portions of the landscape lacking glades. A second important pathway for cattle-wildlife interaction occurs through the influence of native browsing ungulates on woody vegetation. Shrub and tree cover has been increasing in Laikipia over the past century, followed by increases in native browsers in recent decades on ranches where wildlife are allowed to coexist with cattle. Our enclosure experiments in central Laikipia indicate that native browsers suppress shrub encroachment on both dominant soil types. However, the strength of browser effects are three to seven times greater on sandy soils, where two browsers, dik-dik and elephants, are both abundant, compared to heavy clay soils, where elephants are the only dominant browser. In the clay soils, native browsers still exert a significant influence on dynamics of the dominant tree, *Acacia drepanolobium*, and suppress encroachment by subdominant shrub species. Browser effects on woody vegetation likely enhance forage production for cattle and maintain open habitats favored by native grazers for predator avoidance. Taken together, our studies indicate that boma rotation and browser control of shrub encroachment are key interaction pathways that promote cattle-wildlife coexistence in the Ewaso ecosystem.

INTRODUCTION

In East Africa, most native ungulate populations still occur on rangelands outside of formally protected areas, and long-term coexistence of livestock and native species is critical if wildlife is to be conserved in the region (Western, 1989; Prins et al., 2000). Negative relationships between wildlife and livestock on some pastoral rangelands in Kenya have been attributed to poaching and harassment by humans associated with livestock, rather than direct competition for forage (de Leeuw et al., 2001). However, where such direct human effects are removed and livestock are maintained at moderate stocking rates, the magnitude of competition between livestock and native herbivores is a concern for the production of livestock and the conservation of the native fauna. Livestock-wildlife interactions in rangelands are often viewed in terms of competition because herbivores with overlapping habitat and diets have obvious potential for competition. However, multiple pathways of interaction are possible in diverse herbivore communities. Prins (2000) provided a comprehensive review of negative pathways, including direct resource competition, apparent competition, diffuse competition, predation, and competition through habitat modification. He suggested that despite considerable resource overlap between wildlife and cattle, competition is largely asymmetrical and diffuse, with cattle having a competitive effect on some wildlife species, but wildlife often having little or no net competitive effect on cattle (Prins, 2000). Several recent large-scale experiments have demonstrated competition between cattle and native grazers in grasslands under controlled conditions, but the magnitude of competition is often less than expected on the basis of diet overlap (Hobbs et al., 1996; Young et al., 2005; Derner et al., 2006; Odadi et al., 2009).

The relationship between livestock and cattle can also be positive (Arsenault and Owen-Smith, 2002). Prins (2000) discussed two modes of positive cattle-wildlife interactions: facilitation of forage quality or accessibility and facilitation through habitat modification. In diverse herbivore communities, the existence and strength of facilitation can determine the net effect of cattle and wildlife on one another and hence are important to long-term cattle-wildlife coexistence. Facilitation of forage quality or accessibility is usually defined as a short-term effect that bulk-feeding herbivores can have on forage for smaller herbivores (Bell, 1971; Gordon, 1988; Verweij et al., 2006). Facilitation through habitat modification involves long-term effects of different herbivore species on soil nutrient distribution and plant community composition (Arsenault and Owen-Smith,

2002). Our studies in the Ewaso ecosystem have addressed trophic interactions among soils, plants, and herbivores and identified two types of facilitation through habitat modification that have implications for the coexistence of livestock and native ungulates. The first interaction occurs through redistribution of soil nutrients within the landscape, which is a consequence of the use of bomas (temporary livestock corrals) to manage livestock. Boma-derived nutrient redistribution, in turn, has substantial long-term effects on the heterogeneity of forage nutrient content within the landscape, with potential benefits to both cattle and native herbivores. The second interaction is the ecosystem service that native browsers provide by suppressing and reversing shrub encroachment into grasslands, with implications for wildlife and livestock use of the landscape. In addition, the old boma sites are themselves treeless and attract increased wildlife use for this reason as well as for their nutrient-rich grasses. Here we synthesize studies examining these interaction pathways on two widely distributed soil types in the Ewaso ecosystem.

In central Laikipia, the Ewaso ecosystem encompasses a transition in soils, elevation, and vegetation, where gently undulating lava plains dominated by grassland and *Acacia drepanolobium* savanna switch to a more dissected lower plateau on Precambrian metamorphic rocks dominated by *Acacia mellifera*, *A. etbaica*, and *A. brevispica* bushland with a discontinuous grass understory (Ahn and Geiger, 1987; Taiti, 1992; Augustine, 2003b). Black cotton soils (Pellic Vertisols) occur on the lava plains in the south and west, whereas red sandy loams (Ferric and Chromic Luvisols) occur at lower elevations to the north and east (Ahn and Geiger, 1987). These soils differ dramatically in texture, with black cotton containing, on average, 50% clay and 24% sand (Young et al., 1998) and red sands containing 15% clay and 74% sand (Augustine, 2003a). The Mpala Research Centre (MRC) spans this transition zone, which occurs at elevations of 1740–1800 m above sea level. Although these two soils support distinctly different assemblages of plants, native herbivores, and other biota (Table 1), we show that on both of these soil types, herbivore-mediated nutrient heterogeneity and shrub control are important pathways through which cattle and wildlife benefit each other.

LIVESTOCK MANAGEMENT AND NUTRIENT HETEROGENEITY

Tropical rangelands are notoriously poor in mineral nutrients, such that mineral supplementation is recommended

TABLE 1. Comparison of plant and herbivore communities on two widespread soil types in Laikipia, Kenya.

Variable	Red Sands Habitat	Black Cotton Habitat
Soil texture	74% sand, 15% clay	24% sand, 50% clay
Dominant grasses	<i>Digitaria milanjiana</i> , <i>Cynodon dactylon</i> , <i>Pennisetum stramineum</i>	<i>Pennisetum stramineum</i> , <i>Bracharia lachnantha</i> , <i>P. mezianum</i> , <i>Themeda triandra</i>
Dominant shrubs and trees	<i>Acacia mellifera</i> , <i>A. etbaica</i> , <i>A. brevispica</i>	<i>Acacia drepanolobium</i>
Dominant native ungulates	Impala, dik-dik, elephant	Plains zebra, Grant's gazelle, hartebeest, giraffe
Less abundant native ungulates	Plains zebra, Grevy's zebra, eland, waterbuck, giraffe	Elephant, Grevy's zebra, eland, buffalo, oryx

as a standard practice for tropical livestock (McDowell, 1985). Wild herbivore biomass is also strongly affected by large-scale variation in geology and soil nutrient availability (Bell, 1982; Fritz and Duncan, 1994). Furthermore, spatial heterogeneity in soil and plant nutrients in African rangelands can strongly influence the distribution of wild herbivores at multiple spatial scales (McNaughton, 1988, 1990; Blackmore et al., 1990; Ben-Shahar and Coe, 1992; Murray, 1995; Muchiru et al., 2008). Natural sources of soil nutrient heterogeneity include termites (Brody et al., 2010; Fox-Dobbs et al., 2010) and tree canopies (Riginos et al., 2009). Here we discuss a major anthropogenic source of landscape heterogeneity: livestock corrals.

Abandoned livestock corrals, or bomas, are a widespread feature of African rangelands. Bomas are temporary structures consisting of a dense ring of thorn scrub branches that contain and protect livestock overnight from theft and predation for periods ranging from weeks to years. A major consequence of boma use is the concentration of large quantities of dung and urine within a small area, where livestock excrete and redistribute nutrients from the surrounding savanna. Following abandonment, boma sites often support a nutrient-enriched plant community and potentially alter the spatial pattern of nutrient cycling within the ecosystem. Recently abandoned boma sites in East Africa support unique herbaceous plant communities with nutrient enrichment both in soils and grasses (Stelfox, 1986; Augustine, 2003a; Treydte et al., 2006; Muchiru et al., 2009). Studies in South Africa even suggest that plant communities on abandoned sites of human occupation can persist in a nutrient-enriched state for centuries (Blackmore et al., 1990).

SOIL AND GRASS NUTRIENTS ON RED SANDS VERSUS BLACK COTTON SOIL

For increased nutrient heterogeneity to benefit wild herbivores, forage nutrients must be limiting to herbivores

in all or a portion of the landscape during part of the year. Previous studies on nutrient limitations to savanna ecosystem processes and herbivore abundances have primarily relied upon geology or cation exchange capacity as general indices of soil fertility at broad spatial scales (Bell, 1982; Fritz and Duncan, 1994; Olff et al., 2002). We used direct measures of soils and grasses to examine forage nutrient availability on black cotton soils, red sands, and a transition zone between them at MRC in central Laikipia. On the basis of the previous discussion of nutrient limitations to ungulates in Africa, we focus here on N, P, and Ca.

We sampled soil and grass leaf blades at 100 locations within MRC during the wet season in August 2001. We randomly selected 60 locations within the red sands soil type that underlies the majority of MRC, 20 locations within a region of transitional soils between 1740 and 1800 m elevation, and 20 locations within the black cotton soil type above 1800 m elevation in the southwestern portion of MRC. At each location, we sampled 30–40 of the youngest, fully expanded grass leaves from a 1 m² plot dominated by any of the dominant grasses (red sands: *Digitaria milanjiana*, *Cynodon dactylon*, *Pennisetum mezianum*, *Pennisetum stramineum*, *Enteropogon macrostachyus*, *Cymbopogon pospischilii*, *Themeda triandra*, *Sporobolus ioclados*, *Harpachne schimperi*, or *Chloris roxburghiana*; transitional soils: *Digitaria milanjiana*, *Pennisetum stramineum*, *Themeda triandra*, *Cymbopogon pospischilii*, *Pennisetum mezianum*, and *Cenchrus ciliaris*; black cotton soils: *Pennisetum stramineum*, *Themeda triandra*, *Pennisetum mezianum*, *Brachiaria lachnantha*, *Setaria sphacelata*, and *Lintonia nutans*).

Leaves were analyzed for N, P, and Ca content following McNaughton (1988). At each location, we also collected a soil core (15 cm depth). Cores were stored at 5°C at the MRC laboratory, and within 48 hours of collection, a 15 g subsample was extracted with 1 M KCl to measure NH₄⁺ and NO₃⁻ content, and a 2.5 g subsample was

extracted with Mehlich-3 solution to measure extractable P and Ca (Mehlich, 1984). Another 15 g subsample from each core was dried and analyzed for total soil N, P, Ca, and Na following McNaughton (1988). For extractable soil nutrient pools, we report geometric means because of high variability within soil types. Post hoc, pairwise comparisons among soil types were tested using Tukey's honestly significant difference (HSD), and all letters in figures indicate significant differences at the $P < 0.05$ level.

Black cotton soils contain greater concentrations of N and Ca compared to red sands (Figure 1A,C; $F_{2,97} > 9.41$, $P < 0.0002$ for one-way analysis of variance (ANOVA)), but both soils have similar total P concentration (Figure 1B; $F_{2,97} = 2.37$, $P = 0.10$). Mean soil C concentration is more than twice as high in black cotton soils compared with red sands (mean \pm 95% confidence interval = $2.44 \pm 0.35\%$ versus $1.12 \pm 0.13\%$), and soil C:N ratios are also higher in black cotton compared to red sands (17.3 ± 2.4 versus 10.1 ± 0.2). Extractable soil nutrient pools mirrored patterns for total soil nutrients, with inorganic Ca significantly lower on the red sands ($F_{2,97} = 43.9$, $P < 0.0001$; Figure 1F) and inorganic N only marginally lower on red sands ($F_{2,97} = 2.50$, $P = 0.087$; $P > 0.05$ for all pairwise comparisons; Figure 1D). Extractable soil P was similar on red sands and black cotton and lower for the transitional soils ($F_{2,97} = 12.8$, $P < 0.0001$; Figure 1E).

Grass P content was relatively consistent ($F_{2,97} = 1.1$, $P = 0.34$; Figure 1H) and low across the different soil types, reflecting a similar pattern for total and extractable soil P. In contrast to soil nutrient patterns, grass N content was significantly greater on red sands relative to black cotton ($F_{2,97} = 5.2$, $P = 0.007$; Figure 1G). Grass Ca content did not vary across soil types ($F_{2,97} = 0.5$, $P = 0.59$; Figure 1J), even though black cotton soils contain significantly more total and extractable Ca.

Variation in grass nutrient content across soil types has clear implications for large herbivores. Most notably, wet-season forage P content is lower than estimated demands for lactating ruminants on both red sands and black cotton soils (Figure 1H). For example, Murray (1995) estimated minimum forage P content of 3,900 mg/kg dry weight necessary for lactating wildebeest (*Connochaetes taurinus*), and recommendations for lactating cattle are in the range of 3,100–4,000 mg/kg (McDowell, 1985). Despite considerable differences in parent material and properties of red sands versus black cotton soil, our results indicate that forage P content is likely to affect growth rates and distribution of wild grazers in both habitats. Calcium can also be a critical nutrient for large herbivores in tropical grasslands (McNaughton, 1988, 1990;

Murray, 1995), but in the Ewaso ecosystem, grass calcium content is relatively constant across soil types, insensitive to variation in soil Ca availability, and sufficient to meet demands of grazing ungulates (Figure 1F,J).

Nitrogen content of grasses during the wet season on both the red sands and black cotton soils also appears sufficient to meet the protein requirements of ungulate grazers. For example, grasslands in the Serengeti ecosystem supporting high wet-season ungulate densities contain leaves with 2.2%–2.6% N dry weight (Murray, 1995), similar to grass leaf N content on black cotton soil (mean = 2.3%, 1 standard error (SE) = 0.1%) and lower than grass leaf N content on red soil (mean = 2.9%, 1 SE = 0.1%). For high-yielding dairy cattle and actively growing beef cattle, optimum N content in the diet is typically in the range of 2.1%–3.2% dry weight (McDowell, 1985; Whitehead, 1995). We note that our analysis does not address dry-season N limitations, when forage N content below 1% N can limit rumen microbes (Van Soest, 1994). Although our results emphasize P as a critical limiting nutrient for ungulates in Laikipia, the significantly lower N content in black cotton grasses compared to red sands suggests that future studies in the black cotton habitat should consider factors influencing seasonal and spatial variation in grass protein content.

INFLUENCE OF ABANDONED BOMAS ON LANDSCAPE NUTRIENT HETEROGENEITY

In the Ewaso ecosystem, shortgrass and shrub-free lawns on the order of 0.2–1 ha in size are a widespread and conspicuous feature of the landscape. These shortgrass lawns are derived from abandoned livestock bomas, contain nutrient-enriched soil, and support a unique plant community dominated primarily by the stoloniferous grass *Cynodon plectostachyus* (Young et al., 1995; Augustine, 2003a). In the red sands habitat, abandoned boma sites can persist in this shrub-free, shortgrass state for at least four decades and likely for centuries (Augustine, 2003a). In the black cotton soils, *Cynodon* lawns usually develop to a *Pennisetum stramineum*-dominated but still shrub-free stage over one to three decades and likely remain in the latter state many decades more (K. E. Veblen, unpublished data). Hereafter, we refer to all of these nutrient-enriched, shrub-free communities that have developed on abandoned boma sites as "glades." In some of our studies, we used aerial photographs from the 1960s to determine ages of abandoned boma sites, and we examined soils, plant nutrients, and herbivore distribution in relation to glades created by boma abandonment during the past four decades (young glades) versus

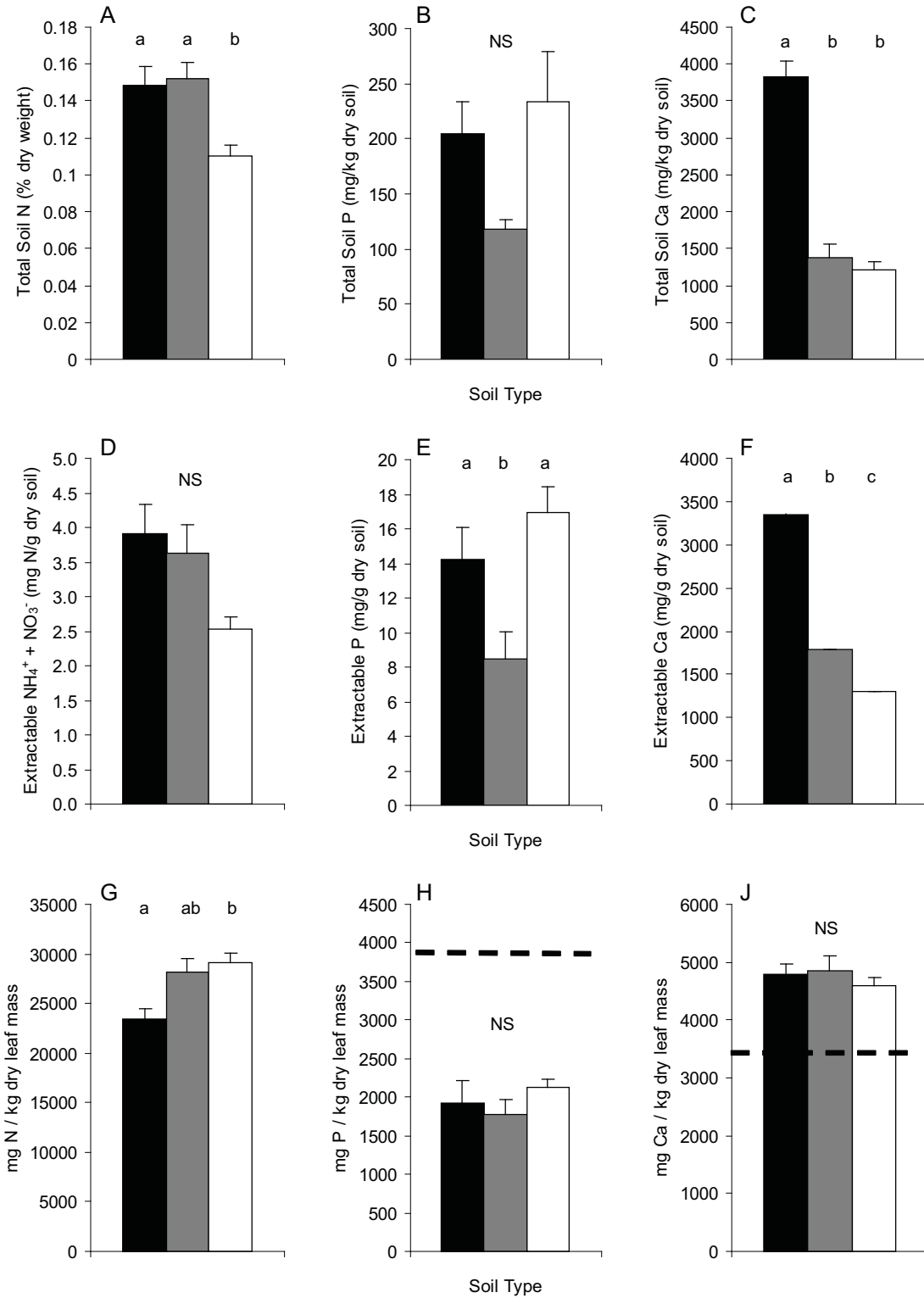


FIGURE 1. Variation in concentrations of N, P, and Ca in (A–C) the total soil pool, (D–F) inorganic soil pool, and (G, H, J) wet-season grass leaves across soil types ($n = 60$ red soil sampling locations, 20 transition soil locations, and 20 black cotton soil locations) at the Mpala Research Centre in central Laikipia. Dashed lines in (H) and (J) show forage phosphorus and calcium requirements for lactating wildebeest (Murray, 1995).

those derived from bomas abandoned more than 40 years ago (old glades).

In the red sands habitat, soil nutrient content is substantially enriched on abandoned boma sites relative to the surrounding landscape and also varies in relation to the age of abandoned boma sites. Over the first four decades following boma abandonment, soil carbon and nitrogen decline relatively rapidly, while soil phosphorus is more tightly retained; old glades contain 1.9 times more N and 7.4 times more P than surrounding soils (Augustine, 2003a). Analysis of soil phosphorus availability using the Mehlich-3 extractant (Mehlich, 1984) from soil cores (0–15 cm depth) collected at four glades and four paired bushland sites revealed 27 times more extractable phosphorus in glade versus bushland soils (Figure 2, left; paired $t_3 = 4.82$, $P = 0.02$). In the black cotton habitat, soil cores (0–30 cm depth) collected from nine glades and nine black cotton sites showed 1.84 times more total soil N in glades, whereas phosphorus availability measured using the Olsen-P extractant (Olsen and Sommers, 1982) revealed 20 times more extractable phosphorus in black cotton glades compared to nonglade soil (nitrogen: $t_8 = 4.47$, $P = 0.0002$; phosphorous: $t_8 = 3.48$, $P = 0.008$; Figure 2, right). Although the Olsen extraction appears to provide lower estimates of soil P availability compared to

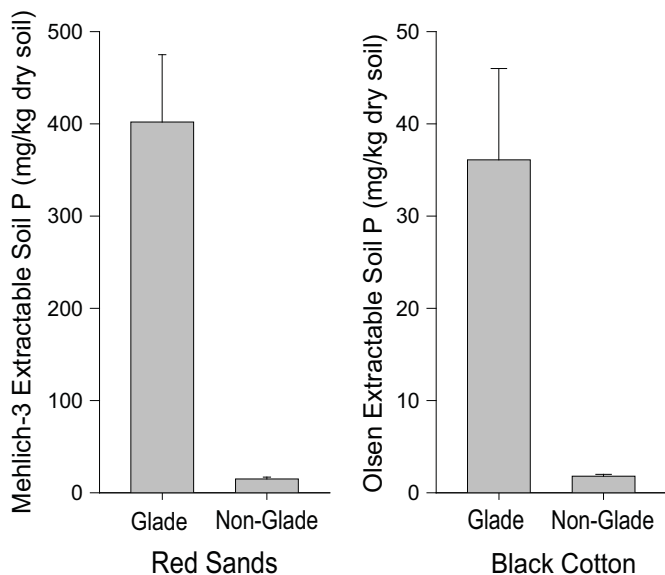


FIGURE 2. Differences in extractable soil phosphorus content of glade and surrounding nonglade soils for the red sands (four glade versus four paired nonglade sites; paired $t_3 = 4.82$, $P = 0.02$) and black cotton soil (nine glade versus nine paired nonglade sites; $t_8 = 3.48$, $P = 0.008$) at Mpala Research Centre in central Laikipia.

the Mehlich extraction, both methods revealed the ≥ 20 -fold larger soil P pools in glade compared to nonglade soils.

A study of grass nutrient content in the red sands habitat during the wet season evaluated variation associated with glades, topography, and plant species (Augustine, 2004). Results from this study, combined with previous analyses of spatial variation in grass species distributions (Augustine, 2003b), illustrate the variation in forage P content that a selectively foraging impala could experience in the red sands habitat (Figure 3). Mineral requirements specific to impala have not been evaluated; hence, we rely upon previously discussed requirements on the order of 3100–4000 mg P/kg dry matter for wildebeest and cattle (McDowell, 1985; Murray, 1995). Although a selectively foraging ungulate moving through the red sands habitat experiences substantial small-scale variation in forage P content among grass species and topographic positions, access to P-rich forage in glades is clearly important for meeting dietary demands (Figure 3). Within the nutrient-poor red sands habitat, P content of grasses is similar to grasslands in the Serengeti ecosystem of Tanzania, which

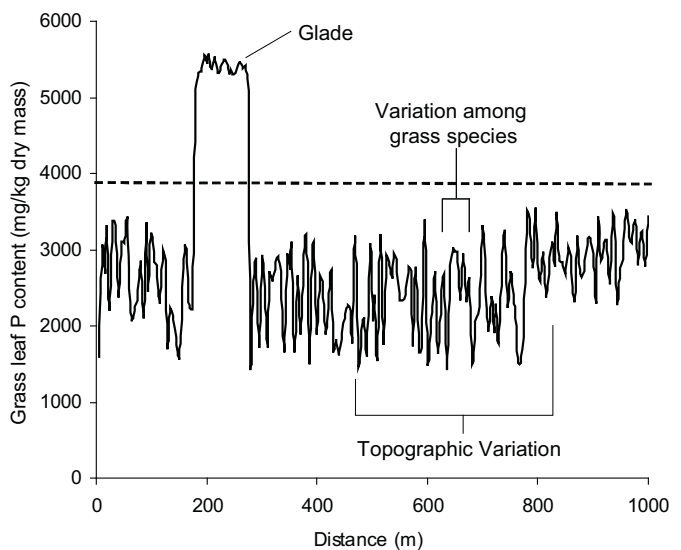


FIGURE 3. Spatial representation of variation in forage phosphorus content that an herbivore in the red sands landscape of Laikipia, Kenya, might encounter while traveling along a 1 km transect beginning at a ridge, passing through a glade, and ending in a drainage, based on forage P content analyses (Augustine, 2004) and grass species distributions in the red sands habitat (Augustine, 2003b). Variation at scales of 5–15 m results from the patchy distribution of dominant grasses. The dashed line shows the forage P requirement measured for lactating wildebeest (Murray, 1995).

migratory ungulates are only able to use during the dry season, outside of calving and peak lactation periods. In contrast, P content in glades is similar to the shortgrass Serengeti plains to which ungulate herds migrate in the wet season for calving (McNaughton, 1990). Phosphorus content in glade grasses at MRC is also similar to grassland “hot spots” in the Serengeti ecosystem that support high concentrations of resident herbivores, including impala (McNaughton, 1988). If a selectively foraging impala were able to acquire a dietary intake of 2800 mg P/kg forage from the red sands bushland habitat, for example, by foraging in lowlands and feeding on red sands grasses such as *Cynodon dactylon* and *Pennisetum stramineum*, the impala would still need to acquire 42% of its forage from glades in order to achieve an overall dietary P content of 3900 mg P/kg.

Similar measures of grass nutrient content in black cotton glades have not yet been conducted. However, the soil P and N enrichment documented in black cotton glades combined with low grass P content found in grasses on the background black cotton soil suggests that (1) grasses on black cotton glades are likely to be enriched in N and P and (2) the level of P enrichment may be important for meeting nutritional requirements of wild grazers. Quantitative measures of how grass nutrient content varies in the black cotton habitat in relation to glades versus other factors such as seasonality, termite mounds, topography, and plant community composition are clearly needed.

INFLUENCE OF ABANDONED BOMAS ON UNGULATE DISTRIBUTION

On the basis of the previous findings for forage nutrient content, it is not surprising that in the landscape encompassing both black cotton and red sands habitats, some native ungulate species exhibit preferential use of abandoned bomas. In both habitats, we used dung group surveys of transects in abandoned bomas compared to the surrounding background vegetation to quantify these patterns. In the red sands habitat, we measured dung group densities in December 1999 at (1) all known glades abandoned between 10 and 40 years ago ($n = 38$), (2) glades abandoned >40 years ago ($n = 16$), and (3) a grid of transects distributed systematically across all bushland habitat at MRC ($n = 46$). Dung groups were counted within three randomly located 20 m transects using a 2 m width for impala dung and a 4 m width for all other species at each glade site and within a 50 × 4 m area for each bushland transect. Cattle dung group counts could possibly include cape buffalo dung, but direct counts of both species

indicated that buffalo were extremely rare (65 times less abundant than cattle) in the study area (D. J. Augustine, unpublished). Data were analyzed by standard one-way ANOVA, with Tukey's HSD for pairwise comparisons.

In the black cotton habitat, we measured dung group densities in August 2003 at five glades abandoned <42 years ago and five glades abandoned >42 years prior to sampling. Inside each of the 10 glade sites we identified and counted all herbivore dung within two 400 m² blocks (except at one site where we had only one block). We also sampled dung group densities outside of each of the 10 glade sites along two 4 × 100 m transects, one located 100 m away from the boma site and one located 200 m away. Data were analyzed as a split-plot ANOVA, treating glade age as the main plot effect and location (inside, 100 m or 200 m) as the subplot effect. Pairwise comparisons were made with planned orthogonal independent contrasts testing (1) inside versus outside and (2) 100 m versus 200 m.

In the red sands habitat, impala dung group densities were 21–35 times greater in old and young glades compared with surrounding bushland habitat (Figure 4; $F_{2,95} = 28.2$, $P < 0.0001$). For zebra (*Equus burchelli* and *E. grevyi* combined), dung group densities were four to five times greater in glades compared with surrounding bushland (Figure 4; $F_{2,95} = 11.98$, $P < 0.0001$). For eland (*Taurotragus oryx*), densities were four times greater in young glades versus bushland habitat, with intermediate densities in old glades (Figure 4; $F_{2,95} = 11.82$, $P < 0.0001$). For cattle, densities were three times greater in glades compared to surrounding bushland habitat (Figure 4; $F_{2,95} = 29.6$, $P < 0.0001$). Waterbuck (*Kobus ellipsiprymnus*) did not show selection for glades ($F_{2,95} = 2.19$, $P = 0.12$). The two browsers (elephant, *Loxodonta africana*, and giraffe, *Giraffa camelopardalis*) also did not select glades ($F_{2,95} < 0.65$, $P > 0.53$).

In the black cotton habitat, dung group densities of hartebeest (*Alcelaphus buselaphus*) and Grant's gazelles (*Gazella granti*) were three to seven times higher inside boma sites of both age classes relative to surrounding bushland (Figure 5; inside versus outside, hartebeest: $F_{1,16} = 5.56$, $P = 0.03$; Grant's gazelles: $F_{1,16} = 8.75$, $P = 0.01$). Cattle densities were three times higher in young glades (new: in versus out, $F_{1,16} = 3.92$, $P = 0.07$), whereas oryx (*Oryx beisa*) densities were six times higher in old glades (old: in versus out, $F_{1,16} = 8.10$, $P = .01$). Eland showed an inconsistent response to black cotton glades (location, $F_{2,16} = 0.54$, $P = 0.59$). In contrast to the red sands habitat, elephant dung density was six times higher in newer (<42 years) boma sites in black cotton habitat (new: in versus

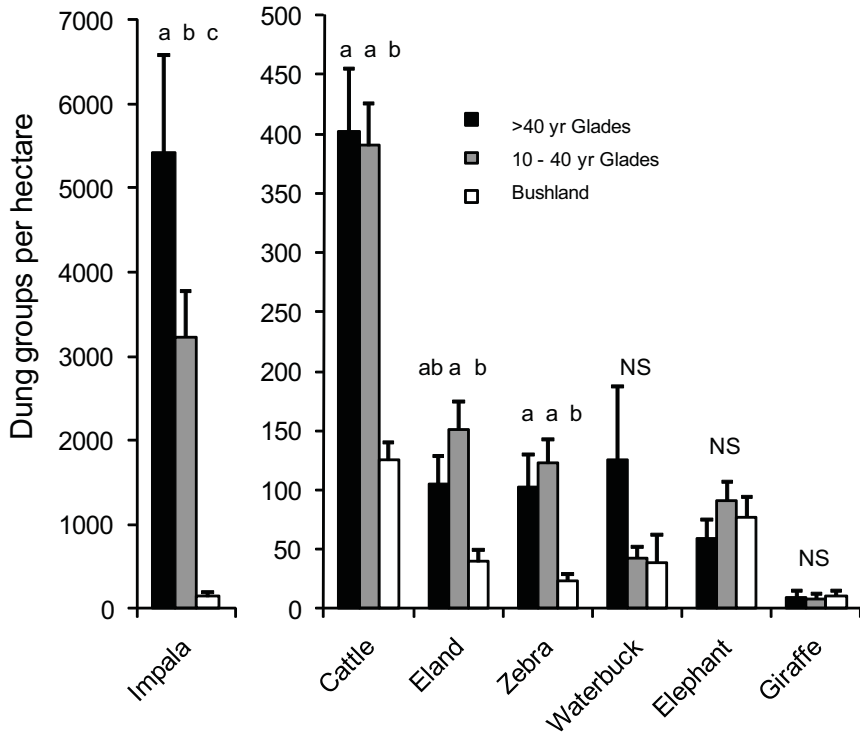


FIGURE 4. Selection of old glades (>40 years since boma abandonment, $n = 16$ sites) and young glades (10–40 years since boma abandonment, $n = 38$ sites) relative to surrounding bushland habitat ($n = 44$ sites) for ungulates in the red sands landscape in central Laikipia, Kenya, as indexed by dung group densities. “Zebra” includes both plains and Grevy’s zebra. Error bars show 1 SE above the mean. For each species, bars with different letters indicate significant ($P < 0.05$) differences between the three habitats, and NS indicates species with no significant differences among the three habitats.

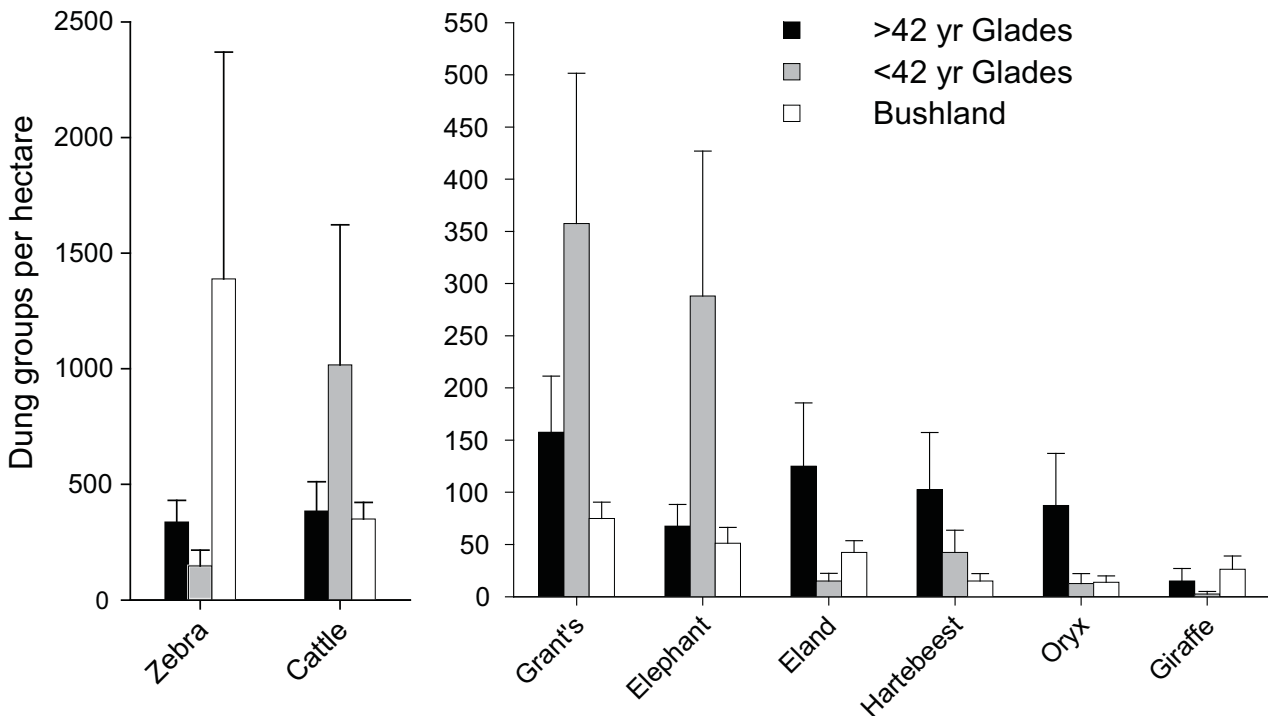


FIGURE 5. Selection of old glades (>42 years since boma abandonment, $n = 5$ sites) and young glades (<42 years since boma abandonment, $n = 5$ sites) relative to surrounding savanna habitats (100–200 m distant from glades, $n = 10$ sites) on black cotton soil in central Laikipia, Kenya, as indexed by dung group densities. “Zebra” includes both plains and Grevy’s zebra. Error bars show 1 SE. For each species, bars with different letters indicate significant ($P < 0.05$) differences between the three habitats, and NS indicates species with no significant differences among the three habitats.

out, $F_{1,16} = 5.62$, $P = 0.03$). Giraffe avoided boma sites (in versus out, $F_{1,16} = 7.67$, $P = 0.06$). Likewise, zebra densities were not elevated inside black cotton glades and instead showed a nonsignificant trend toward avoidance of glades relative to woodland (location, $F_{2,16} = 1.52$, $P = 0.25$).

We have also used infrared camera monitors to conduct more detailed analyses of how glades influence seasonal and spatial distribution of impala in the red sands habitat (Augustine, 2004). Camera monitors showed that impala preferentially used glades compared to surrounding bushland in both wet and dry seasons but increased glade use ninefold during wet compared to dry seasons (Figure 6A). Furthermore, impala density was highly correlated with the distance to the nearest glade or abandoned boma (Figure 6B), with impala density declining to extremely low levels in areas where glades were more than 600 m distant.

Overall, our studies demonstrate that across diverse soil types, the management of livestock via bomas creates nutrient hot spots within the landscape. These hot spots have a strong influence on wild ungulate distribution and potentially influence overall carrying capacity. Our work on impala showed that (1) glades are critical for meeting wet-season phosphorus requirements, (2) impala show strong preferential use of glades, especially during the wet season, and (3) portions of the landscape distant from glades support few impala. Fine-scale distribution analyses have not been conducted for other wild herbivores, but many species show clear preferential use of glades (Figures 4 and 5). Our surveys have also documented some notable differences between red sands and black cotton habitats, especially with zebra and elephant use of glades. Factors such as differences in grazing pressure or in the structure and composition of the plant communities in the two habitat types may be involved and merit future research attention.

Our studies also suggest that anthropogenic glades can contribute to the viability of ungulate species of conservation concern in the Ewaso ecosystem. Although species such as plains zebra and Grant's gazelles may be adaptable to livestock-dominated landscapes, others such as impala, hartebeest, eland, waterbuck, and buffalo may require deliberate management efforts (Georgiadis et al., 2007a). The hartebeest population in Laikipia is the largest of only three distinct populations of *A. buselaphus* remaining in Kenya that are hybrid between two morphotypes (*A. b. cokei* and *A. b. lelwel*), the remainder having been extirpated by human activities. Hartebeest have been declining in Laikipia over the past decade and serve as one of several focal species for conservation efforts in the region (Georgiadis et al., 2007b). In the black cotton habitat, hartebeest are strongly attracted to glades, especially

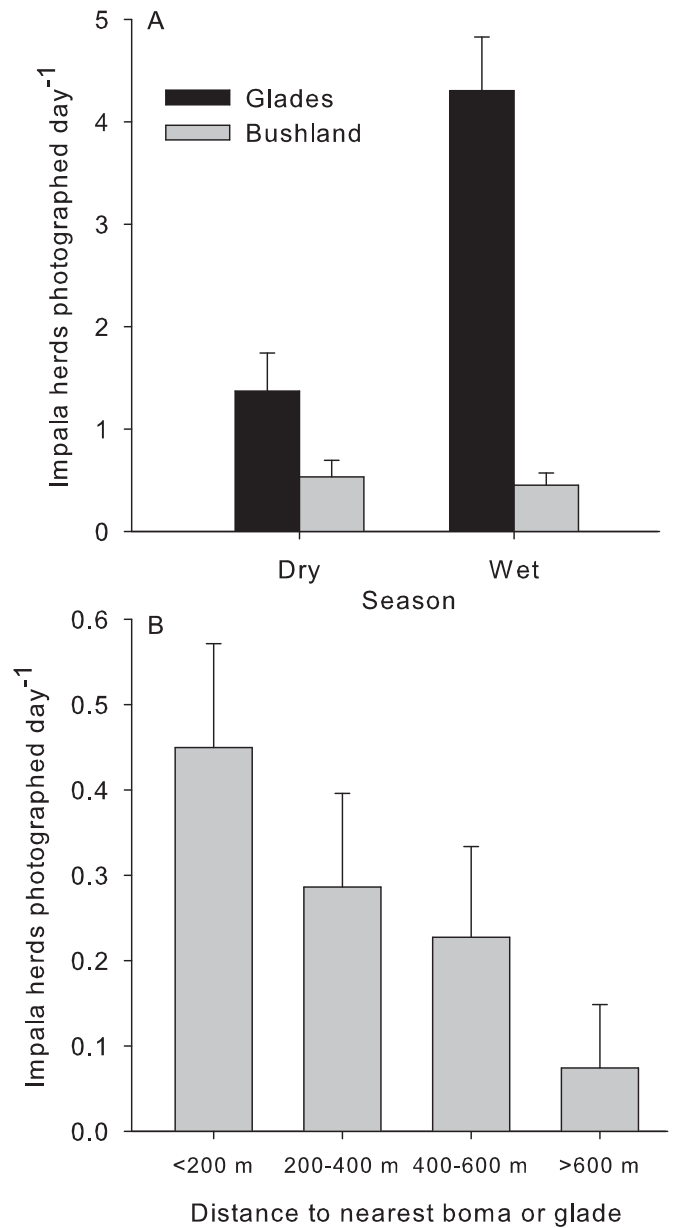


FIGURE 6. (A) Seasonal variation in the abundance of impala in glades versus adjacent red sands bushland habitat and (B) spatial variation in wet-season impala abundance within bushland habitat as a function of the distance to the nearest glade or abandoned boma in Laikipia, Kenya, 2001–2002. Impala herds were present in glades at a significantly higher rate during wet versus dry seasons (season \times habitat interaction: $F_{1,27} = 23.96$, $P < 0.001$). Error bars show 1 SE above the mean, and the number above each bar in (B) shows the number of locations sampled within each distance class. Reprinted from Augustine (2004) with permission; © The Wildlife Society.

younger glades (Figure 5). Hartebeest also preferentially forage on abandoned bomas in southern Kenyan rangelands (Stelfox, 1986). Hartebeest are primarily associated with open, treeless grasslands; provision of nutrient-rich glades in combination with such open areas may be one important means to enhance habitat for the species.

The Grevy's zebra is another rare and declining species, with much of the remaining population found in the Ewaso ecosystem (Williams, 2002). Grevy's zebra at MRC are primarily found in the red sands and adjacent transitional habitats dominated by *Acacia* bushland. Grevy's zebra habitat use at MRC differs for lactating versus non-lactating mares, with lactating mares selecting the shortest, greenest grass swards in the landscape (Sundaresan et al., 2008). Abandoned bomas are the primary source of these shortgrass swards. Use of glades by Grevy's zebra may be constrained by availability of drinking water (which lactating females require frequently) and the locations of active bomas (which Grevy's zebra avoid; Sundaresan et al., 2008). Although Grevy's zebra avoid areas with herders and cattle in the short term, they also appear to benefit from long-term consequences of boma rotation. Consideration of how water sources and shrub density interact with glade distribution could assist in boma placement and rotation planning to provide critical habitat for such declining wildlife species.

LONG-TERM GLADE PERSISTENCE

Glades in the Ewaso ecosystem persist for at least four decades and could potentially persist for centuries, as reported for nutrient-enriched patches in a southern African savanna (Blackmore et al., 1990). During 1961–2000 at MRC, bomas in the red sands habitat were abandoned at a mean rate of 1.15 per year, while long-term glades (i.e., those present in 1961) were invaded by *Pennisetum* at a rate of only 0.08 per year (Augustine, 2003a). In other words, glade density in the landscape was increasing during this four-decade period primarily because existing glades persisted in a nutrient-enriched, *Cynodon*-dominated state for well beyond 40 years. Soil nitrogen can be lost from glades over time via several pathways, including leaching, denitrification, and volatilization, such that long-term glade persistence likely depends upon nitrogen inputs to replenish these losses. Detailed analysis of glade nitrogen budgets at MRC showed that during dry seasons, impala bed within glades (Figure 6) while foraging in adjacent bushland, causing a substantial net input of nitrogen via dung and urine deposition (Augustine et al., 2003). This N input may facilitate long-term glade persistence in the *Cynodon*-dominated state and represents a

pathway by which impala benefit all ungulate grazers that make use of glades, including livestock.

In the black cotton soils, there is more rapid transition from *Cynodon*-dominated glades to glades dominated by *Pennisetum stramineum* (in as few as 20–30 years), but the latter also persist for a minimum of 40 years, and probably much longer. In these black cotton soils, the long-term persistence of glades may be associated with increased termite activity (not seen in the red soil glades), which not only enriches soil fertility but also changes soil texture and reinforces the treelessness of glades. Another factor may be the length of time a boma is occupied by livestock, which in black cotton soils can be limited by rainy-season accessibility. In addition, a recent study of multiple proximate glades in black cotton soils in Laikipia (L. McGeoch, unpublished data) has shown that the areas between glades within 150 m of each other have elevated tree densities and concomitant low use by herbivores, perhaps because of low predator visibility (see below). This result suggests that although bomas can be useful in enhancing wildlife habitat, details of boma density, configuration, and persistence can produce emergent patterns that will also need to be considered.

Taken together, our studies have several implications for boma and nutrient management in this ecosystem. First, boma rotation is key to glade formation and hence ungulate hot spots, indicating boma placement can be used as a tool to attract wild ungulates into particular locations in the future. Fertilization at the hectare scale, particularly with phosphorus, may also be a means to induce herbivore hot spots in desired locations. Sedentarization of bomas or elimination of boma use may have negative long-term consequences for wildlife species such as impala, hartebeest, Grevy's zebra, eland, and Grant's gazelle. Long-term persistence of glades may also be contingent on use by wild ungulates. In bushlands on red soils, where shrub-free glades attract herbivores year-round, dung and urine inputs from native ungulates such as impala can prevent long-term nitrogen loss from glades and hence can maintain them in a shortgrass, *Cynodon*-dominated state (Augustine et al., 2003). In purely grassland habitats, soil and plant nitrogen in glades may decline, and *Pennisetum* cover may increase over time. However, enriched P content in glade grasses is likely to persist for decades in all soil types and to be an important wet-season forage resource for native ungulates.

NATIVE BROWSERS AND RANGELAND SHRUB ENCROACHMENT

Worldwide, rangeland ecosystems are experiencing increases in woody plant abundance and associated declines

in their suitability for cattle production (Scholes and Archer, 1997; Van Auken, 2000). Shifts from grassland to shrubland may be related to changes in climate (Polley et al., 1997; Morgan et al., 2007), fire frequency and grazing intensity (Dublin et al., 1990; Roques et al., 2001; Tobler et al., 2003), and browsing pressure (Dublin et al., 1990). In some areas of Africa, woodlands have declined in protected areas coincident with a concentration of elephants into these areas (e.g., Laws, 1970; Dublin et al., 1990; Van de Vijver et al., 1999). Conversely, woodland expansion is often observed in African rangelands managed for cattle production (Scholes and Archer, 1997; Oba et al., 2000; Roques et al., 2001; Tobler et al., 2003). A consequence of lowered tree or shrub densities may be increased availability of understory nutrients (Treydte et al., 2007), whereas increased densities of trees and shrubs can negatively affect grass productivity (Scholes and Archer, 1997; Smit and Rethman, 2000). High densities of spinescent *Acacia* shrubs can also physically impede cattle access to the understory, effectively reducing forage availability.

Our studies in Laikipia have addressed the effects of native browsers on woody plant dynamics on rangelands where native fauna coexist with cattle. Here we first present baseline information on the abundance of native browsers in the red sands and black cotton landscapes and the history of woody plant dynamics in the district. We then synthesize results of exclosure studies in both red sands and black cotton soils, addressing the effect of native browsers on woody plant dynamics. Finally, we discuss the long-term implications for both cattle and wildlife.

HISTORIC TRENDS IN SHRUBS AND BROWSERS IN THE EWASO ECOSYSTEM

The distribution of woody vegetation and elephants across the Ewaso ecosystem has changed substantially since settlement by European ranchers in Laikipia began in 1912. As reviewed by Thouless (1995), none of the early European explorers, hunters, and ivory traders who traveled through the Ewaso ecosystem during 1880–1910 found elephants in central Laikipia, and this area consisted mostly of open grass plains. Laikipia is now dominated by *Acacia* bushland on red soils and contains extensive areas of *A. drepanolobium* woodland on black cotton soils (Taiti, 1992; Young et al., 1998; Augustine, 2003b; Table 1). As recently as a few decades ago, much of Laikipia was open grassland on both the red and black soils (Heady, 1960; T. P. Young, personal communications with living ranch owners and herders).

Early in the twentieth century, elephants in this region were found only in Samburu district to the north of

Laikipia, but by the 1950s elephants were increasing and expanding their range toward Laikipia (Thouless, 1995). Heavy poaching during the 1970s and 1980s strongly affected elephant numbers and distribution in Samburu. By the 1990s, telemetry studies identified a significant population of elephants (estimated at ~800 individuals) that regularly migrated 80–100 km between pastoral rangelands in Samburu and the commercial ranches in Laikipia (Thouless, 1995). Our studies have examined savanna dynamics on the commercial rangelands in Laikipia utilized by this migratory elephant population. Our own surveys of ungulate densities at MRC during 2000–2002 (distance sampling of 93 km of ground transects in the red sands habitat at 6 month intervals; densities calculated following Thomas et al., 1998) show a continued migration of substantial numbers of elephants into this region during June–October each year (Table 2). In addition, the *Acacia* bushland habitat on the red soils supports high densities of dik-dik, a small antelope that forages predominantly on woody vegetation (Table 2). Dik-dik were unlikely to have been abundant in grasslands that dominated Laikipia early in the twentieth century. Rather, the high abundance of dik-dik and migratory elephants are likely a response, in part, to increases in woody vegetation. Other browsing species also likely to have increased as the density of woody species has increased include giraffe, eland, steinbuck, and kudu.

Current landscape-scale estimates of shrub and tree cover in central Laikipia are approximately 28% for the red sands (Augustine, 2003b) and 31% for the black cotton soils (Riginos et al., 2009). A continental-scale analysis of woody cover in African savannas predicts that in the long-term absence of disturbances (i.e., no browsers or

TABLE 2. Densities of dik-dik and elephant (number/km²) in the red sands habitat at Mpala Research Centre during dry seasons (March) and wet seasons (August) of 2000–2002. CI, confidence interval.

Season	Dik-dik		Elephant	
	Mean density	95% CI	Mean density	95% CI
2000 dry season	130	(99, 170)	0.0	(0.0, 0.0)
2000 wet season	140	(102, 194)	5.2	(1.4, 19.8)
2001 dry season	139	(106, 182)	0.04	(0.01, 0.39)
2001 wet season	139	(119, 164)	2.9	(1.3, 6.4)
2002 dry season	145	(121, 173)	0.3	(0.1, 1.7)
Five-survey mean	139	(124, 156)	1.7	(0.8, 3.4)

fire), the rainfall-limited bound for woody cover on both soil types in central Laikipia based on 500 mm mean annual precipitation is approximately 56% (Sankaran et al., 2005). Continued increases in shrub and tree abundance toward this maximum could have at least two negative effects on herbivores. First, high densities of shrubs and trees can substantially suppress grass production (Smit and Rethman, 2000; Smit, 2004) and hence reduce forage for cattle. In the black cotton habitats, sites with a low density of trees were found to have double the grass production as sites with a high density of trees (Riginos et al., 2009). Further research is needed to quantify the effects of tree density on grass productivity in the red sands habitat. Second, woody encroachment is likely to directly affect some native wild herbivores by reducing the quality of the habitat available to them. In the black cotton habitat, a recent study examined patterns of herbivore use in *A. drepanolobium* woodland habitats that varied from 240 to 2,784 trees per hectare, or 6 to 45% canopy cover. All but the largest herbivore species (elephants) spent significantly more time in areas with low tree density and avoided areas with high tree density (Riginos and Grace, 2008). This preference was independent of grass cover or species composition. Rather, herbivore habitat preference was strongly related to visibility; in more open habitat with low tree density and cover, predators are more visible, making those areas favorable for vulnerable herbivore species. Thus, areas with high tree density represent lower-quality habitat for small- and medium-sized herbivores, including the declining hartebeest. Areas with high tree density, in contrast, actually attracted elephants and experienced more damage per tree (Riginos and Grace, 2008). These relationships suggest that elephants and other native browsers can have important feedbacks on landscape-scale woody vegetation dynamics, with potential benefits to native grazers and cattle alike.

EFFECTS OF NATIVE BROWSERS ON SHRUB AND TREE DYNAMICS IN LAIKIPIA

Two large-scale herbivore exclusion experiments at MRC have demonstrated the effects of native browsers on shrubs and trees. In 1999, a set of exclosures was established in the red sands habitat to examine effects of browsers on bushlands dominated by *A. mellifera*, *A. etbaica*, and *A. brevispica* (Augustine and McNaughton, 2004). Exclusion of browsers for just three years led to rapid shrub encroachment, measured in terms of shrub cover, density, and biomass (see Table 4). This response was due to the effects of two vastly different native species. First, high densities of dik-dik (*Madoqua kirkii*) strongly

suppressed growth of shrubs less than 0.5 m high; exclusion of dik-dik led to rapid recruitment of shrubs into taller height classes, which was the primary determinant of increases in shrub density. Second, browsing elephants focused mainly on large (>2.5 m high) shrubs, significantly suppressing rates of change in shrub cover and above-ground biomass (Augustine and McNaughton, 2004).

On the black cotton soils, the Kenya Long-term Exclusion Experiment (KLEE), initiated in 1995, has examined browser effects on woodland dynamics (Young et al., 1998). Studies at this site have confirmed that cattle do not eat the dominant woody plant, *Acacia drepanolobium* (Odadi et al., 2007), whereas native browsers regularly feed on this species. We used three measurements from the KLEE plots to examine how the exclusion of native browsers has affected woodland encroachment in this ecosystem. First, we monitored annual changes in size of *A. drepanolobium* in KLEE plots from which all large herbivores have been excluded and in KLEE plots to which all large herbivores have access. Briefly, we measured crown breadth, diameter at breast height, and height of all *A. drepanolobium* trees in two 150 × 10 m strip transects at each plot each year during 2004–2007 (see Goheen et al., 2007). We use this data set to quantify differences in canopy cover of adult *A. drepanolobium* (>1 m) between the ninth and twelfth year of large-herbivore exclusion and also changes in height of large trees (>2.5 m) during this time. Second, we measured the height, diameter at 30 cm above ground, and location for every tree >1 m tall within the central hectare of plots exposed to large herbivores and plots from which large herbivores had been excluded. We use these data to compare differences in density and biomass of *A. drepanolobium* stemming from the 10 year exclusion of large herbivores. Third, we measured the cover of all shrub species other than *A. drepanolobium* in the KLEE plots in 2001, which we use to quantify effects of herbivores on the rare shrub species after six years of herbivore exclusion. We used mixed-model ANOVA to analyze these measurements, treating large-herbivore exclusion as a fixed factor and replicate as a random factor.

Large herbivores reduced the density of tall (>1.0 m) *A. drepanolobium* by 32% ($F_{1,2} = 16.14$, $P = 0.06$), reduced mean canopy cover by 28% ($F_{1,2} = 2.54$, $P = 0.25$), and reduced woody biomass of *Acacia drepanolobium* by 29% ($F_{1,2} = 5.88$, $P = 0.14$; Figure 7). Even more dramatic was the increase in canopy cover of the several species of subordinate trees and shrubs, which accounted for a relatively small fraction of total woody abundance (Table 3). Density of subordinate species was not affected by the exclosure treatment, but established plants that had been suppressed by constant browsing were released when

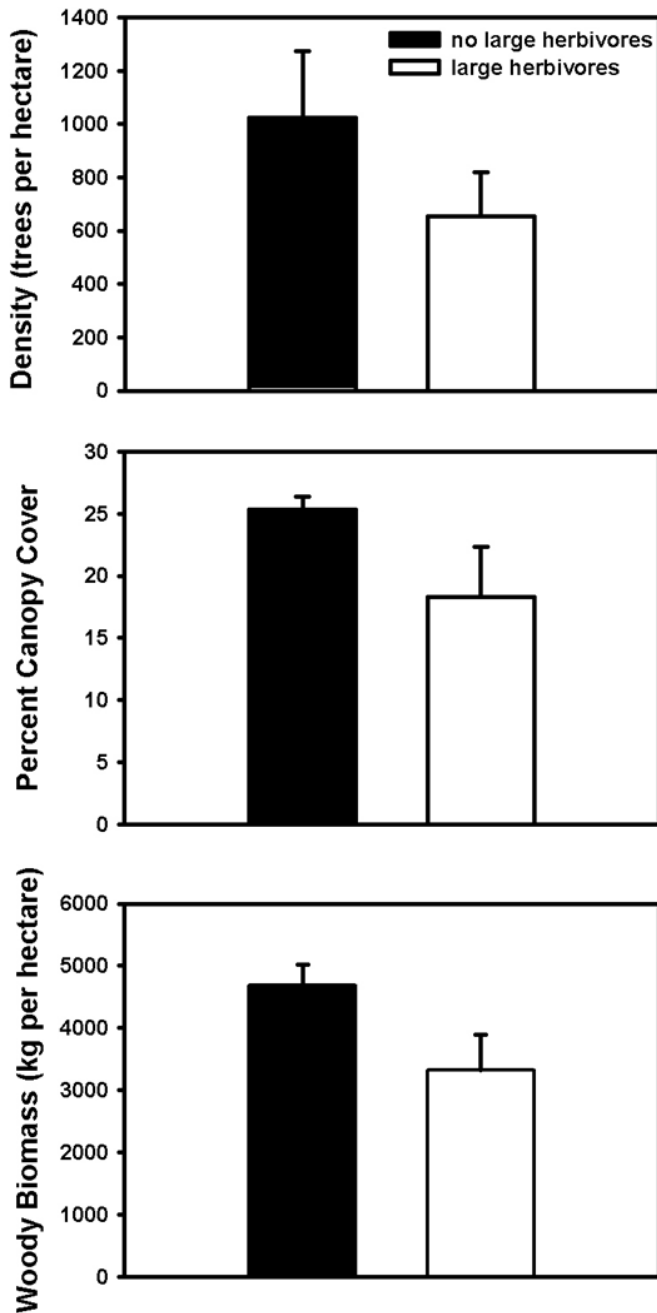


FIGURE 7. Effects of removing large herbivores on the density of tall (>1.0 m) individuals, percent canopy cover, and woody biomass of *Acacia drepanolobium* in the Kenya Long-term Exclusion Experiment. Error bars show 1 SE above the mean; $n = 3$ enclosures and 3 paired control sites for each comparison.

protected from herbivory. The mean canopy sizes of some species increased by as much as twentyfold, and the percent contribution to woody cover across all these species was 12.8% in enclosures compared to 3.8% in the presence of browsers (Table 3).

Our studies have shown that browsers strongly influence woody vegetation dynamics in both soil types, and they also highlight differences in the strength of browser effects (Table 4). Following the experimental removal of native browsers, the cover, density, and biomass of shrubs have been increasing on both soils, but at three to seven times greater rates on red sands compared to black cotton soils (Table 4). One potential factor underlying these rate differences may be high dik-dik densities combined with substantial elephant browsing pressure in the red sands, compared to elephants being the only high-density browser in the black cotton habitat.

A second important factor influencing shrub encroachment rates may be differences in herbivore resistance traits of the dominant *A. drepanolobium* on black cotton soils compared to the dominant *Acacia* species in the red sands. Results for the subdominant shrub species on the black cotton soil, which showed a fourfold increase in cover over just six years (Table 3), also indicate that browsers exert less control over *A. drepanolobium* compared to other co-occurring woody species. Ant symbionts that occur on *A. drepanolobium* effectively protect host trees and greatly reduce browse intake by elephants (Goheen and Palmer, 2010). In addition, subordinate species in the black cotton habitat may experience low rates of growth and reproduction on black cotton soils relative to red soils and therefore may not be able to compensate after being browsed by large herbivores (Harper, 1969; Holt and Lawton, 1994). Fire is another management tool that has substantial potential to influence shrub dynamics and interact with the effects of browsing ungulates (Dublin et al., 1990). There is widespread belief among ranchers, pastoralists, herders, and ecologists that fire, and probably intentional burning, was once far more frequent and widespread in Laikipia in previous centuries and that it suppressed woody plant densities. Fire effects may be stronger in the black cotton habitat because of the continuous understory grass cover, but grass cover in the red sands would likely have been great enough in at least some years to carry a fire. In addition, there can be synergistic effects of fires and herbivores. In a recent study in the black cotton habitat at MRC, burnt *A. drepanolobium* trees were found to survive the fires themselves but later to succumb to increased browsing pressure in the burned areas (Okello et al., 2008). Using ground and satellite-derived measurements of canopy cover, we estimate that although shrub cover on unburned KLEE plots accessible to native wild herbivores was 18% (Figure 7), the combination of fire and native herbivore presence reduced average canopy cover to 13%. These findings emphasize the need to understand herbivore responses to

TABLE 3. Differences in canopy cover of nine subdominant shrub species in the black cotton habitat after six years of large-herbivore exclusion. Although these species are typically rare within the plant community, following browser exclusion, they exhibited more rapid rates of increase than the dominant woody species, *Acacia drepanolobium*. For three species, there was insufficient sample size for reliable statistical analysis. Here n.a. denotes statistic is not applicable.

Species	Mean Percent Canopy Cover		Ratio	F	P
	Herbivores excluded	Herbivores present			
<i>Cadaba farinosa</i>	3.36	1.42	2.4	15.5	0.0002
<i>Balanites aegyptiaca</i>	4.23	1.06	4.0	36.4	<0.0001
<i>Acacia mellifera</i>	2.95	0.89	3.3	4.59	0.038
<i>Lycium europaeum</i>	0.86	0.36	2.4	n.a.	n.a.
<i>Rhus natalensis</i>	0.92	0.04	22.0	2.72	0.14
<i>Grewia</i> spp.	0.17	0.02	6.9	7.80	0.019
<i>Boscia angustifolia</i>	0.15	0.03	4.4	3.67	0.07
<i>Acacia brevispica</i>	0.14	0.01	10.6	n.a.	n.a.
<i>Lippia javanica</i>	0.05	0.004	12.5	n.a.	n.a.
Total	12.82	3.84	3.3	n.a.	n.a.

fires in semiarid rangelands in order to take full advantage of burning as a management tool.

CONCLUSIONS

Two themes in African wildlife conservation have emerged over the past decade. The first is the underlying importance of habitat heterogeneity across multiple spatial scales in sustaining biodiversity (du Toit et al., 2003; Cromsigt and Olff, 2006). The second is the critical role of nonprotected lands, especially managed rangelands, in sustaining Africa's large mammalian fauna (Prins et al., 2000). These themes are related, in that protected areas of Africa often do not encompass sufficient heterogeneity across scales to maintain the range of habitats that sustain diverse and abundant mammalian communities. Our studies show that facilitation via habitat modification is an important pathway for cattle-wildlife interactions in semiarid rangelands. First, nutrient-enriched patches created by abandoned cattle bomas can persist for decades to centuries and provide a key source of nutrient-rich forage for both native and domestic grazers. Nutrient-rich glades that develop from abandoned bomas in the red sands habitat not only sustain local impala abundance but are also maintained as glades by nitrogen inputs from impala (Augustine et al., 2003). Such feedbacks and interactions among cattle bomas, soil and plant nutrients, and

wild ungulates indicate that ranch managers can influence the long-term distribution and abundance of wild ungulates through the placement and rotation of current bomas. Second, although cattle can directly compete with native grazers for forage (Young et al., 2005), native browsing ungulates can provide an important compensatory benefit to cattle by controlling shrub encroachment. There is even evidence that the ability of elephants to reduce forb cover may interact with effects of cattle grazing in a manner that reduces competition between cattle and zebra (Young et al., 2005). Soils have a strong influence on the structure of woody plant communities and rates of shrub encroachment, but the influence of native browsers appears to be robust across such variation.

To directly measure the importance of such facilitation through habitat modification, we would ideally compare ranches with dynamic boma management and the presence of native fauna to ranches where bomas are not rotated and native fauna are excluded. An example of the latter is provided by a large ranching enterprise in the coastal savannas of Tanzania. There the 462 km² Mkwaja ranch was managed for cattle production using a system of permanent paddocks where cattle were kept at night; native ungulates were rare throughout the property (Tobler et al., 2003; Treydte et al., 2006). Over a 48 year period, this intensive, cattle-only ranching operation proved to be economically and ecologically unsustainable, primarily because of severe bush encroachment that developed in

TABLE 4. Summary of the effects of native browsing ungulates on woody plant dynamics at the Mpala Research Centre in central Laikipia, Kenya. Browser effects in the red sands habitat are from Augustine and McNaughton (2004) and Young and Augustine (2007). Browser effects in the black cotton habitat are derived from Gadd et al. (2001), Goheen et al. (2007), Riginos and Young (2007), and this chapter (see Figure 7).

Dynamic	Red sands (<i>A. etbaica</i> and <i>A. mellifera</i>)	Black cotton (<i>A. drepanolobium</i>)
Seed production	No effect	Reduced by half in the presence of browsers
Twig growth rate	Annual twig growth rates negative or zero in the presence of dik-diks; positive and rapid in the absence of dik-diks; no detectable browser effects above dik-dik foraging height	Simulated giraffe browsing resulted in compensatory twig regrowth (i.e., no negative short-term effect on twig biomass), but this may occur at the expense of long-term growth and/or seed production
Sapling recruitment	Recruitment into 0.5–1.5 m height class reduced sixfold by browsers, primarily due to effects of dik-dik	Enhanced in the presence of large herbivores, despite suffering greater browse damage; enhanced recruitment likely due to reduced density of conspecific adult trees
Shrub growth in large size class	Browser presence reduced canopy volume and height for shrubs >2.5 m tall, primarily due to elephant damage	Browser presence reduced vertical growth by 49% over three years for trees >2.5 m tall, primarily due to elephant damage
Net browser effect on woody plant abundance		
Change in shrub density	No change in the presence of browsers; rapidly increasing (+137 individuals ha ⁻¹ yr ⁻¹) with browser removal	Adult trees >1.0 m increasing (+37 individuals ha ⁻¹ yr ⁻¹) with browser removal
Change in shrub cover	Shrub cover increasing rapidly with browser removal (+1.92% per year) and declining (-0.75% per year) in the presence of browsers	<i>A. drepanolobium</i> cover increasing slowly with browser removal (+0.7% per year); cover of other shrub species three times greater after six years of browser exclusion.
Woody biomass accumulation	Near zero (-26 kg ha ⁻¹ yr ⁻¹) in the presence of browsers; rapidly increasing (+962 kg ha ⁻¹ yr ⁻¹) with browser removal.	Increasing with browser removal (+137 kg ha ⁻¹ yr ⁻¹)

wide bands around the permanent paddocks (Tobler et al., 2003). Similarly in Laikipia, ranches intolerant of browsing wildlife are often characterized by greater tree densities. Although numerous ecological factors differ between coastal savanna and the Ewaso ecosystem, the long-term patterns observed in these rangelands illustrate the potential importance of boma rotation and browsing ungulates in sustaining the Ewaso ecosystem.

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