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Impact of Land Subdivision and Sedentarization on Wildlife in Kenya's Southern Rangelands

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Abstract

Subdivision and sedentarization of pastoral communities is accelerating rapidly across the African rangelands, posing a severe threat to wildlife populations, but few studies have looked quantitatively at the ecological impact of sedentarization. Here we look at the impact of sedentarization on wildlife by comparing ecologically matched subdivided and unsubdivided Maasai pastoral lands (ranches) in semiarid southern Kenya. We found no significant difference in livestock densities on the two ranches but there was a significantly higher wildlife density on the unsubdivided ranch, in both dry and wet seasons. Nonetheless, the unsubdivided ranch still had a higher percentage of grass biomass and ground cover and lower grazing pressure than the subdivided ranch. Distribution of homesteads (bomas) was mostly random on the subdivided ranch, with little area unaffected by human settlement. On the contrary, the unsubdivided ranch had a highly clumped boma distribution pattern, resulting in much of the land being relatively far from permanent human settlement. We show that the regular distribution and permanence of settlements following subdivision and sedentarization greatly reduces wildlife populations both through direct displacement and a reduction of forage. Relative to mobile pastoralism on open rangelands, sedentarization leads to reduced seasonal movements of livestock, lowered grass biomass, and slower grass recovery after very dry periods. This study points to the need to maintain mobile, large-scale herd movements to avoid the heavy impact on grasslands associated with sedentarization of pastoral settlement and herds.

Key Words: grass biomass, land tenure, livestock, Maasai, pastoralism, wildlife conservation

INTRODUCTION

Most arid and semiarid regions of the world have seen progressive sedentarization of pastoral populations over the past two millennia (McPeak and Little 2005). Sedentarization refers to the settlement of previously nomadic or seminomadic peoples into permanent homesteads, with a corresponding decrease in the mobility of people and livestock (Salzman 1980). In Kenya, the causes of sedentarization are reviewed in Groom (2007), and include economic, political, demographic, and environmental factors and, in recent years, legal subdivision of communal lands (Njoka 1979; Roth and Fratkin 2005). Sedentarization has led to a rapid decrease in the mobility of pastoral herds and households throughout the country (Fratkin 1992; Schwartz et al. 1995; Roth 1996). Many studies report negative environmental consequences of land subdivision and sedentarization (e.g., Salzman 1980; Stanley 2000; Ntiati 2002; Seno and Shaw 2002; Worden et al. 2003; Schwartz 2005).

Despite the scale and speed of sedentarization of pastoral lands across Africa and the potential impact on people, rangelands, and wildlife, few studies have looked at the ecological impact of sedentarization. Exceptions include work by Norton-Griffiths (1998), Worden (2007), Boone (2005), and Boone et al. (2005). More recently, Western et al. (2009) used 33 yr of continuous aerial monitoring of ecologically matched ranches to show that wildlife on a subdivided and settled ranch in eastern Kajiado District in Kenya declined sharply relative to the adjacent communally grazed ranch. They attributed the decline to the distribution and permanence of settlements rather than differences in human and livestock density. However, the aerial study was unable to distinguish the exact mechanisms whereby the increase in permanent settlement caused a decline in wildlife. In this study we monitored seasonal changes in standing crop biomass of grasslands in the same two ranches in order to investigate whether the decline in wildlife was 1) due to the direct physical displacement of wildlife by settlements (i.e., loss of range) or 2) the indirect effects on grassland productivity (i.e., loss of forage).

METHODS

Study Area

We compared the same two areas as Western et al. (2009): Mbirikani Group Ranch and Kaputei individual ranches. However, in this study we sampled only a portion of Kaputei, the Merueshi section, which neighbors Mbirikani, as opposed

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to the entire Kaputei ranches. Merueshi excludes the somewhat wetter areas of Kaputei to the north and provides a very close match with Mbirikani in terms of livestock and wildlife prior to sedentarization. To test the match, we compared the figures for wildlife and livestock production on both ranches for the period 1974 to 1978, prior to subdivision. Using 19 aerial counts covering both ranches and using production estimates ($\text{kcal} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$) based on species densities (Western et al. 2009), we found no significant differences in wildlife or livestock (Mbirikani wildlife production 1924 ± 710 SD, Merueshi 1712 ± 1173 SD, $t=1.02$; $P=0.32$; Mbirikani cattle production 32183 ± 10959 SD, Merueshi 22700 ± 17592 SD, $t=1.80$; $P=0.94$; Mbirikani sheep and goat production 7036 ± 3333 SD, Merueshi 5226 ± 3343 SD, $t=1.38$, $P=0.19$). The results confirm that the two ranches were ecologically closely matched prior to the subdivision of Merueshi.

Both Mbirikani and Merueshi ranches are located in the Amboseli-Tsavo ecosystem in southern Kenya (Fig. 1), which, at the time of study, supported abundant and diverse wildlife outside as well as inside the protected areas. Both ranches are classified as Agroclimatic Zones V and VI (arid to semiarid; Sombroek et al. 1982), with temperatures ranging between 8°C at night to 35°C in the day (Altmann et al. 2002). Rainfall is erratic, averaging $350\text{--}500 \text{ mm} \cdot \text{yr}^{-1}$ along a west-east gradient (Worden et al. 2003). Droughts are frequent and have been recorded at least once a decade since 1930 (Campbell 1999; Roth and Fratkin 2005).

Mbirikani is bordered to the east by the Chyulu Hills National Park and by Amboseli National Park to the southwest. A perennial river and associated swamps on the southern border were the only natural permanent water sources on the ranch. The Loitokitok water pipeline with many access points ran along the western portion of the ranch.

Merueshi borders Mbirikani to the north and was formally part of the larger Kaputei Group Ranch cluster. There was no natural permanent water on Merueshi, but the Loitokitok pipeline supplied abundant water along the western portion of the ranch. At the time of study there was one functioning borehole. A seasonal river, the Kiboko River, runs through

Merueshi, providing water in the dry season via temporary, hand-dug wells.

A summary of the key characteristics of each ranch is given in Table 1. Although Merueshi is much smaller than Mbirikani, livestock density on both ranches was similar, and on both ranches the dominant vegetation type was thinly bushed grassland with areas of denser bush.

The population on Merueshi was far more sedentary than Mbirikani's population during the study period, reflecting subdivision and sedentarization that began in the early 1980s (Grandin et al. 1991). By 1981, more than 90% of Kaputei household heads were living in a permanent boma (homestead), compared with only 46% on Mbirikani (Grandin et al. 1991). In 1984, a decision was made by the members of Merueshi Group Ranch to subdivide and privatize the land. Formal demarcation of the plots began in 1991 and was completed in 1997 when title deeds were issued (Merueshi chairman, personal communication, June 2006). Mean plot size on Merueshi was 1.5 km^2 (range $0.7\text{--}4.6 \text{ km}^2$; Groom 2007). Many plots, totaling 99 km of fence line, were enclosed by 2006.

Fieldwork Methods

We investigated the impact of subdivision on wildlife and pasture conditions using subdivided Merueshi as our experimental ranch and unsubdivided Mbirikani as the control. Based on the ecological similarities of Merueshi and Mbirikani and the similarities in livestock and wildlife densities on the two ranches prior to subdivision, we set up monthly measurements of wildlife, livestock, pasture, and human variables to compare the status of herbivores and pastures postsubdivision of Merueshi. The monitoring was conducted over the course of a year (2005), spanning two wet and two dry seasons. Wildlife and livestock variables included density, production, and distribution; pasture variables included pin-frame measurements of grass biomass, ground cover, grazing pressure, and greenness (the latter three measured as a percentage); and human variables included population density, settlement size, and the spread of settlements. The methodology has been described in detail in Groom (2007).

Animal Counts. Wildlife and livestock populations were counted monthly (December 2004 to November 2005 inclusive) using strip transects (Burnham et al. 1980; Caro 1999a) or point transects. On Mbirikani, a minimum of 22 strip transects 4 km in length were laid out each month in a stratified random sampling design according to habitat (Krebs 1999) and wildlife abundance. The start and end points of each transect were determined by a global positioning system (GPS; GPS III+, Garmin). Speed never exceeded $15 \text{ km} \cdot \text{hr}^{-1}$ and the driver and single observer were constant for all transect and counts. Monthly transects took three full days and were usually completed within the first week of each month. Transects were carried out throughout the day, but the counting order was randomized each month to avoid bias. In total, 1132 km on 283 transects were driven in the course of the 12 counts.

The strip width at any point on a transect was determined by the maximum distance at which a Thomson's gazelle (the smallest animal counted) was considered visible either side of the car (see Caro 1999a) and varied with vegetation density

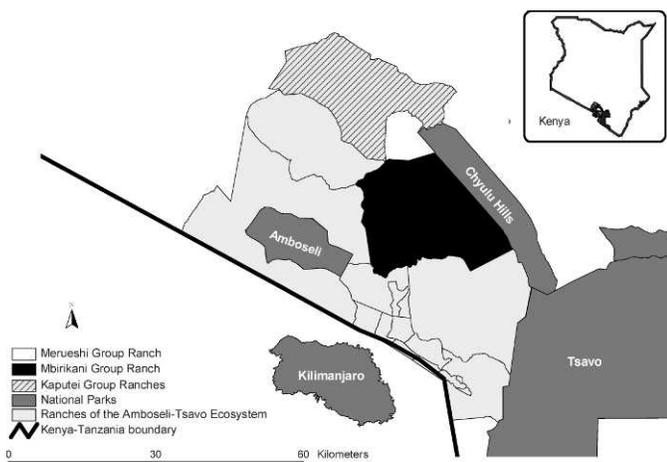


Figure 1. Map of the Amboseli-Tsavo ecosystem showing Mbirikani and Merueshi group ranches and surrounding national parks. Inset shows the location of the study area within Kenya.

Table 1. Key features of Mbirikani and Merueshi ranches, Kenya (2006).

	Mbirikani	Merueshi
Land status	Unsubdivided	Subdivided
Pastoralists	Mobile	Sedentary
Area	1 300 km ²	183 km ²
Members	4 650	117
Total population	> 10 000	2 000
Mean human density	> 7.7 · km ⁻²	10.9 · km ⁻²
Mean permanent boma density ¹	0.35 · km ⁻²	0.66 · km ⁻²
Mean hut density	0.71 · km ⁻²	0.87 · km ⁻²
Livestock	60 000–90 000	11 000
Mean livestock density	57.6 · km ⁻²	60.0 · km ⁻²

¹Figures exclude temporary bomas because numbers of temporary bomas fluctuated significantly. At all times there were considerably more temporary bomas on Mbirikani (unsubdivided) than on Merueshi (subdivided).

(Western 1973). At every sighting, the species, group size, GPS position, and distance and angle from the vehicle were recorded using a digital range finder (Yardage Pro 500, Bushnell Sports Optics Worldwide) and an angle board (Buckland et al. 2001:263). The area of each transect was calculated by multiplying width by length for all the different sections of one transect and summing all sections (Burnham et al. 1980). Species density was calculated by summing the total number of individuals of each species divided by the area sampled (Mduma 1995; Caro 1999a). Caro (1999b) found that this method gives densities that are strongly correlated with densities obtained through other ground-based methods.

Point transects were used where line transects could not be driven. They included one habitat on unsubdivided Mbirikani (where rocky terrain made vehicle access difficult), and the whole of subdivided Merueshi Group Ranch because of the obstruction of fence lines. Fifty randomly chosen point transects were sampled each month on Merueshi and 25 in the habitat not amenable to transect sampling on Mbirikani. The point transects were reached by bicycle or foot. The radius of the circular area to be counted was chosen according to visibility and measured by range finder. Once in position, the observer stood still for 3 min before counting to allow animals time to settle down and resume their activity. Data were recorded as for strip transects.

Circular point transects use the same counting technique as belt transects (Sutherland 1996) and give very similar density estimates (Ruelle et al. 2003; Guidetti et al. 2005). Given that the counts were conducted in areas where foot and bicycle traffic was not uncommon, we did not expect any bias in wildlife behavior between transects done by vehicle or accessed by foot. Indeed statistical comparison of the two counting methods in the two key habitats showed no evidence for a systematic bias; in only 2.8% of cases ($N=72$ tests) were there significant differences in the density estimates obtained by the different methods (Groom 2007).

We used animal densities to compare species abundance between the two ranches and estimated energy production per unit area per year to derive a common metabolic equivalent using the method of Western et al. (2009).

Pasture Conditions. Pasture characteristics were measured every 500 m along each 4-km strip transect, and twice at each

point transect. The characteristics were measured using the pin-intercept method (Sutherland 1996; Mwangi and Western 1998) in which a wooden A-frame supports 10 metal pins of 1 m in length, angled at 33° to the vertical. The frame was placed at a randomly selected site at each sampling point and mean number of grass blades touching each pin was calculated, then an overall mean taken. The mean intercepts were calibrated against plant biomass using the clipped-plot method described by Mwangi and Western (1998). The regression equation used in this study is given by $y=135.94x$ ($R^2=0.752$), where y is dry weight and x is the mean hits per pin.

Every grass blade touching a pin was scored as grazed or not grazed. We derived the percent-grazed estimate from a ratio of the two (Western 1973). The step-point method was used to measure ground cover (Strauss and Neal 1983; Sutherland 1996), with two repetitions (later averaged) at each sampling point.

Settlement and Human Population Survey. A survey of all permanent bomas (those occupied for ≥ 3 mo) was carried out in 2005 on both ranches. Settlement location was recorded by GPS. In addition, once each wet and dry season in 2004, 2005, and 2006, the GPS positions of all temporary bomas (those occupied for < 3 mo) were recorded. All surveys were carried out by one of two trained Maasai enumerators by interviewing respondents 16 yr or older. The enumerators recorded the number of men, women, and children sleeping at the boma that night.

Data Analysis

For comparison between ranches, both animal and pasture data were averaged by season. Pasture characteristics (greenness and percentage of deviation from the overall biomass mean) were used to classify the months into wet or dry seasons. Following the methodology of Mose (2005), any months with grass showing $\geq 25\%$ greenness were classified as wet, all other months as dry. On this basis, January, February, April, May, June, November, and December were classified as wet months, and March, July, August, September, and October classified as dry.

Transect count data and plant data were analyzed using nonparametric statistics (Mann–Whitney U tests) in SPSS (version 12.0) because the large number of zeros in the data set precluded parametric statistics (Caro 1999a). We used total wildlife production as a measure of wild herbivore grazing pressure on pasture plots (Western 1983). An index of dispersion (Fowler et al. 1998) was used to measure the spread of the bomas within each ranch.

We used a general linear regression model to look at the response of average monthly wildlife densities to the average distances to the permanent settlements, grass biomass, livestock densities, seasonality, and interaction between grass biomass and the distance to the permanent settlements across the two sites. Average distance to permanent settlement from points of wildlife sightings were calculated using the nearest-neighbor feature extension in ArcView version 3.2. The data were analyzed based on monthly averages over the entire study period, calculated by taking the average of all data points (grass biomass, livestock sightings, wildlife sightings) on all transects

in a single month, and months were categorized into seasons as explained above.

The general linear regression model used was:

$$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \beta_5 X_1 X_2 + \varepsilon \quad [1]$$

Where y =wildlife density, X_1 =distance to permanent settlements, X_2 =grass biomass, X_3 =livestock densities, X_4 =seasonal effect and ε =error. The data spanned 24 mo. Assumptions of the general linear regression model (linearity, independence, homoscedasticity, and normality) were met. We then applied sequential analysis of variance (ANOVA) on the model (Chambers 1992). Our model design was balanced, and thus the most correlated covariate was analyzed first in the model. Data were pooled across sites to fit the global model but subsequent correlation analysis was carried out to investigate differences between ranches. Distance to water was not included in the model because it was highly correlated with settlement distribution and the individual effects could not be distinguished.

RESULTS

Wildlife

Mbirikani (unsubdivided) had significantly higher densities of wildlife than Merueshi (subdivided) for both dry and wet seasons ($W=69\,581.50$, $P < 0.01$ and $W=94\,077.00$, $P < 0.01$ respectively; Fig. 2). These differences were found to be significant for wild grazers, browsers, and mixed-feeders independently, in both seasons (Table 2), consistent with the results of aerial counts (Western et al. 2009).

Pasture

Tables 3 and 4 give descriptive statistics for pasture conditions on each ranch in dry and wet seasons and the results of Mann-Whitney U tests of significance of the differences. Seasonal results show that, with the exception of biomass in the dry season, Mbirikani had significantly greater grass biomass and ground cover than Merueshi. Merueshi grass was significantly more heavily grazed than that in Mbirikani.

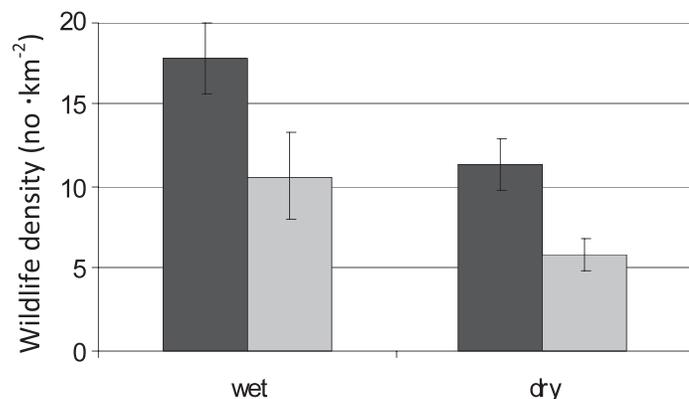


Figure 2. Mean densities (no. · km⁻²; ± SE) of wildlife in dry and wet seasons. Dark bars represent unsubdivided Mbirikani; light bars subdivided Merueshi.

Mean monthly grass biomass on Mbirikani was consistently and significantly greater than on Merueshi (paired samples t test: $t_{11}=5.021$, $P < 0.01$; Fig. 3). Monthly percentage of grass cover was also significantly higher on Mbirikani than on Merueshi (paired samples t test: $t_{11}=4.855$, $P=0.01$). Grass biomass on both ranches showed temporal fluctuations that correlated significantly with the previous month's rainfall (Pearson's correlation: $R=0.777$, $P < 0.01$ and $R=0.657$, $P=0.02$ for Mbirikani and Merueshi respectively). However, the variance of grass biomass on Mbirikani (2 258.44) was more than double that on Merueshi (1 000.79), a difference approaching significance ($F_{11,11}=2.26$, $P=0.096$).

Seasonal changes in the standing mass of grass were derived by measuring the biomass difference from one month to the next. Differences between months gave the rate of grass increase or decrease in $\text{g} \cdot \text{m}^{-2}$ over the preceding month. The most significant departures in rate of change between the two ranches occurred during the growth recovery phase following the seasonal rains in March and October. In the 2-mo growth phase following the rains, the rate of grass growth was significantly greater on Mbirikani than on Merueshi (directional paired t test; $T_3=2.48$, $P=0.045$). In addition, peak biomass (May and December) was significantly higher on Mbirikani than on Merueshi (directional paired t test; $T_1=7.20$, $P=0.04$).

Monthly ratios of herbivore production ($\text{kcal} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$) to grass biomass (Fig. 4) show that the relative grazing pressure, normalized for grass biomass, was far higher on Merueshi in most months and was significantly higher over the full year of monitoring (Paired t test, $T_{11}=-2.44$, $P=0.03$).

Livestock

Livestock densities during the period of study were not significantly different between Merueshi and Mbirikani in either season (dry: Mbirikani $31.1 \cdot \text{km}^{-2} \pm 4.42$ SE, Merueshi $46.3 \cdot \text{km}^{-2} \pm 7.35$ SE, $P=0.84$; wet: Mbirikani $52.4 \cdot \text{km}^{-2} \pm 7.49$ SE, Merueshi $73.4 \cdot \text{km}^{-2} \pm 8.93$ SE, $P=0.33$).

Settlement Patterns

There were 450 permanent bomas and 930 households on Mbirikani Group, amounting to 2.1 households per boma. Permanent bomas showed a highly clumped distribution ($\chi^2_{86}=1\,290.9$, $P < 0.01$) around permanent water sources (Fig. 5). There were many temporary bomas present year-round on Mbirikani. In the dry season, temporary bomas on Mbirikani were found mostly within 10 km of the pipeline road (or other source of permanent water). In the wet season, temporary bomas occurred mostly on the eastern portion of the ranch at the base of the Chyulu Hills (Fig. 5).

Permanent bomas on subdivided Merueshi also showed a clumped distribution ($\chi^2_{52}=104.3$, $P < 0.01$). However, when the bomas clustered around the three small shopping centers (Ilkelunyeti, Merueshi, and Ol Donyo Sambu; Fig. 6) were excluded, the remaining bomas (79%) showed a random distribution ($\chi^2_{49}=63.1$, $P > 0.05$). There were approximately 120 permanent bomas and 160 households on Merueshi, amounting to 1.3 households per boma, significantly fewer than on Mbirikani ($W=24\,691.50$, $Z=-6.764$, $P < 0.01$).

Table 2. Descriptive statistics and Mann–Whitney U test results for comparison between densities of different wildlife guilds on Mbirikani (unsubdivided) and Merueshi (subdivided). Grazers included zebra, wildebeest, Thomson’s gazelle, oryx, and Coke’s hartebeest; browsers included gerenuk, giraffe, and lesser kudu; and mixed feeders included eland, Grant’s gazelle, and impala.

	Wildlife guild	Ranch	Mean ± SE	Median (inter-quartile range)	W	Z	P
Dry season ¹	Grazers	Mbirikani	7.7 ± 1.49	0.0 (0.00–3.57)	72 354.50	–5.210	< 0.01 ³
		Merueshi	3.0 ± 0.68	0.0 (0.00–0.00)			
	Browsers	Mbirikani	0.9 ± 0.21	0.0 (0.00–0.00)	73 579.50	–5.761	< 0.01 ³
		Merueshi	0.2 ± 0.07	0.0 (0.00–0.00)			
	Mixed feeders	Mbirikani	2.8 ± 0.55	0.0 (0.00–1.28)	74 499.50	–3.719	< 0.01 ³
		Merueshi	2.5 ± 0.51	0.0 (0.00–0.00)			
Wet season ²	Grazers	Mbirikani	13.5 ± 2.03	0.0 (0.00–10.15)	96 422.00	–6.007	< 0.01 ³
		Merueshi	8.0 ± 2.55	0.0 (0.00–0.00)			
	Browsers	Mbirikani	1.2 ± 0.36	0.0 (0.00–0.00)	100 294.50	–5.983	< 0.01 ³
		Merueshi	0.5 ± 0.16	0.0 (0.00–0.00)			
	Mixed feeders	Mbirikani	3.0 ± 0.50	0.0 (0.00–2.52)	98 511.50	–5.527	< 0.01 ³
		Merueshi	2.1 ± 0.35	0.0 (0.00–0.00)			

¹N=235 transects on Mbirikani and 297 on Merueshi.

²N=338 transects on Mbirikani and 327 on Merueshi.

³Indicates Mbirikani value is greater than Merueshi value.

Factors Accounting for the Differences in Wildlife and Pasture Conditions

The ANOVA results (Table 5) give the contribution of each predictor variable after fitting the overall mean, and each of the predictor variables in order from top to bottom. Distances to boma and grass biomass were significant contributors to the model. ($F_{1,18}=13.31$, $P<0.01$; $F_{1,18}=12.56$, $P<0.01$ respectively), suggesting that both the displacement effects of the more regularly distributed settlements and the lower grass biomass on subdivided Merueshi contributed to the lower wildlife densities and could not be separated. No significant interaction was found between distance from boma and grass biomass ($F=0.96$, $P=0.34$). Livestock densities and seasonality were not significant factors in explaining wildlife densities ($F=0.04$, $P=0.84$ and $F=1.21$, $P=0.29$, respectively).

We ran a separate analysis of the impact of “distance to settlement” on wildlife densities on each ranch to detect any differences between them. We found no significant correlation between wildlife density and distance to settlement on Merueshi in either the dry season ($r_s=0.088$, $P=0.13$) or wet season ($r_s=0.097$, $P=0.08$), but a highly significant correlation for both the dry season ($r_s=0.307$, $P<0.01$) and wet season ($r_s=0.355$, $P<0.01$) on Mbirikani.

DISCUSSION

Land subdivision and pastoral sedentarization pose major threats to the conservation of rangeland areas (Darling and Farver 1972; Salzman 1980; Seno and Shaw 2002; Roth and Fratkin 2005). Despite the rapidity of sedentarization of pastoral rangelands around the world, little rigorous and controlled study has been conducted of its impact on wildlife populations.

A long-term aerial study of group ranches in Kenya by Western et al. (2009) provides direct evidence that subdivision and sedentarization of mobile pastoral societies led to steep declines in wildlife populations. The long-term study added weight to earlier comparative studies in the areas (Worden 2007) that found lower wildlife densities on subdivided ranches, but lacked the evidence to rule out ecological differences predating subdivision. Western et al. (2009) concluded from an analysis of 33 yr of aerial counts on ecologically matched ranches that the key factor accounting for the lower wildlife densities on subdivided ranches was the distribution of settlements, rather than the absolute densities of livestock, humans, or settlement. They found no significant differences in livestock densities between an unsubdivided ranch (Mbirikani) and an adjacent subdivided ranch (Kaputei) in pre-, during, or postsubdivision phases (Western et al. 2009,

Table 3. Dry season descriptive statistics of four grass characteristics on Mbirikani (unsubdivided) and Merueshi (subdivided) group ranches, including results of the Mann–Whitney U tests comparing the two ranches.

	Ranch	Mean ± SE	Median (inter-quartile range)	W	Z	P
Biomass ($\text{g} \cdot \text{m}^{-2}$)	Mbirikani	116.4 ± 4.9	68.0 (40.8–149.5)	663 938.00	–0.056	= 0.96
	Merueshi	90.3 ± 3.1	68.0 (40.8–108.8)			
Ground cover (%)	Mbirikani	33.8 ± 0.8	28.0 (14.0–58.0)	402 148.00	–4.908	< 0.01 ¹
	Merueshi	24.7 ± 0.5	23.0 (16.0–31.3)			
Grazing (%)	Mbirikani	58.2 ± 1.4	62.5 (21.4–100.0)	483 487.00	–8.595	< 0.01 ²
	Merueshi	76.8 ± 1.5	100.0 (57.1–100.0)			

¹Indicates value for Mbirikani is higher than for Merueshi.

²Indicates value for Mbirikani is lower than for Merueshi.

Table 4. Wet season descriptive statistics of four grass characteristics on Mbirikani (unsubdivided) and Merueshi (subdivided) group ranches, including results of the Mann–Whitney U tests comparing the two ranches.

	Ranch	Mean \pm SE	Median (inter-quartile range)	<i>W</i>	<i>Z</i>	<i>P</i>
Biomass ($\text{g} \cdot \text{m}^{-2}$)	Mbirikani	181.4 \pm 4.6	135.9 (54.4–244.7)	613 077.00	–8.323	< 0.01 ¹
	Merueshi	118.9 \pm 5.3	81.6 (54.4–135.9)			
Ground cover (%)	Mbirikani	45.8 \pm 0.6	46.0 (25.0–46.0)	567 125.50	–11.892	< 0.01 ¹
	Merueshi	32.0 \pm 0.6	31.0 (22.0–40.0)			
Grazing (%)	Mbirikani	36.6 \pm 0.9	29.4 (0.0–62.5)	1 537 593.00	–2.168	= 0.03 ²
	Merueshi	40.5 \pm 1.4	40.0 (0.0–66.7)			

¹Indicates value for Mbirikani is higher than for Merueshi.

²Indicates value for Mbirikani is lower than for Merueshi.

table 3). This is consistent with our finding of no significant difference in livestock densities between Mbirikani and Merueshi (a representative part of Kaputei) in the current study.

In addition, the aerial count data presented in Western et al. (2009) showed no significant difference in the number of huts on Mbirikani and Kaputei during the period of this study ($P=0.31$), nor in the human population size ($P=0.15$). This suggests that neither the number of settlements nor the human population size accounts for the different wildlife densities observed on Mbirikani and Merueshi. Settlement distribution patterns were, however, significantly different ($P < 0.01$) and far more clumped on Mbirikani than on Kaputei (Western et al. 2009).

Despite the conclusion that the distribution of settlements was a key factor explaining the lower wildlife densities on the subdivided group ranch, the aerial study by Western et al. (2009) did not measure pasture conditions on the ground or measure distance of wildlife to settlements. As a result, the study pointed to the need to measure both variables on the ground in order to distinguish whether loss of pasture due to sedentarization or the physical displacement effects of more regularly spaced permanent settlements, or both, explained wildlife losses following subdivision.

Our year-round ground study reaffirms the aerial study of Western et al. (2009) that the distribution of settlements, rather than the number of settlements or human population size per

se, explain the loss of wildlife due to land subdivision and sedentarization. The ground study goes a step further in discriminating the causal mechanisms of settlement displacement of wildlife. It shows that both direct displacement by settlements and the indirect consequence of lower grass biomass in the vicinity of settlements explains wildlife densities.

In elaborating the effects of settlement on wildlife, we found a strong correlation between wildlife density and distance from settlement on unsubdivided Mbirikani for both wet and dry seasons, but no effect on subdivided Merueshi. The findings that both reduced grass availability and settlement displacement affect wildlife densities are supported by the results of an ANOVA analysis that show wildlife densities were highly significantly correlated with both factors independently but show no interactive effects.

These findings support our field observations that establishment of permanent settlements on private land parcels following subdivision creates a relatively uniform distribution of human habitation and year-round grazing by livestock. This occurs because each landowner takes up residence on his own plot in order to supervise it, since his livestock is now restricted to his own specific land parcel. For example, subdivided Merueshi Group Ranch had 79% of its homesteads distributed randomly across the ranch, following the distribution of land parcels in a mosaic across the whole ranch, resulting in low grass biomass throughout the area. In contrast, Mbirikani bomas were concentrated in a clumped pattern around water sources, thus reducing low grass cover to a limited area of the

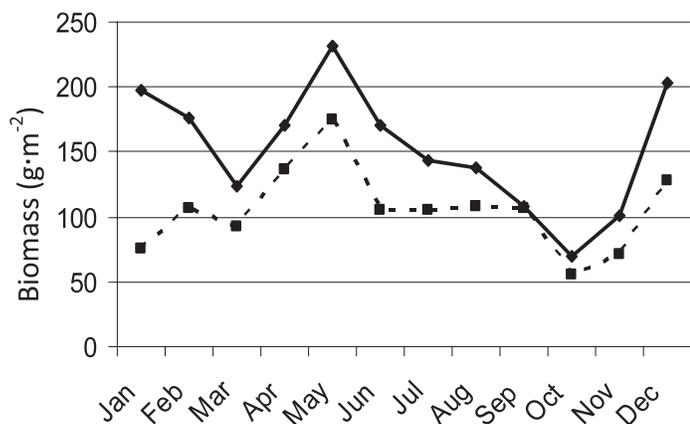


Figure 3. Temporal changes in biomass on Mbirikani (unsubdivided) and Merueshi (subdivided). The solid line represents Mbirikani; the dashed line Merueshi.

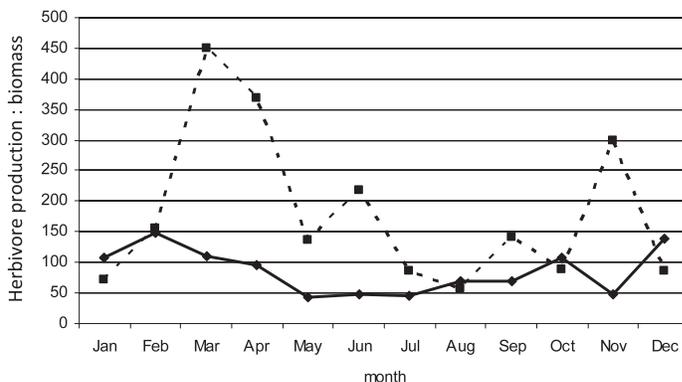


Figure 4. Ratio of herbivore production ($\text{kcal} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$) to grass biomass ($\text{g} \cdot \text{m}^{-2}$) on unsubdivided Mbirikani (solid line) and subdivided Merueshi (dashed line).

Table 5. Sequential analysis of variance, giving the contribution of each predictor variable to the model after fitting the overall mean and sequentially adding each of the predictor variables. Sample size $N=24$ (all data combined). Response: wildlife densities.

	Df	SS	MS	F	P
Distance to boma	1	275.67	275.67	13.31	$P < 0.01$
Grass biomass	1	260.14	260.14	12.56	$P < 0.01$
Livestock densities	1	0.84	0.84	0.04	$P = 0.84$
Season	1	25.09	25.09	1.21	$P = 0.29$
Distance to boma × grass biomass	1	19.92	19.92	0.96	$P = 0.34$
Residuals	18	372.73	20.71		

ranch. Ranch members were able to do this because of the free access to the whole ranch for grazing.

This study's finding of higher grass biomass on Mbirikani than on Merueshi contrasts with the finding of de Leeuw (1991) that pasture biomass on Kaputei was higher than that on Mbirikani in the early 1980s, prior to full sedentarization. This supports our conclusion that the lower pasture biomass on Kaputei (Merueshi) results from subdivision and is not the result of prior ecological differences. The findings suggest that grass cover and biomass on sedentarized ranches is falling in response to consistent grazing pressure. The loss of production poses a problem for pastoral communities that subdivide and settle their lands as well as for wildlife.

We further established from our study that biomass recovery after a dry period was slower and lower on Merueshi than on Mbirikani (Groom 2007). This finding is consistent with modeling predictions that sedentary populations of grazers reduce plant production (Boone 2005; Leloup 2006). The decline in plant cover on Merueshi and the slower recovery of plant biomass after rains also fits with earlier experimental findings on the impact of sustained heavy herbivory on grasslands in the Amboseli ecosystem (Georgiadis et al. 1989).

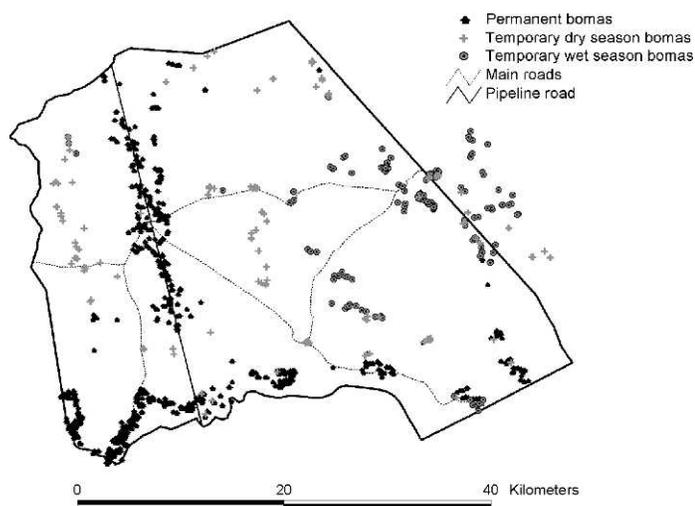


Figure 5. Spatial location of permanent and temporary seasonal bomas on Mbirikani Ranch, Kenya.

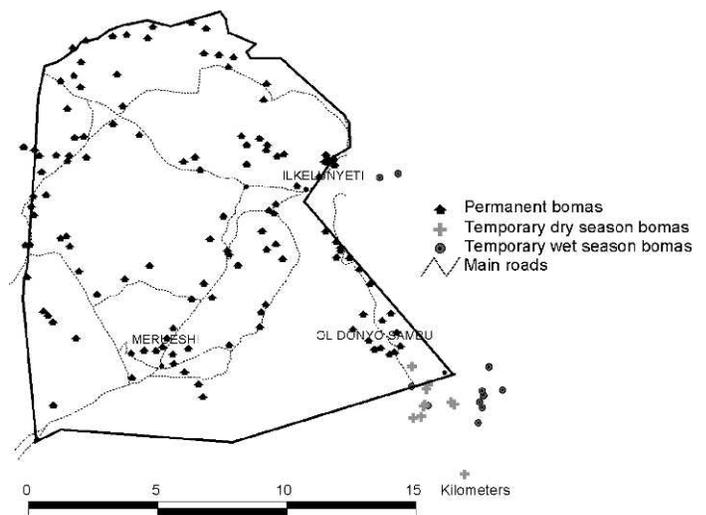


Figure 6. Spatial location of permanent and temporary seasonal bomas on Merueshi Ranch, Kenya.

The reduced biomass in subdivided areas such as Merueshi displaces wildlife to the higher-biomass grasslands of the surrounding open-range ranches, including Mbirikani. The regular distribution of settlements also physically displaces wildlife because of the constant human disturbance associated with permanent settlements, as well as the heavy year-round activity of livestock (Fritz et al. 1996). Other developments stemming from sedentarization, such as fencing of land parcels and water holes will also have repercussions on rangeland productivity and wildlife and livestock populations (e.g., Boone and Hobbs 2004).

Other explanations for the decline of wildlife on Merueshi have been examined for the Kaputei–Mbirikani comparison and ruled out as major factors (Western et al. 2009). They include variability in levels of predation and poaching. However, poaching rates in eastern Kajiado have been generally curbed by the training and deployment of community scouts (R. Bonham, personal communication, May 2007) across the region. Despite almost 100 km of fencing surrounding several land parcels on Merueshi, fences were still too few, too fragmented, and of insufficient quality to exclude wildlife, as evidenced by the spread of wildlife across Merueshi recorded on our ground monitoring. Finally, there is no reason to suspect that predation would account for the lower wildlife densities on Merueshi. Predators were far fewer on Merueshi because of the wider spread of human impact resulting from permanent settlement (R. J. Groom, personal observation). We therefore conclude that the lower wildlife densities on Merueshi can be accounted for by direct displacement effects and the indirect effects of lowered pasture abundance as a result of sedentarization.

The Kenya–Tanzania border area supports the richest mammalian fauna on the planet (Little 1996; Institute for Applied Ecology 1998). Most of this region is currently designated for land subdivision and permanent settlement. Our study shows that such permanent settlement causes a loss of grassland biomass and leads to a sharp drop in wildlife. Land subdivision schemes that encourage uniform, permanent, small-scale settlement and year-round livestock grazing on

small holdings are therefore likely to reduce the productivity and resilience of savanna ecosystems (Graham 1988; Boone et al. 2005), threaten regional biodiversity (Gosnell et al. 2006), and reduce livestock productivity and the drought resilience of pastoral systems. Given that the rangelands support the greatest remaining populations of megafauna (Flannery 2001), the sedentarization of mobile pastoral economies currently taking place around the world poses an imminent threat to the world's wildlife populations, and especially to large migratory herds of wildlife.

This study adds to the conclusions of Western et al. (2009) that the most significant impact of subdivision stems from curtailing seasonal livestock and wildlife mobility and the ecological consequences this has on pasture production and resilience. Land privatization need not, however, lead to fragmentation and sedentarization, as several authors have pointed out (Boone et al. 2005; Mwathi et al. 2005; Burnsilver and Mwangi 2007). Recent exchanges among pastoral peoples have begun exploring methods of securing land tenure while keeping the rangelands open and herds mobile in the interests of sustaining the productivity and resilience of grasslands and biodiversity (Curtin and Western 2008).

IMPLICATIONS

This paper adds support to a growing body of evidence demonstrating the adverse impact of pastoral sedentarization on the grasslands and wildlife of the East African savannas. Sedentarization reduces wildlife abundance through both the direct displacement effects of settlement and the indirect effects of persistent grazing on grassland biomass and growth rates. Given the need for security of tenure among pastoral peoples as pressure on land increases, the pressure to subdivide communal land and switch from nomadic to sedentary lifestyles will also increase. The challenge is thus to explore land tenure systems that maintain the mobility of ungulate herds and the productivity and drought resilience of rangelands, while providing people the land security they need. Shared title of unspecified plots in a large-scale communal rangeland, rather than allocation of a specific land parcel, is one option. In areas of key conservation significance, where the private and nongovernmental sectors are involved, payment for ecosystem services can also be used to maintain open, intact ecosystems where wildlife and livestock coexist. Moreover, some of the models for conservation of private lands in the United States, such as easements and land trusts, could potentially be adapted to the African system. Such possibilities need to be explored in order to minimize the subdivision of remaining rangelands and the consequent devastating ecological impacts.

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