



# The impact of subdivision and sedentarization of pastoral lands on wildlife in an African savanna ecosystem

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## ABSTRACT

This study looks at the impact of subdivision and sedentarization of pastoral lands on wildlife numbers and production in a savanna ecosystem of southern Kenya. The study uses aerial counts over a period of 33 years to compare changes in wildlife populations on two adjacent and ecologically similar Maasai group ranches. During the period under study, one group ranch was subdivided and settled. The other remained communally owned under shifting seasonal use. Wildlife populations decreased sharply on the privatized ranch following subdivision and increased steadily on the adjacent ranch where pastoralists continued mobile pastoralism. The results of multivariate analysis show that sedentarization and settlement distribution accounts for wildlife declines on the subdivided ranch. Both the direct displacement of wildlife and the reduction in grass production following a switch from seasonal to permanent grazing associated with sedentarization are discussed as causes of wildlife loss. Given the demand for title deeds among pastoralists to counter land losses, the resulting sedentarization is likely to become the biggest threat to wildlife in the East African savannas.

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## 1. Introduction

Arid and semi-arid grasslands cover over 40% of the earth's land surface, account for a quarter of all ecoregions, half of all endemic bird species (Satterfield et al., 1998; White et al., 2000) and contain the greatest remaining concentrations of terrestrial megafauna on earth (Flannery, 2001). The importance of the megafauna in the world's grassland biomes declined sharply at the end of the Pleistocene when the majority of genera became extinct in the Americas and much of Eurasia and Australia (Martin, 1984). Africa was exceptional in retaining the considerable diversity and concentration of its megafauna until the advent of colonialism in the 17th century. But even within Africa, rapid human population growth, land development and the spread of firearms since colonial times have exterminated much of the megafauna in West, South and central Africa (Simon, 1962). East Africa was exceptional in sustaining relatively intact megafauna well into the 20th century.

In recent decades, however, East Africa's megafauna has declined sharply due to rising human and livestock populations (Du Toit and Cumming, 1999), land developments, cultural change, meat hunting and commerce (Western and Manziollo-Nightingale, 2004). Countrywide censuses of Kenya over the last 30 years

show wildlife numbers to have shrunk by between 35% and 50% (Grunblatt et al., 1996). Most of the early decline was attributed to the spread of farming into the humid periphery of pastoral lands (Ottichilo et al., 2000). In contrast, the drier sub-arable lands under customary pastoral ownership and communally owned group ranches remained relatively open and wildlife abundant (Western and Manziollo-Nightingale, 2004). A group ranch is defined as a livestock production system or enterprise where a group of people, generally the traditional occupants, jointly own freehold title to land yet continue to herd their own livestock (Ministry of Agriculture 1968).

The accelerating pace of land subdivision in pastoral areas over the last decade has raised concerns that the impact of land fragmentation on migratory wildlife populations and pastoralists is spreading into the semi-arid and arid lands (Ntiati, 2002; Worden, 2007). The concern arises in large measure from the increasing support of subdivision by pastoralists after initial skepticism.

The driving force for subdivision and sedentarization of pastoral lands in the early 1970s was government policy rather than pastoral inclination. Government policy called for the commercialization of the rangelands by privatizing land and improving herd management and range practices (Graham, 1988; Kimani and Pickard, 1998; Lane, 1998). The policy was founded in part on the belief that pastoral culture rested on the value of herd size rather than quality and productivity of livestock, leading to overstocking and land degradation (Ruttenberg, 1971). At first, pastoralists opposed

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or ignored government policy on the grounds that their herds needed to move seasonally to maintain milk yields and avoid harsh droughts (Western and Manzollilo-Nightingale, 2004). This view was given weight by a number of studies showing that traditional pastoralism was not only as productive as commercial ranching, but highly adapted to the drylands by virtue of resilient livestock breeds and seasonal migrations (Western, 1982; Ellis and Swift, 1988).

These studies, together with emerging ecological views on the importance of scale and mobility to the productivity and resilience of the drylands (Walker and Noy-Meir, 1982; McNaughton, 1985), led to concerns that land subdivision is a threat to pastoral livelihoods and wildlife alike. The continuing relevance of these concerns was recently highlighted in exchanges between East African pastoralists and American ranchers. The exchanges focused on the degradation caused by a century of land parceling and livestock development in the arid west of the United States (Curtin and Western, 2008).

Despite continuing concerns over their inability to survive on small subdivisions, most pastoralists now support subdivision (Ntiati, 2002) for fear of losing their land to outsiders (Manzollilo-Nightingale and Western, 2006). Other factors contributing to this shift in attitude include rising population pressure, poverty, alienation of land for farming and conservation, and the influence of market economies (Rutten, 1992). Even as they await legal subdivision, and often to accelerate the process, many pastoralists are voluntarily settling wherever water and social services permit, resulting in locally clustered sedentarization.

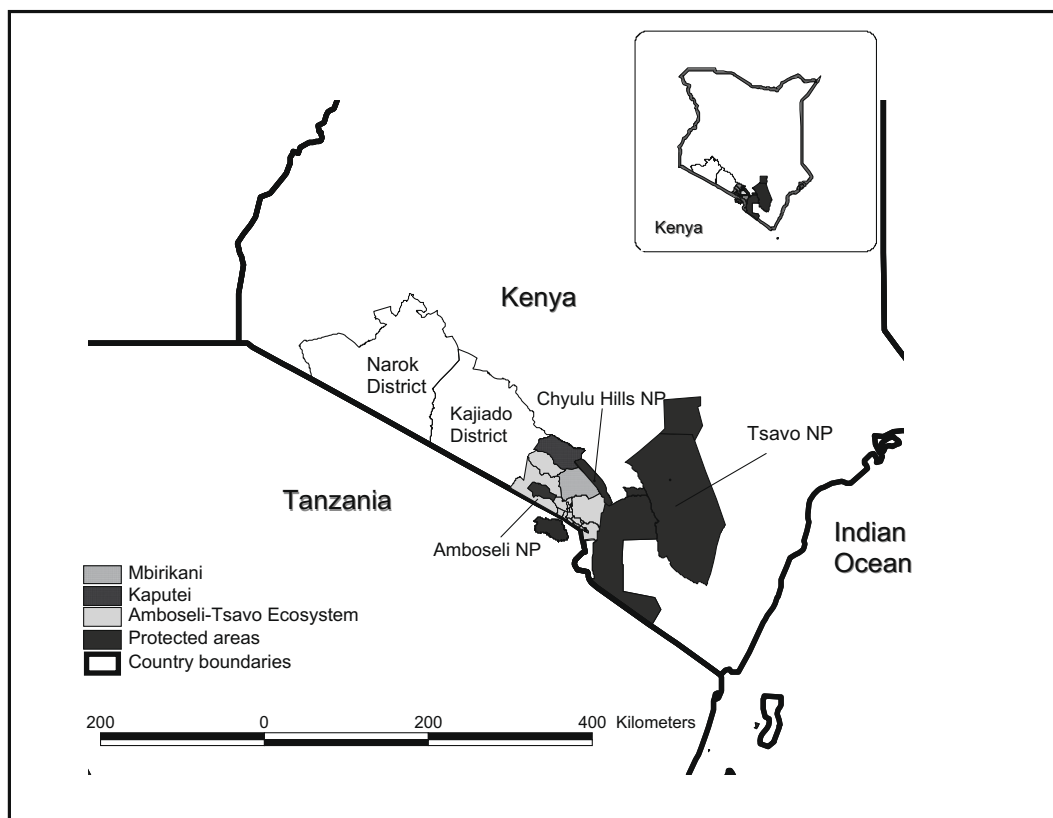
The pace of subdivision is likely to see most of the remaining open pastoral lands around Kenya's premier protected areas carved into small allotments within the next several years. The parks and reserves most at risk include Masai Mara, Amboseli, Tsavo West

and Nairobi National Park. A number of recent articles have drawn attention to the threat of legal subdivision but offer no quantification of the nature of its impact or its likely scale (Rutten, 1992; Kimani and Pickard, 1998; Ntiati, 2002; Worden, 2007).

The lack of quantification on the impact of subdivision stems from the lack of case studies comparing the response of wildlife on legally subdivided group ranches to ecologically similar group ranches under continued mobile pastoralism. One of the few areas where the impact of subdivision has been studied is the Amboseli ecosystem in the Kajiado district of Kenya. Here several studies have begun to look at the impact of subdivision on pastoral societies (Ntiati, 2002; BurnSilver and Mwangi, 2007; Groom, 2007; Worden, 2007; BurnSilver et al., 2008) and the consequences for wildlife (Groom, 2007; Worden, 2007). These studies suggest that land fragmentation will reduce herd productivity and increase the drought risk to pastoralists, particularly among poorer families (Worden, 2007). Worden (2007) also gives some evidence to show that wildlife numbers decline significantly in the vicinity of permanent settlements compared to seasonally mobile settlements.

One of the weaknesses of post-hoc studies comparing subdivided and un-subdivided locations is that they lack the before-and-after control for distinguishing ecological from land use differences (e.g. Groom, 2007). One study that does provide before and after control is the Amboseli Research and Conservation Program (Western, 1994). Established in 1967, the study covers both the Ilkisongo section and the transition from free-ranging traditional pastoralism to subdivision in the Kaputei section of Maasailand.

Here we draw on a 33-year ecological monitoring program to look at the impact of legal subdivision on wildlife in Kaputei section compared to the adjacent Ilkisongo section where mobile pastoral herding practices continued. We assess the impact of



**Fig. 1.** Map of the study area in Kajiado District of Kenya (grey). The area covered by the aerial counts (black) encompasses Amboseli National Park and borders Tsavo National Park to the east (protected areas are dotted). The inset shows the location of the study area within Kenya.

subdivision on 17 large herbivore species using before and after measures on adjacent subdivided and un-subdivided ranches. The species counted included zebra (*Equus burchelli*), wildebeest (*Connochaetes taurinus*), kongoni (*Alcelaphus buselaphus*), Thompson's gazelle (*Gazella thomsonii*), Grant's gazelle (*Gazella granti*), impala (*Aepyceros melampus*), oryx (*Oryx beisa*), eland (*Taurotragus oryx*), buffalo (*Syncerus caffer*), elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardis*), ostrich (*Struthio camelus*), gerenuk (*Litocranius walleri*), black rhino (*Diceros bicornis*), warthog (*Phacocoerus africana*), lesser kudu (*Tragelaphus imberbis*), and waterbuck (*Kobus ellipsiprymnus*).

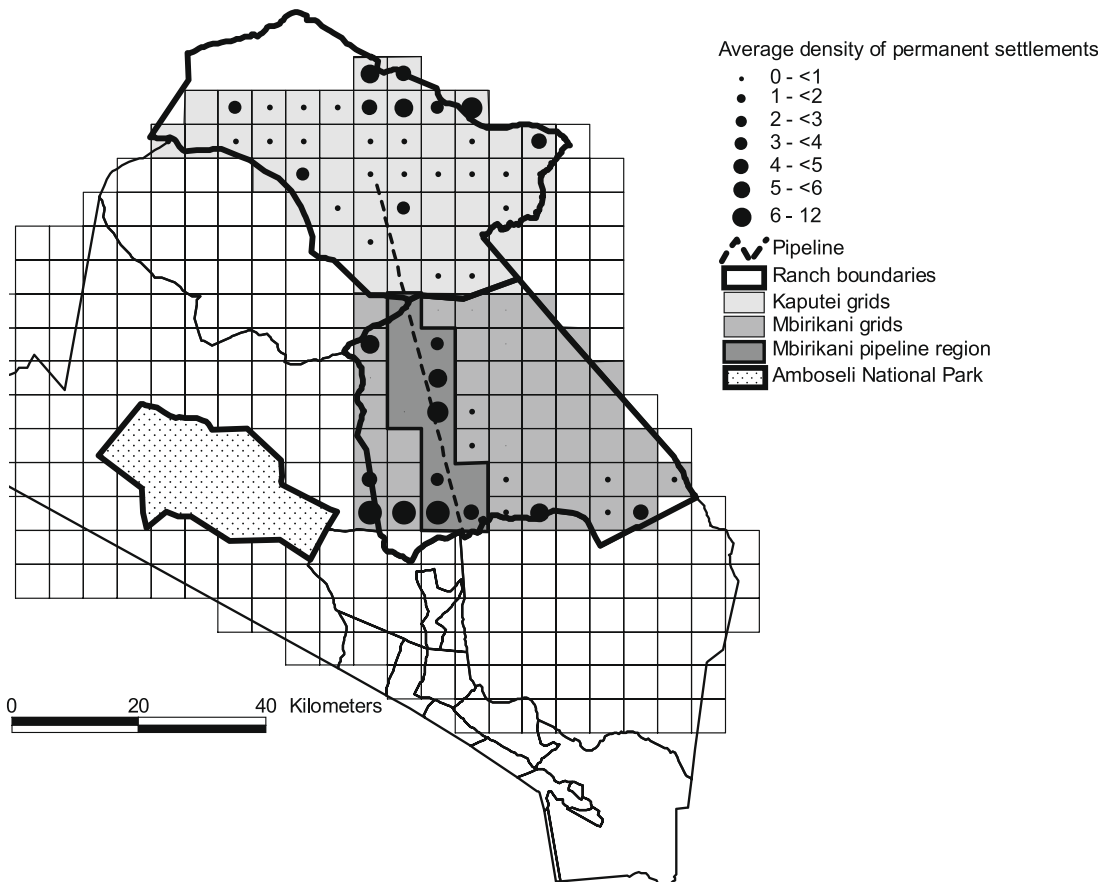
### 1.1. Study area

The 14 sections of Maasailand cover a wide range of climatic and ecological conditions (Jacobs, 1965). Subdivision has occurred in the wetter rather than drier portions of the rangelands, introducing an ecological bias into a comparative study of the impact of sedentarization on savanna ecosystems. To minimize this bias, we studied two adjacent sections of Maasailand, Kaputei and Ilkisingo, both in eastern Kajiado District, southern Kenya (Fig. 1).

The two ranches share a similar climate and ecology (Groom, 2007). Aerial counts of eastern Kajiado by one of us (DW) have been conducted since the early 1970s (Fig. 1). Within the count area we selected the Kaputei ranches and Mbirikani group ranch for comparison. Mobile pastoralism was practiced on both ranches until the 1970s. In the late 1970s, however, Kaputei was subdivided into individual private ranches. Mbirikani remained communal and open to herders and wildlife, with the exception of a small

strip in the west of the ranch. In that strip, in the 1980s, a number of families voluntarily settled along the Loitokitok–Sultan Hamud water pipeline (Fig. 2).

Both ranches are semi-arid and classified as Agroclimatic Zones V and VI (Sombroek et al., 1982). In Amboseli, mean monthly maximum temperatures range from the mid-30s °C in February to low 20s °C in July (Altmann et al., 2002). No in situ climate records are available due to the dearth of climate stations in the study area. To characterize the rainfall patterns in the two areas we used satellite derived rainfall estimates generated from cold cloud duration and rainfall station data (African Data Dissemination Service <http://earlywarning.usgs.gov/adds/>). Rainfall on both ranches ranged between 350 and 700 mm annually over the last 12 years. To determine the magnitude of difference in rainfall between the two areas we performed a paired *t*-test, further calculating an effect size using the pooled standard deviation of total annual ( $t = 1.14$ ,  $p = 0.277$ ) and mean monthly rainfall ( $t = 0.76$ ,  $p = 0.461$ ). An effect size of 0.116 for annual rainfall indicated a non-overlap of less than 14.7% in mean annual rainfall distributions in the two areas (over 85% overlap). Similarly, an effect size of 0.06 for the mean monthly rainfall indicated a small non-overlap of less than 7.7% (over 92% overlap) in the mean month by month rainfall distributions in the two group ranches. There is a slight rainfall gradient across both ranches associated with the Ukambani uplands to the north and the Chyulu Hills to the east. Rainfall is bimodal, with short rains generally falling in November and December and long rains from March to May (Ntiati, 2002). Droughts are frequent. During the past century droughts were recorded in 1933–1935, 1943–1946, 1948–1949, 1952–1953, 1960–1961, 1972–



**Fig. 2.** Map of the study area showing the 5 × 5 km grids covered in aerial counts of eastern Kajiado since 1973 and the boundaries of the two study ranches, Kaputei and Mbirikani, relative to Amboseli National Park. The voluntarily settled portion of Mbirikani is shown along the pipeline together with the density and dispersal of settlements on both ranches.

1976, 1983–1984 and 1994–1995 (Campbell, 1999). So far this century 2001 and 2005–2006 have been severe drought years (Ojwang et al., 2006). The severest drought in the 33-year study occurred in 1973–1976. Wildlife and livestock numbers fell during this drought and rose again in the ensuing wet years (Western, 1994).

The ecology of the Amboseli ecosystem prior to subdivision has been described in detail in Western (1973, 1994). Wildlife and livestock migrated widely during the rains and concentrated in the Amboseli Basin to the south, the Chyulu Hills to the east and the plains north of Sultan Hamud during the dry season.

The Kaputei ranches included in our study cover 1364 km<sup>2</sup> in total, divided among 15 individual ranches (Fig. 2). The Chyulu Hills National Park borders the Kaputei ranches to the southeast. The Nairobi–Mombasa highway lies to the north. There are approximately 16,000 Kaputei Maasai living on Kaputei ranches and 80–100,000 head of livestock, based on aerial counts (see results). Until the late 1970s, water was sparsely distributed in the south and east. In the 1980s, the pipeline passing through the western part of the Kaputei ranches to the Mombasa Road was tapped to provide a string of new watering points. New dams and boreholes have also been constructed. These developments have made daily watering possible over most of the ranches.

Mbirikani Group Ranch covers 1331 km<sup>2</sup>, bordered on the eastern edge by the Chyulu Hills National Park and on its western boundary by Amboseli National Park (Fig. 2). The group ranch is owned and run communally by over 4000 members of Ilkisono Maasai (Groom, 2007). Based on aerial counts (see results), there are approximately 12,000–16,000 people living on the ranch, along with some 50–80,000 head of livestock. Permanent water on the ranch is scarce and is restricted to a few swamps and rivers in the south of the group ranch and water outlets along the pipeline to the west. As a result, most herders drive livestock further to water than on Kaputei and water them less frequently (DW, personal observation).

### 1.2. Land subdivision and settlement

Kajiado District was divided into 52 group ranches after the passage of the Land Group Representatives Act of 1968 (Kimani and Pickard, 1998). Group ranch titles were given to the customary pastoral communities. The southern Kaputei section was divided into 15 small group ranches in the early to mid-1970s (Njoka, 1979). The group ranches averaged 150 km<sup>2</sup> in size. The group ranches were further subdivided into individual private ranches in the early 1980s (Kimani and Pickard, 1998). On one group ranch studied intensively by Groom (2007), the mean size of the individual plots was 1.5 km<sup>2</sup> (0.7–4.6 km<sup>2</sup>) and plots were separated mostly by thorn fencing. We refer to these private ranches collectively as the Kaputei ranches.

The Ilkisono section was divided into several large group ranches in the mid-1970s, including the Mbirikani Group Ranch. Of the six group ranches in Ilkisono, only Kimana has been entirely subdivided. Mbirikani group ranch has only subdivided a small arable portion of its land adjoining Kimana. Subdivision of the remaining lands is now (2009) progressing rapidly but had not taken place during our study period (1972–2006).

The division of Kaputei into individual ranches led to sedentarization in the 1980s. Each owner attempted to settle his land and manage livestock on his own holding. The group ranch designation of Mbirikani, in contrast, gave occupants joint title to the land, but did not initially change traditional seasonal migrations or foraging strategies. A comparison of the pre- and post-settlement changes on Kaputei and Mbirikani therefore provides a natural experiment of the impact of legal land subdivision (privatization) on wildlife abundance and seasonal movements.

## 2. Methods

The two areas selected for comparative study, the Kaputei ranches and Mbirikani Group Ranch, were similar in terms of environmental characteristics, wildlife ecology, human population density and patterns of livestock use at the start of study in 1973. Livestock densities were, however, higher on Kaputei than Mbirikani. Differences in land tenure patterns between Kaputei and Mbirikani were used in a natural experiment (cf Hsieh et al., 2006). The Kaputei ranches were used as the experimental treatment to test the impact of subdivision on wildlife. Mbirikani was used as the control representing continued mobile pastoralism.

We used 29 aerial counts covering the period 1974–2006 to study the impact of land subdivision on wildlife. The 33-year study was divided into three periods, corresponding to the settlement phases on Kaputei independently of the analysis. The divisions were determined by the course of legal subdivision and from continuous observations by DW over the actual physical progress of subdivision. Little permanent settlement took place on Kaputei before legal subdivision across all the ranches in the early 1980s. Until then, permanent settlement was confined to the north of the ranch close to the Mombasa Road. We refer to the period before 1982 as the pre-settlement phase. Permanent settlement began over most of the Kaputei ranches in the early 1980s. Settlement was slow and erratic at first, due to the traditional inclination of pastoralists to move in response to drought and rains. By the early 1990s, most pastoralists had settled or attempted to settle. We refer to the period from 1982 to 1992 as the settlement phase. We refer to the period from 1992 onwards as the post-settlement phase. No subdivision took place on Mbirikani during this time, except for opportunistic voluntary settlement along the pipeline in the mid- to late 1980s, amounting to 20% of the group ranch (Fig. 2).

In comparing changes in wildlife and livestock production on Mbirikani and Kaputei, we found the results were not significantly affected by the inclusion of the pipeline area. However, because this study is concerned with the impact of permanent settlement resulting from land subdivision and privatization, we excluded the pipeline section of Mbirikani because of the permanent clustered settlements it contained (Fig. 2).

The aerial counting method used has been described fully in Pennycuik and Western (1972) and Western (1976). The counts covered 8500 km<sup>2</sup>, divided into UTM grids measuring 5 km on a side. Transect lines were flown through the centre of each grid on a north–south axis 90 m above ground. Counting strips were nominally 150–200 m wide. Within each strip, rear-seat observers counted all wild and domestic animals the size of Thomson gazelles (25 kg) and larger. Animal herds too numerous to count by eye were photographed and later counted under a binocular microscope. The sample fraction was typically 8–10% of total counting area. Population estimates were calculated from the sample fraction using the Jolly II equation (Jolly, 1969). Settlements were counted according to type. These included traditional Maasai dung huts, thatch-roofed huts, tin-roofed huts and brick buildings. All non-traditional Maasai hut types are permanent. In recent years an increasing number of traditional huts have also become permanent (Worden, 2007). All settlement types were combined in assessing the impact of settlements on wildlife.

Wildlife and livestock population estimates of Kaputei and Mbirikani were calculated from the counting grids covering each ranch. However, scaling down population estimates from the entire Ilkisono ecosystem to ranch levels greatly inflated the standard error of estimates due to both the fewer sampling units and the seasonality of wildlife movements on the ranches. The total Ilkisono Monitoring System covered 8500 km<sup>2</sup> using 22 transect

lines up to 100 km+ in length, and encompassed wet and dry season wildlife ranges. In contrast, Kaputei and Mbirikani ranches covered 15% of that area, included half as many aerial transects averaging one third the length, and had seasonal wildlife movements.

To reduce the dilution effect of small sampling units on the standard errors, we pooled the individual species numbers to derive total wildlife production, total livestock production and combined wildlife and livestock production. We initially look at the impact of subdivision on aggregated wildlife numbers. We subsequently converted wildlife numbers into aggregated production figures for two reasons. First, the use of production figures rather than total population counts normalizes the difference in area between the two ranches by giving a unit area figure. Second, production rather than numbers and densities takes into account differences in metabolism and turnover rates among species to give a common energetic equivalence per unit area for all species (Coe et al., 1975). Animal production was calculated for each species using the equation  $P = N 13.8M_s^{0.67}$ , where  $N$  is the population size or density and  $M_s$  is the mean kcal equivalent of adult mass (Western, 1983). Unit weights were based on values given in Western (1973). The mass scaling exponent of 0.67 was used rather than 0.75 for consistency and comparison with earlier work in the Amboseli Ecosystem (Western 1991). The most appropriate scaling exponent (Glazier, 2005; White and Seymour, 2005; Clauss et al., 2007; Beuchat et al., 1997) is a subject of debate but will not affect the outcome of our results.

To determine the impact of subdivision on wildlife, we used three measures of human activity and three measures of wildlife response. Measures of human activity included total livestock production, total number of huts as a measure of settlement density, and the proportion of grids with any settlement as a measure of the spatial distribution of human activity. The average number of occupants per hut was 4.54 for traditional huts, 4.08 for thatched huts and 4.36 for tin-roofed or brick huts. These numbers were derived from questionnaire surveys in 2005/2006 (Groom, 2007) and are similar to hut counts in the 1970s Western, D (unpublished data). The number of occupants per hut has thus remained relatively constant over the study period and gives a direct and reliable measure of human population size. Settlement numbers also give a better measure of human impact, taking into account evidence that occupied settlements displace wildlife (Worden, 2007). For example, highly clustered settlements typical of the traditional seasonally mobile pastoralism on Mbirikani are likely to displace wildlife from the immediate vicinity and leave much of the seasonal range free for wildlife. Permanent settlements scattered through Kaputei, in contrast, are likely to displace wildlife over a far larger area. We have, for this reason, treated the number of huts and spread of settlements as independent variables for the purpose of measuring human impact of subdivision on wildlife.

Measures of wildlife response to subdivision included aggregate wildlife numbers, production of all species (total wildlife production) and the correlation of wildlife production with antecedent rainfall as an indicator of the seasonality of wildlife movements in each ranch. Differences in aggregated wildlife numbers and wildlife production on Kaputei and Mbirikani in each settlement

phase were investigated using paired  $t$ -tests. Data were log or square-root transformed where necessary. Seasonality of production was tested by correlating production figures with antecedent rainfall over the preceding 40 days (Western, 1975) using Spearman's correlation tests.

Once significant changes in wildlife numbers, production and seasonality were established, we investigated the potential causes of these changes. Several different analyzes were used to test the relative contributions of human settlement characteristics and livestock patterns on changes in wildlife production over the study period. First, human population size and rate of population growth were compared between the ranches. The spatial spread of settlement on the two ranches was then compared using the proportion of grids occupied by settlements. Finally, a general linear model (GLM) was used to investigate the effects of human-related variables on the response variable 'wildlife production'. The global model used was:

$$y = \beta_0 + \beta_1X_1 + \beta_2X_2 + \beta_3X_3 + \varepsilon$$

where  $y$  = wildlife production,  $X_1$  = spatial settlement spread,  $X_2$  = ranch effect,  $X_3$  = livestock distribution,  $\varepsilon$  = error.

An ANOVA was used on the global model to test the relative importance of each of the explanatory variables.

### 3. Results

#### 3.1. Animal populations and production

Paired  $t$ -tests illustrate that wildlife numbers were similar on the two ranches in the pre-settlement phase, still similar but starting to diverge in the settlement phase and significantly higher on Mbirikani than Kaputei in the post-settlement phase (Table 1).

For Mbirikani, six wildlife species (zebra, wildebeest, Thompson's gazelle, Grant's gazelle, giraffe and ostrich) showed positive trends. None were significant. Only impala and black rhino showed a significant decline. On Kaputei, four wildlife species (zebra, kongoni, elephant and gerenuk) showed positive trends, but only zebra was statistically significant. Six species (Thomson's gazelle, Grant's gazelle, impala, eland, buffalo and giraffe) showed significant negative trends.

Using wildlife production instead of total numbers gives similar results

Wildlife production was similar on Mbirikani and Kaputei in the pre-settlement and settlement phases, but diverged significantly post-settlement (Table 2). Wildlife production values for each aerial count illustrate this divergence in Fig. 3. Wildlife increased in parallel on both ranches from the 1970s to 1980s, following a severe drought. However, wildlife production declined steeply on Kaputei and rose on Mbirikani in the post-settlement phase during the 1990s. By the 1990s, wildlife production on Mbirikani was more than twice that of Kaputei ( $T = 2.698$ ,  $P = 0.043$ ) (Fig. 4).

Livestock and total herbivore production levels during the pre-settlement phase were significantly higher on Kaputei than Mbirikani. However, this initial difference narrowed to insignificance during the settlement and post-settlement phases (Table 2).

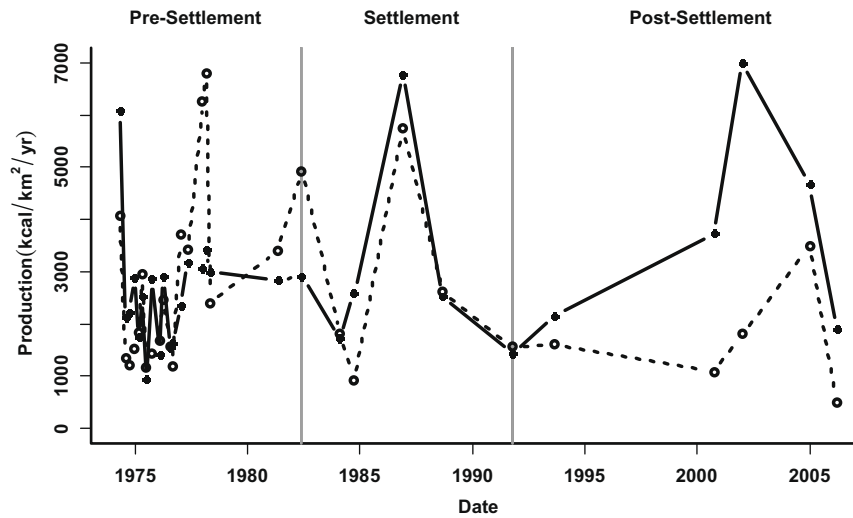
**Table 1**  
Mean wildlife population estimates and standard errors for Kaputei and Mbirikani ranches during the three settlement phases, with results of paired  $t$ -tests comparing the two ranches (no transformation of data necessary).

Phase	$N$	Mbirikani	SE	Kaputei	SE	Statistic	$P$ Value
Pre-settlement	17	8801	859	8570	1072	$T_{16} = -0.225$	0.825
Settlement	6	11,514	2006	9566	1909	$T_5 = -1.106$	0.319
Post-settlement	6	12,291	3018	5282	1264	$T_5 = -2.664$	0.045

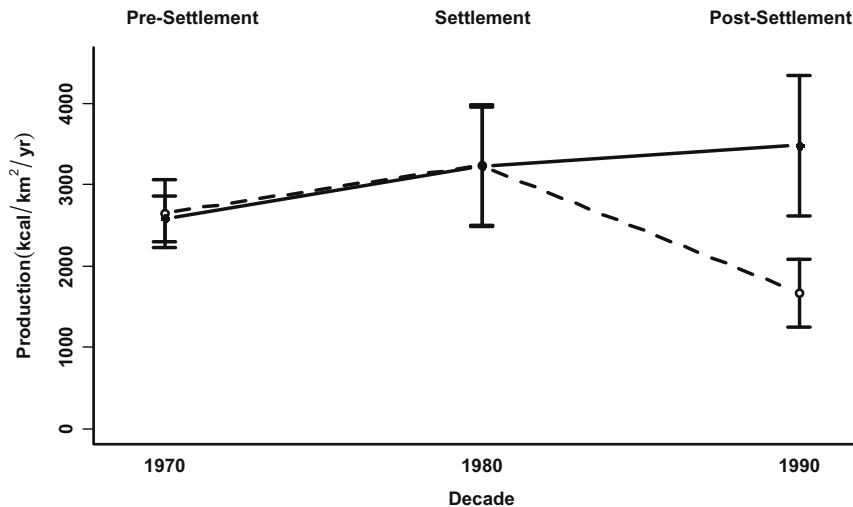
**Table 2**

Average production values (kcal/km<sup>2</sup>/year) for wildlife, livestock and all herbivores combined by settlement phase. Values are means, standard errors, *t*-test statistic, and *P* values. *N* = total number of counts. Wildlife data were square-root transformed and livestock and total herbivore data were log transformed.

Herbivore group	Phase	<i>N</i>	Mbirikani	SE	Kaputei	SE	Statistic	<i>P</i> Value
Wildlife	Pre-settlement	17	2579.17	278.99	2644.76	419.86	<i>T</i> <sub>16</sub> = 0.158	0.876
	Settlement	6	3227.69	729.02	3232.41	752.68	<i>T</i> <sub>5</sub> = 0.140	0.894
	Post-settlement	6	3478.81	863.03	1669.02	412.49	<i>T</i> <sub>5</sub> = 2.698	0.043
Livestock	Pre-settlement	17	6597.02	1135.37	12116.29	1140.54	<i>T</i> <sub>16</sub> = -4.336	0.001
	Settlement	6	7852.49	1035.62	14475.16	2724.65	<i>T</i> <sub>5</sub> = -1.528	0.187
	Post-settlement	6	12242.33	3861.21	18119.73	2661.10	<i>T</i> <sub>5</sub> = -2.093	0.091
All herbivores	Pre-settlement	17	9176.20	1314.48	14761.05	1008.88	<i>T</i> <sub>16</sub> = -4.773	<0.001
	Settlement	6	11080.00	1219.40	17707.57	3203.69	<i>T</i> <sub>5</sub> = -1.352	0.234
	Post-settlement	6	15721.14	4329.50	19788.76	2958.08	<i>T</i> <sub>5</sub> = -1.495	0.195



**Fig. 3.** Changes in wildlife production on Mbirikani and Kaputei during pre-settlement, settlement and post-settlement phases. The solid line represents Mbirikani, the dashed line Kaputei.



**Fig. 4.** Summary of decadal changes in wildlife production on Mbirikani (solid lines) and Kaputei (dotted lines).

We examined the correlation of animal production on Kaputei and Mbirikani during the three settlement phases (Table 3), and the correlation of wildlife production with antecedent rainfall on each ranch for each phase using Spearman correlation tests.

Wildlife production between the two ranches was significantly correlated (*r*<sub>s</sub> = 0.659, *P* = 0.004) during the pre-settlement phase

in the 1970s. In this decade, production figures were highly correlated with rainfall on both ranches (Mbirikani; *t* = -3.356, *P* = 0.002, Kaputei; *t* = -2.828, *P* = 0.009), indicating that animal production on both ranches changed in relation to seasonal patterns, in a similar way. Wet seasons had significantly higher wildlife production than dry seasons on both ranches. In the

**Table 3**

Spearman correlation tests of differences in wildlife, livestock and total herbivore production between Kaputei and Mbirikani during all three settlement phases.

Phase	N	Wildlife		Livestock		Total herbivores	
		$r_s$	P Value	$r_s$	P Value	$r_s$	P Value
Pre-settlement	17	0.66	0.004	0.32	0.209	0.31	0.224
Settlement	6	0.77	0.072	0.03	0.957	-0.03	0.957
Post-settlement	6	0.66	0.156	0.37	0.468	0.66	0.156

subsequent settlement and post-settlement phases however, the correlation in wildlife production between Kaputei and Mbirikani declined to insignificance (Table 3). The divergence in seasonality corresponds to a declining abundance and mobility of wildlife on Kaputei.

Neither livestock nor total herbivore production was significantly correlated with rainfall or between Kaputei and Mbirikani during any settlement phase (Table 4), indicating that livestock use of both ranches, unlike wildlife, did not vary seasonally.

### 3.2. Wildlife responses to human activity

Having demonstrated that wildlife numbers and production declined significantly on Kaputei and increased on Mbirikani, we investigated factors that might account for the decline, including the rate of change in human population, settlement numbers, the spatial spread of settlements (i.e. the proportion of grid cells occupied by settlement), and changes in the livestock population.

To test whether the divergence in wildlife production on Kaputei and Mbirikani can be explained by differences in settlement intensity or human population growth, we looked at wildlife re-

sponses to total hut numbers as an indicator of human population size over the three settlement phases. Growth in the numbers of huts over the 33-year study period was highly correlated between ranches (Pearson's correlation:  $r = 0.908$ ,  $P < 0.001$ ) (Fig. 5). Furthermore, we found no differences in the number of huts on each ranch during any of the settlement phases (pre-settlement  $T_{16} = -2.003$ ,  $P = 0.059$ , settlement  $T_5 = -1.907$ ,  $P = 0.115$  and post settlement  $T_5 = -1.131$ ,  $P = 0.309$ ). Neither human population size (log transformed,  $F = 2.09$ ,  $P = 0.154$ ) nor the rate of change in human population ( $T = 0.53$ ,  $P = 0.590$ ) were significantly different between the two ranches.

These results indicate that neither the number of settlements, nor the increasing human population per se, could explain the decline of wildlife on Kaputei, given that the same trends took place on Mbirikani where wildlife increased more than two-fold after the 1970s drought.

We next tested whether there was any significant change in the distribution pattern of settlements resulting from sedentarization by using the proportion of occupied grids on each ranch. Settlements occupied a significantly higher proportion of the study area in Kaputei than in Mbirikani ( $T = 4.76$ ,  $P < 0.001$ , Fig. 2).

Given the significant difference in wildlife production between Mbirikani and Kaputei in the post-settlement phase, we used a General Linear Model to evaluate the relative contributions of both the proportion of the area occupied by human settlement and the impact of livestock production on wildlife production during this period. Because there were no significant differences in the total numbers of huts on each ranch ( $F = 2.09$ ,  $p = 0.1544$ ), we excluded the hut counts from the analysis. An ANOVA on the global model showed that settlement spread was the most significant variable in explaining wildlife production ( $F = 30.133$ ,  $P < 0.001$ , Table 5).

**Table 4**

Spearman correlation tests of differences in wildlife, livestock and total herbivore production between Kaputei and Mbirikani during settlement phases.

Phase	N	Wildlife		Livestock		Total herbivores	
		$r_s$	P Value	$r_s$	P Value	$r_s$	P Value
Pre-settlement	17	0.659	0.004	0.321	0.209	0.311	0.224
Settlement	6	0.771	0.072	0.029	0.957	-0.029	0.957
Post-settlement	6	0.657	0.156	0.371	0.468	0.657	0.156

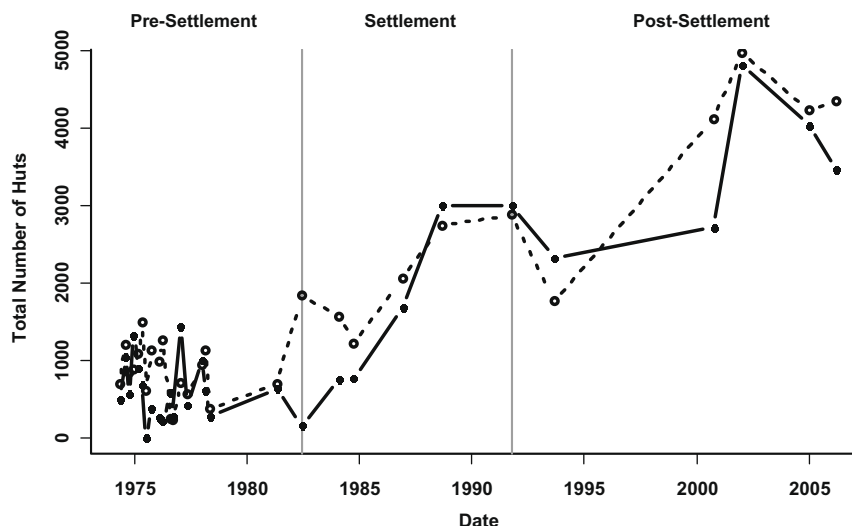


Fig. 5. Total number of huts on Kaputei (dashed line) and Mbirikani (solid line) over the period 1974–2006.

**Table 5**

Results of the GLM global model illustrating the importance of the spatial spread of settlement in affecting wildlife production.

Response: wildlife production			Residual Df	Residual deviance	F	P Value
Variable	Df	Deviance				
NULL			12	1167,74,703		
Settlement spread	1	582,65,660	11	585,09,043	30.133	<0.001
Ranch	1	400,02,556	9	185,06,487	10.344	0.006
Livestock	1	30,37,679	8	154,68,808	1.571	0.245

#### 4. Discussion

The results show that wildlife decreased sharply after the legal subdivision of pastoral lands in eastern Kajiado. This finding amplifies Worden's (2007) conclusion that sedentarization affects both the distribution and movements of wildlife in other areas of the Amboseli ecosystem. A multivariate analysis shows that the uniform spread of permanent settlements resulting from subdivision largely accounts for the wildlife decline. Our findings do not imply that human and livestock populations are unimportant in wildlife declines in rangeland areas. There is abundant evidence to suggest otherwise. Western (1989) showed that, normalizing for rainfall, wildlife densities in livestock areas are depressed relative to national parks. Du Toit and Cumming (1999) showed that increases in livestock across Africa explain much of the wildlife decline.

Poaching is a possible explanation for wildlife losses in eastern Kajiado. Poaching levels have, however, been sufficiently contained by community and Kenya Wildlife Service anti-poaching forces to see a steady rise in wildlife populations on Mbirikani (Fig. 3) and across eastern Kajiado generally (Western and Manzollilo-Nightingale, 2004). Two more plausible explanations for the impact of sedentarization on wildlife abundance are, first, the direct disturbance of wildlife due to displacement by settlement and, second, the impact of settlements on pasture conditions.

First, under traditional pastoral practices common to both ranches in the 1970s, settlements moved seasonally and were concentrated in relatively small areas at any one time. The concentration and seasonal movement of settlements left large areas vacant on both ranches, as in the rest of the ecosystem (Western, 1975). Wildlife was able to shift seasonally in response to local settlement concentrations and pasture availability. In contrast, the more uniform and permanent settlement pattern due to subdivision on Kaputei, left few undisturbed areas for wildlife.

Second, the continuous livestock grazing that results from permanent settlement and abandonment of free-range movements reduces grassland production far more than the short intensive grazing associated with migratory herbivore populations (Boone, 2005).

These two hypotheses are not mutually exclusive and are more than likely additive in their effects. The even spread and permanence of settlements associated with subdivision is, in other words, likely to reduce wildlife numbers both by direct displacement and by suppressing grassland productivity.

A number of studies point to both direct displacement and reduction of pasture as serious threats to wildlife in the event of large-scale sedentarization of the rangelands in eastern Africa. For example, Worden (2007) found reduced concentrations of wildlife in dry season areas of the Eselenkei region of the Amboseli ecosystem, where permanent settlement and livestock concentrations were high. There is also good evidence to show that basal cover and quality of grass increases under a moderate and continuous grazing regimen (e.g. Owen and Weigert, 1981; Guevara et al., 2002), but declines sharply under continuous intensive grazing (Boone, 2005). Boone (2005) found in modeling the effects of subdivision on vegetation in South Africa that high palatability grasses

declined, low palatability grasses increased and overall annual net primary productivity decreased as woody cover rose with year-round grazing of pastures. Groom (2007) demonstrated a significantly lower grass biomass and ground cover on Kaputei compared to Mbirikani. Given that stocking rates have increased faster on Mbirikani than Kaputei and narrowed the production differences, it is likely that the lower grass biomass on Kaputei is due to continuous, intensive grazing rather than stocking rates per se.

Our studies of the impact of subdivision of Kaputei ranches on wildlife point to the need to distinguish between subdivision as a legal instrument for granting land titles (land privatization) and the physical impact of changes in settlement patterns in time and space. Our results suggest that, even in the absence of fencing, land owners who establish permanent settlements on their individual holdings are likely to reduce wildlife and pasture more than seasonally mobile herders.

Sedentarization can also take place without subdivision, as happened in parts of the Amboseli ecosystem in response to social amenities and in anticipation of subdivision (Western and Manzollilo-Nightingale, 2004). Such settlement is, however, highly localized and its impact will be dwarfed by legal subdivision underway across southern Maasailand.

The distinction between legal land titling and sedentarization is important in assessing the ecological impact of land fragmentation on livestock production, wildlife and habitat. Physical fragmentation of land, whether through settlement or fencing, is occurring rapidly in rangelands around the world (Curtin and Western, 2008; Gosnell et al., 2006; Anantha Ram et al., 1999). The ecological impact of physical land fragmentation has been widely documented for livestock production (Du Toit and Cumming, 1999; Boone et al., 2005), habitat and biodiversity (Knight et al., 1995; Holdt et al., 2004; Gosnell et al., 2006).

The accelerating pace of sedentarization due to subdivision poses the largest single threat to wildlife and the health of Kenya's rangelands, in our estimation. Sedentarization poses a particularly grave threat to the Kenya-Tanzania Rift Valley borderlands, an area identified as the richest vertebrate location in Africa (Boitani et al., 1998).

It is therefore important to explore alternative methods of land privatization that avoid sedentarization, fragmentation, and loss of rangeland productivity and resilience (Manzollilo-Nightingale and Western, 2006; Worden, 2007; BurnSilver et al., 2008; Curtin and Western, 2008).

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