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INFLUENCE OF CATTLE MANAGEMENT ON HABITAT SELECTION BY IMPALA ON CENTRAL KENYAN RANGELAND

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Abstract: In sub-Saharan Africa, the widespread practice of corralling livestock overnight in thorn-scrub "bomas" creates nutrient-enriched patches within rangelands that can subsequently support unique plant communities for decades to centuries after boma abandonment. These nutrient-rich patches (glades) may be preferentially used by native ungulates that coexist with livestock. To evaluate the potential link between cattle management via bomas and habitat for impala (*Aepyceros melampus*), I examined seasonal patterns of habitat selection by impala and land-scape variation in grass nutrient content on a commercial cattle ranch in central Laikipia, Kenya. Studies using automated, infrared camera monitors showed that impala selected nutrient-rich glades 2.6 times more frequently than surrounding *Acacia* bushland habitat during dry seasons, and 9.6 times more frequently during wet seasons. Significantly greater impala presence in glade versus bushland habitat during dry seasons suggests that impala presence may be related to reduced predation risk in shrub-free glades. The large, significant increase in impala presence in glades from dry to wet seasons suggests that impala distribution also is linked to the availability of nutrient-rich forage. In particular, grass nutrient analyses showed that wet-season phosphorus (P) concentrations in grasses throughout the bushland landscape ($\bar{x}$ = 2,125 mg P/kg dry matter, varying from 1,789 to 2,922 mg P/kg across topographic positions and from 1,508 to 3,215 mg P/kg among grass species) were below recommended levels for pregnant and lactating ruminants, while mean P concentrations in glade grasses ($\bar{x} \pm$ SE = 5,346 ± 2.92 mg P/kg) exceeded recommended levels. Results suggest that management to increase the relocation rate and distribution of current cattle bomas can have a positive, long-term effect on the local distribution and abundance of impala.

Savannas often are characterized by a high degree of spatial heterogeneity in soil and plant nutrients that can significantly influence the distribution and abundance of wild herbivores (McNaughton 1988, 1990; Blackmore et al. 1990, Ben-Shahar and Coe 1992, Seagle and McNaughton 1992, Murray 1995, Young et al. 1995). In African savannas, which cover some 65% of the continent and primarily are used as pastoral or commercial rangeland, heterogeneity in soil and plant nutrients is created not only by natural variation in topography and geology but also through the effects of livestock management. On both pastoral and commercial African rangeland, cattle often are corralled nightly in brush-ringed complexes, or bomas, where significant quantities of dung and urine accumulate. Bomas subsequently are abandoned and colonized by a unique, nutrient-enriched plant community as the manure layer becomes mixed with mineral soil (Stelfox 1986, Blackmore et al. 1990, Reid and Ellis 1995, Young et al. 1995, Augustine 2003a). In central Kenya, soil carbon and nutrient content declines in bomas during the first 4

decades after abandonment, but bomas >40 years old remain significantly nutrient enriched relative to surrounding soils for an unknown period (Augustine 2003a), possibly up to centuries (Blackmore et al. 1990). Nutrient-enriched plant communities developed on abandoned boma sites are a widespread feature of African savannas (Blackmore et al. 1990, Reid and Ellis 1995, Turner 1998) and potentially could be an important source of mineral-rich forage for native ungulate herbivores (Stelfox 1986, McNaughton 1988, Ben-Shahar and Coe 1992, Young et al. 1995).

In the Laikipia district of central Kenya, approximately 6,500 km^2 of savanna are managed primarily for commercial livestock production. No formally protected natural areas exist in the district, but management for wildlife on private lands contributes significantly to the local economy through wildlife consumption and ecotourism. Research on wildlife in Laikipia has focused primarily on the plains zebra (*Equus burchellii*), the most abundant native ungulate in the district (Georgiadis et al. 2003). Less is known about habitat use or population dynamics of the impala, the second most abundant ungulate species (Augustine 2002). The impala is a mid-sized (approx 40–60 kg) member of Bovidae distributed from the Transvaal in South Africa to central Kenya and Uganda in East Africa (Jarman

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and Jarman 1973). Impala are most common in transition zones between open grassland and closed bushland or woodland, and are relatively sedentary ungulates with year-round home ranges varying from 50 ha (Murray 1982) to 581 ha (du Toit 1990). Despite their limited mobility, impala respond to the climatic variability of semi-arid environments by grazing during wet seasons—when grasses are abundant—and shifting to a predominantly browse diet during dry seasons (Dunham 1982, Hansen et al. 1985, Klein and Fairall 1986, Meissner et al. 1996).

In Laikipia, impala are especially abundant (averaging 20 individuals/km^2) in *Acacia* bushland communities that dominate on red, sandy soils distributed across central and northern regions of the district (Augustine 2002). One distinctive feature of this bushland landscape is a 2-phase vegetation mosaic consisting of discrete, short-grass plant communities lacking woody vegetation (1% of the landscape) embedded within the background *Acacia*-dominated community (99% of the landscape; Young et al. 1995). These open, short-grass communities (hereafter, glades) are derived from cattle bomas abandoned prior to 1961 (Augustine 2003a). Glades are dominated by the perennial, stoloniferous grass *Cynodon plectostachyus*, while the surrounding bushland landscape contains a discontinuous herbaceous layer and a shrub layer dominated by *Acacia* species (Augustine 2003b). Glades typically are 0.5–1.0 ha in size and occur at a mean density of 1.2 per km^2 within the study area (Augustine 2003a). Glades are widely distributed throughout the landscape but often are locally clumped in their distribution (along ridgelines and at the base of granitic inselburgs) such that some portions of the landscape have higher glade densities while other areas, up to several square kilometers, lack glades.

To evaluate the potential link between cattle management via bomas and impala habitat, I measured variation in grass mineral content and seasonal patterns of habitat selection by impala on a commercial cattle ranch in central Laikipia. Two hypotheses have been proposed to explain high rates of glade use by ungulates: (1) reduced predation risk associated with the absence of shrubs and hence high visibility in glades, and (2) high-quality forage provided by nutrient-rich grasses (Young et al. 1995). I examined the relative importance of forage quality versus other factors as determinants of impala habitat selection by evaluating the use of glade versus bushland habitat during dry seasons, when plant biomass in glades is of similar or lower quality than in surrounding bushland habitat, and again during wet seasons, when mineral-rich forage becomes available in glades. If impala select glades only on the basis of forage quality, they are predicted to exhibit high rates of glade use in wet seasons but no preferential use of glades during dry seasons. If impala select glades only on the basis of nonforage factors such as the lack of shrubs in glades and the resulting high degree of visibility, they are predicted to exhibit similar rates of glade use during dry and wet seasons. If impala select glades on the basis of both forage quality and nonforage factors, they are predicted to preferentially use glades relative to bushland during dry seasons, but then significantly increase their use of glades from dry to wet seasons. To examine these predictions, I quantified seasonal patterns of habitat selection by impala using infrared camera monitors and evaluated these patterns in relation to the mineral content of forage grasses and seasonal variation in forage availability.

METHODS

Study Area

I conducted my research at the Mpala Research Centre and Ranch (MRC; 37°53′E, 0°17′N) within *Acacia* bushland habitat occurring on well-drained, red sandy loam soils (Ahn and Geiger 1987). The study area encompassed 82 km^2 in central and southern MRC bounded on the west by the 1,740-m elevation contour, on the east by the Ewaso Nyiro River, on the south by the MRC property boundary, and on the north by the property boundary with Soit Nyiro ranch. The shrub layer was dominated by *Acacia mellifera, A. etbaica*, and *A. brevispica* (mean shrub cover = 28%), and the understory was dominated by patchily distributed perennial grasses (Augustine 2003b). Abandoned cattle bomas were distributed throughout the study area and likely varied widely in the number of years since they were abandoned. I defined glades as bomas abandoned >40 years ago based on aerial photographs and soil mineralogical analyses. Glades were dominated by *Cynodon plectostachyus* (Augustine 2003b). Permanent rivers occur along the northern and eastern borders of MRC, and dams are well distributed throughout. Mean annual rainfall (1972–2000) was 508 mm (SD = 225 mm; CV = 0.44). Rainfall is trimodal, with long rains in April–May and smaller peaks occurring typically in August and October. A predictable dry season occurs during January–March. The MRC supports cattle man-

aged for market production using traditional Maasai herding methods. All cattle are contained overnight in bomas. Native predators include spotted hyaena (*Crocuta crocuta*), lion (*Panthera leo*), leopard (*Panthera pardus*), and African wild dogs (*Lycaon pictus*).

Impala Habitat Selection

Passive infrared camera monitors (Forestry Suppliers, Jackson, Mississippi, USA) were used to measure seasonal patterns of impala presence in glade and bushland habitats. I studied 8 glades and 8 paired bushland sites during March 2001–February 2002, with dry-season measurements in March 2001 and February 2002 and wet-season measurements during April–August 2001. I selected 3 glade sites because they were the focus of studies of forage productivity and nutrient cycling (Augustine 2002), and I randomly selected 5 additional glade sites from a pool of all known glades within the study area. Cameras were rotated randomly among sites with 1 positioned at the glade edge (facing into the glade) and 1 positioned 150–200 m from the glade in bushland habitat at the same topographic position. Bushland cameras were always mounted such that shrubs did not block the camera's infrared detection beam. Cameras were mounted at 1 m height and left in place for 48 or 72 hr. A 6-min delay was used between photographs, and I analyzed all data in terms of herds photographed/24 hr. I pooled multiple measurements of the same site within a season and based statistical tests on variation among the 8 paired study sites (i.e., variation among true replicates).

To further examine impala distribution within the bushland landscape, the field team conducted additional sampling with the infrared camera monitors during wet seasons in July–August 2001 and April–May 2002. Cameras were placed at randomly selected points within the study area that were located >200 m from any glades or other abandoned bomas (other abandoned bomas were those abandoned <40 yr ago). Cameras were left in place for 48 or 72 hr, and data were again analyzed in terms of impala herds photographed/day. Locations ranged from 216 to 1,001 m from existing glades and abandoned bomas. I combined these data (*n* = 37 sites) with the 8 bushland sites sampled in the seasonal habitat-selection study (all 150–200 m from glades) to examine whether impala presence in bushland habitat (*n* = 45 total locations sampled) was related to the distance to the nearest abandoned boma.

To complement the analysis of seasonal patterns of impala habitat selection, we quantified seasonal variation in herbaceous forage availability via monthly measurements of herbaceous biomass at 3 glade and 3 bushland study sites. For each site and month, both live and standing dead biomass were measured by canopy interception using a calibrated 10-point pin frame (see Augustine 2003*b* for regression equations), and productivity was measured using 1-m³ moveable grazing cages (Augustine 2002).

Grass Nutrient Analyses

To evaluate landscape-scale availability of mineral nutrients in grasses from bushland habitat and glades, we sampled leaves from dominant grasses in the bushland habitat at 60 randomly selected locations within the study area during the wet season in August 2001. At each of the 60 random locations, 30–40 of the youngest, fully-expanded leaves were sampled from the nearest 1-m² plot dominated by any of the 10 most abundant grasses at MRC (Augustine 2003*b*): *Digitaria milanjiana, Cynodon dactylon, Pennisetum mezianum, P. stramineum, Enteropogon macrostachyus, Cymbopogon pospischilii, Themeda triandra, Sporobolus ioclados, Harpachne schimperii,* or *Chloris rhoxburghiana.* Only leaves of the dominant grass species were sampled at each plot unless 2 of these species were co-dominant (both >25% cover), in which case leaves of both species were collected and analyzed separately. We sampled grass leaves rather than all live biomass because impala are relatively selective feeders, and this measure has been used to assess forage quality for ungulates in other African grasslands (McNaughton 1988, 1990; Georgiadis and McNaughton 1990). Leaves of *Cynodon plectostachyus* also were sampled from 3 1-m² plots at each of 6 glades for comparison to bushland grass samples. As upper and lower topographic positions were infrequently sampled by the random locations, leaves of *C. dactylon* also were sampled from 6 swards located at lowland positions along water drainages and 3 swards located at upper hillslope and ridge positions. Only leaf samples from the random locations were used for comparison of grass nutrients in bushland versus glade habitats, but the additional lowland and ridgeline sampling points were used in comparisons among grass species and topographic positions. Leaf samples were air dried and delivered to Syracuse University (Syracuse, New York, USA). Leaves were analyzed for nitrogen (N) content by Dumas combustion with
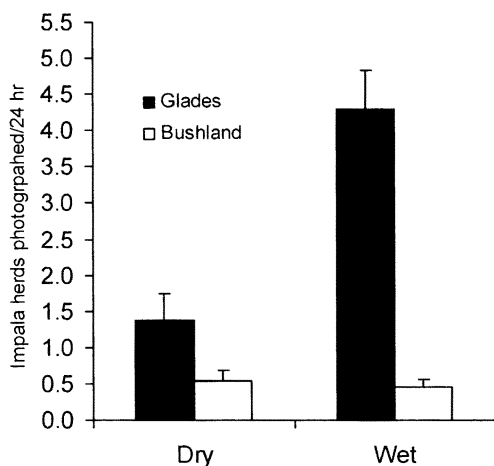
Fig. 1. Seasonal patterns of impala presence in glade versus bushland habitats in Laikipia, Kenya, 2001–2002. Impala were present in glades at a significantly higher rate during wet versus dry seasons (season × habitat interaction: $F_{1,27} = 23.96$, $P < 0.001$). Error bars show 1 standard error around the mean.

a Carlo-Erba CN Analyzer (Milan, Italy) and for total P, calcium (Ca), and sodium (Na) by inductively coupled plasma spectroscopy (Leman Labs PS3000, Hudson, Massachusetts, USA) in simultaneous mode following procedures described by McNaughton (1988).

Statistical Analyses

I analyzed variation in impala presence in relation to community and season as a blocked 2 × 2 factorial analysis of variance (ANOVA), and variation in grass nutrient content was analyzed with standard 1-way ANOVAs. In the analysis of impala presence in relation to distance from the nearest abandoned boma, the high degree of heteroscedasticity in the data violated assumptions required for standard linear regression. Therefore, I analyzed results from all 45 sampling locations with least absolute deviation (LAD) regression, which minimizes the sum of absolute deviations between the model and observed values, rather than the traditional sum of squared deviations (Cade and Richards 1996, Cade et al. 1999). This regression approach estimates the conditional median for the response variable, and rank-score tests for the regression provide an appropriate test for linear models with nonconstant variance (Cade et al. 1999). These data also are presented in terms of the mean impala herd detection rates for each of 4 distance classes (<200, 200–400, 400–600, and >600 m to the nearest glade or boma).
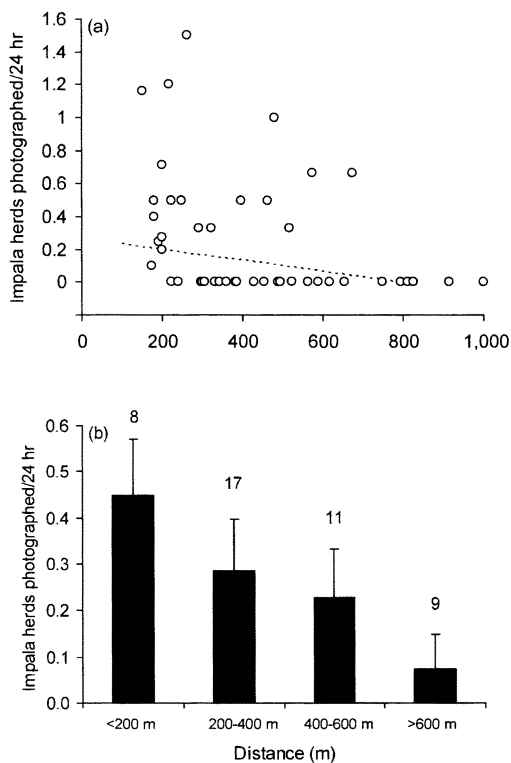

Fig. 2. Variation in impala abundance within bushland habitat during the wet season as a function of the distance to the nearest abandoned boma in Laikipia, Kenya, 2001–2002. Data are shown for all 45 sampling sites (a) as well as the mean detection rates (±1 SE) within each of 4 distance classes (b). The dashed line in (a) shows the median fit based on least absolute deviation regression. The number above each bar in (b) shows the number of locations sampled within each distance class.

RESULTS

Seasonal Patterns of Habitat Selection

Impala were present at higher rates in glade versus bushland habitat in all seasons, but the magnitude of this difference increased significantly from dry to wet seasons (Fig. 1; habitat × season interaction: $F_{1,21} = 24.36$, $P < 0.001$). Analysis of the simple effects by season showed that impala herds were photographed 2.6 times more frequently in glades versus bushland during dry seasons ($t = 2.14$, $P = 0.044$) and 9.6 times more frequently in glades versus bushland during the wet season ($t = 9.86$, $P < 0.001$).

Inspection of the relationship between impala herds photographed per day and distance to the nearest abandoned boma (Fig. 2a) showed a triangular (or "factor-ceiling") distribution in the data (Thomson et al. 1996; Cade et al. 1999).
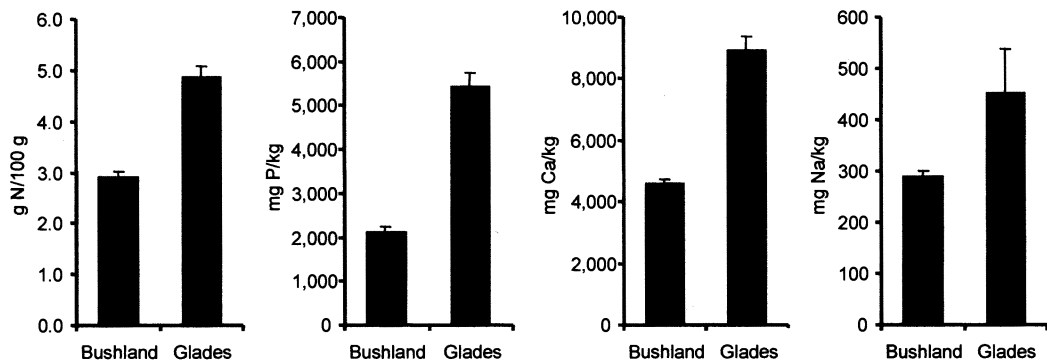
Fig. 3. Mineral nutrient content (nitrogen [N], phosphorus [P], calcium [Ca], and sodium [Na]) of grass leaf blades from 6 glades and 60 randomly selected bushland sampling points at Mpala Research Centre and Ranch in Laikipia, Kenya, 2001–2002. Error bars show ±1 standard error.

Analysis of this distribution demonstrated that the impala herd detection rate decreased significantly with distance from the nearest abandoned boma (Fig. 2a; Rank-score $P = 0.011$). Data also were summarized according to herd detection rates within 4 distance classes (Fig 2b). For locations >600 m from an abandoned boma, the mean rate of impala herd detection was 6 times lower than the rate for locations <200 m from an abandoned boma and 3–4 times lower than the rate for locations 200–600 m from an abandoned boma.

Seasonal Forage Availability

Monthly measurements of herbaceous biomass documented the following patterns of forage availability during the study period. First, during the dry season in March 2001, we found no live aboveground herbaceous biomass at glade or bushland sites. Standing dead biomass averaged only 13 ± 1 g/m² ($\bar{x}$ ± SE) at glades and 29 ± 4 g/m² at bushland sites. Nutrient content of this standing dead biomass was similar in the 2 habitats (0.9 ± 0.1% N for bushland, 1.1 ± 0.2% N for glades) because the biomass consisted primarily of stem material. During the April–August wet season in 2001, live aboveground herbaceous biomass averaged 54 ± 16 g/m² for glades and 33 ± 5 g/m² for bushland sites. During this same period, cumulative aboveground herbaceous productivity was far greater for glades (306 ± 72 g/m²/5 months) than bushland sites (84 ± 12 g/m²/5 months). During the dry season in February of 2002, live aboveground herbaceous forage was again absent from glade and bushland sites, and standing dead biomass was not measured. Although shrub leaf biomass was not measured, green shrub leaves were available at bushland

sites throughout the dry seasons, while no shrubs occurred in glades.

Forage Nutrient Content

Grass leaves from glades were significantly enriched in N, Ca, Na, and especially P relative to mean nutrient content of the dominant bushland grasses ($t_{64} > 3.49$, $P < 0.001$, Fig. 3). Although grass leaf N content differed between glades and bushland, N in bushland grasses was still relatively high (averaging 2.9% N, equivalent to 18% crude protein) and above wet-season requirements for African grazers (Murray 1995). Leaf Na and Ca content also were greater in glades than bushland ($t_{64} > 3.49$, $P < 0.001$). The magnitude of the difference in Na content between habitats was small (300 vs. 440 mg/kg; Fig. 3), and leaf Na content was less than recommended level for lactating ruminants in both habitats (520–1,000 mg/kg). Leaf Ca content in both habitats exceeded lactating ruminant requirements (3,400–6,000 mg/kg; McDowell 1985, Murray 1995).

Glade and bushland grasses differed to the greatest degree in terms of P content, and bushland grasses averaged only 2,288 mg P/kg dry weight. Within the bushland habitat, analyses of variation among grass species showed that *Cynodon dactylon* and *Pennisetum stramineum* were significantly enriched in P (2,800–3,200 mg/kg) relative to other dominant bushland grass species (1,500–2,000 mg/kg, Fig. 4). Variation in leaf N content among the dominant bushland grass species followed similar relative patterns presented for P. Grass P content also varied significantly with topography ($F_{3,78} = 0.0013$) and was greatest at lowland positions (2,920 mg/kg; Fig. 5). From
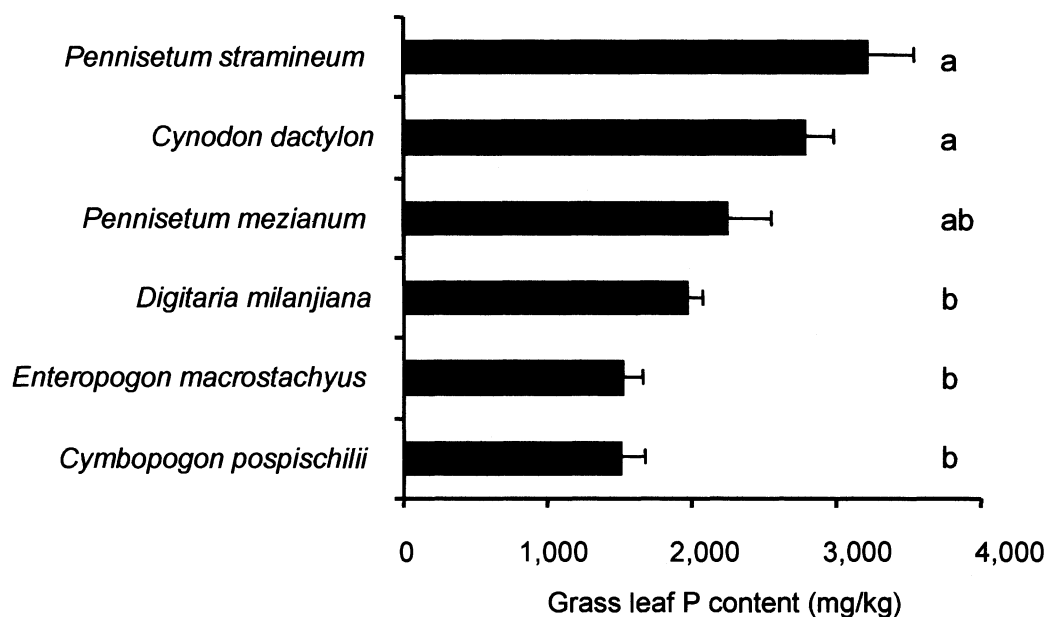
Fig. 4. Variation in grass leaf phosphorus (P) content among dominant grass species in bushland habitat at Mpala Research Centre and Ranch in Laikipia, Kenya, 2001–2002. Error bars show ±1 standard error and letters indicate differences among species at the $P < 0.05$ level.
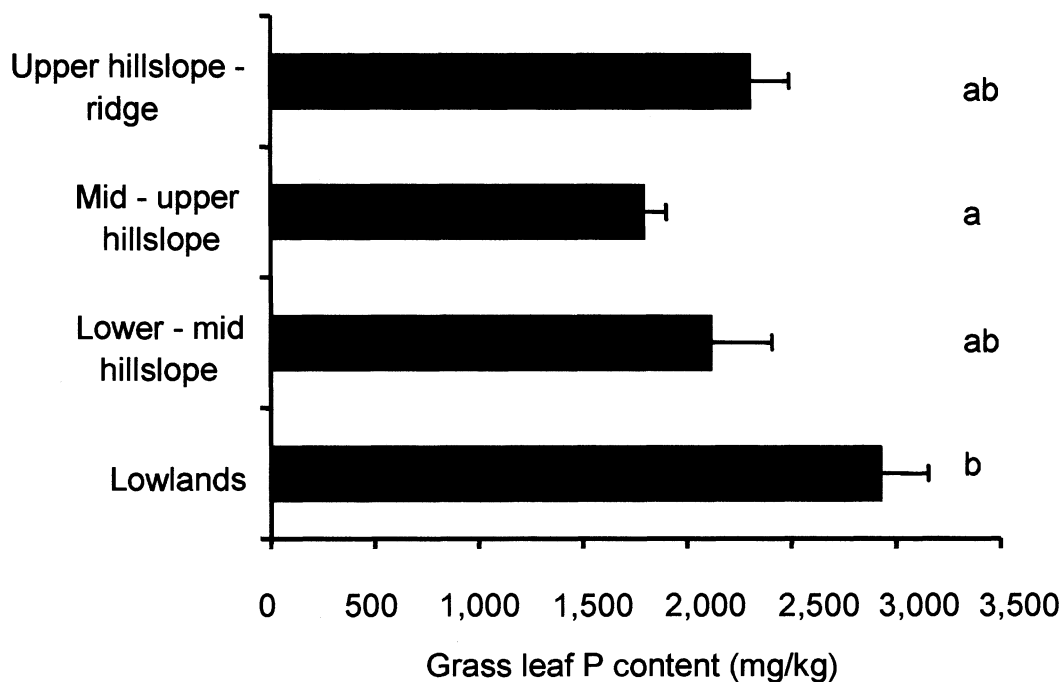

Fig. 5. Topographic variation in grass phosphorus (P) content in bushland habitat at Mpala Research Centre and Ranch in Laikipia, Kenya, 2001–2002. Error bars show ±1 standard error and letters indicate differences among species at the $P < 0.05$ level.

the perspective of large herbivores, wet-season forage P content throughout the bushland habitat (i.e., for all grass species and all topographic positions) is especially low relative to recommended levels for pregnant and lactating females (3,900–6,000 mg/kg; McDowell 1985, Robbins 1993, Murray 1995), while forage P content is adequate in glades (>5,000 mg/kg; Fig 3). In the bushland habitat, forage P content is greater in lowlands (which receive inputs of soil nutrients due to surface runoff from the uplands), and in areas dominated by *Cynodon dactylon* and *Pennisetum stramineum*, but by far the greatest forage P content can be obtained in glades.

DISCUSSION

Analyses of impala habitat selection identified an important link between cattle management and impala habitat quality. The traditional practice of corralling cattle overnight in African rangelands creates fertilized patches within the landscape that provide high-quality forage to cattle and wildlife for decades. As abandoned bomas age and a grass layer develops, grasses are enriched in N, P, and Ca relative to surrounding plant communities (Fig. 3).

Impala were present in glades at significantly greater rates compared to bushland habitat throughout the year. During dry seasons, no live biomass occurred on glades while shrubs in the surrounding bushland provided green forage. Although impala respond to seasonal fluctuations in semi-arid environments by foraging primarily on shrubs during dry seasons (Hansen et al. 1985, Klein and Fairall 1986, Meissner et al. 1996; T. Cerling and D. Augustine, unpublished data), they still preferentially used glades at MRC during the dry season. One explanation is that glades provide bedding sites where predation risk is minimized, but further work is needed to directly assess the effects of predation on impala behavior and population dynamics.

During wet seasons, rates of glade use increased dramatically (Fig. 1), consistent with the hypothesis that forage quality is an important factor underlying glade selection. These findings suggest that glades provide an important source of nutrient-rich forage that is otherwise lacking in this relatively nutrient-poor ecosystem. In particular, P concentrations in glade grasses at MRC (approx 5,000 mg/kg) meet recommended requirements of 4,000–6,000 mg/kg for pregnant and lactating ruminants (McDowell 1985, Robbins 1993). While mineral requirements specific

to impala have not been evaluated, detailed analysis of mineral requirements for wildebeest (*Connochaetes taurinus*) in East African grasslands also showed that the minimum dietary P content in forage for a lactating female was 3,900 mg/kg (Murray 1995). At MRC, wet-season P content in bushland grasses (<3,000 mg/kg) was substantially lower than recommended levels (Fig. 3). Although forage P content is variable in the *Acacia* bushland landscape and ungulates could increase P intake by selectively grazing in lowland swards (Fig. 5) or on *Cynodon dactylon* and *Pennisetum stramineum* (Fig. 4), P intake can be maximized to a far greater degree by foraging in glades. Similarly, in the Serengeti ecosystem of Tanzania, patches of P- and Ca-enriched forage appear to be a critical habitat component for nonmigratory grazers (McNaughton 1988). Furthermore, impala abundance even within bushland habitat was highly correlated with distance to the nearest glade or recently abandoned boma (Fig. 2), providing additional evidence that high-quality impala habitat is tied to the legacy of cattle management via bomas. In contrast to results from Serengeti grasslands in Tanzania (McNaughton 1988, 1990), my analysis also identified Na as a limiting nutrient in all habitats. Geophagy by impala at several locations within the study area (D. J. Augustine, personal observation) may be related to acquisition of this nutrient (Jones and Hanson 1985, Tracy and McNaughton 1995), but how impala meet Na requirements and whether Na restricts their distribution requires further attention.

MANAGEMENT IMPLICATIONS

My study identified an important link between the management of cattle via bomas and long-term impala habitat quality. The widespread use of cattle bomas on commercial and pastoral rangeland is based primarily on the need to protect cattle from theft and predation overnight. Managers rarely consider the long-term implications for nutrient redistribution within the landscape and subsequent effects on wildlife habitat. Previous work showing that nutrient-enriched grassland patches persist on abandoned bomas for >40 years (Augustine 2003a), combined with strong selection of these patches by impala, suggests that ranch managers can manipulate the long-term distribution and abundance of impala on rangelands through careful consideration of boma placement and relocation rates. Conversely, factors that constrain relocation rates, such as increasing sedentarization of bomas around

water points and cattle dips as well as the use of permanent bomas that more effectively deter predators, may cause long-term loss of impala habitat by reducing opportunities for glade development.

ACKNOWLEDGMENTS

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