Contributed Paper

Effects of Private-Land Use, Livestock Management, and Human Tolerance on Diversity, Distribution, and Abundance of Large African Mammals

MARGARET F. KINNAIRD*‡ AND TIMOTHY G. O'BRIEN*‡ †

*Mpala Research Centre, P.O. Box 555, Nanyuki, 10400 Kenya
‡Wildlife Conservation Society, Global Conservation Programs, Bronx, NY, 10460 USA

Abstract: *Successful conservation of large terrestrial mammals (wildlife) on private lands requires that landowners be empowered to manage wildlife so that benefits outweigh the costs. Laikipia County, Kenya, is predominantly unfenced, and the land uses in the area allow wide-ranging wildlife to move freely between different management systems on private land. We used camera traps to sample large mammals associated with 4 different management systems (rhinoceros sanctuaries, no livestock; conservancies, intermediate stocking level; fenced ranches, high stocking level; and group ranches, high stocking level, no fencing, pastoralist clan ownership) to examine whether management and stocking levels affect wildlife. We deployed cameras at 522 locations across 8 properties from January 2008 through October 2010 and used the photographs taken during this period to estimate richness, occupancy, and relative abundance of species. Species richness was highest in conservancies and sanctuaries and lowest on fenced and group ranches. Occupancy estimates were, on average, 2 and 5 times higher in sanctuaries and conservancies as on fenced and group ranches, respectively. Nineteen species on fenced ranches and 25 species on group ranches were considered uncommon (occupancy < 0.1). The relative abundance of most species was highest or second highest in sanctuaries and conservancies. Lack of rights to manage and utilize wildlife and uncertain land tenure dampen many owners' incentives to tolerate wildlife. We suggest national conservation strategies consider landscape-level approaches to land-use planning that aim to increase conserved areas by providing landowners with incentives to tolerate wildlife. Possible incentives include improving access to ecotourism benefits, forging agreements to maintain wildlife habitat and corridors, resolving land-ownership conflicts, restoring degraded rangelands, expanding opportunities for grazing leases, and allowing direct benefits to landowners through wildlife harvesting.*

Keywords: camera trapping, Kenya, Laikipia, large mammals, livestock, occupancy, private lands, species abundance, species richness

Efectos del Uso Privado de Suelo, Manejo de Ganado y la Tolerancia Humana sobre la Diversidad, Distribución y Abundancia de Mamíferos Mayores Africanos

Resumen: *La conservación exitosa de mamíferos terrestres mayores (vida silvestre) en tierras privadas requiere que los propietarios estén empoderados para manejar la vida silvestre para que los beneficios sean mayores que los costos. El Condado Laikipia, Kenia, predominantemente carece de cercos, y los usos de suelo en el área permiten que la vida silvestre se mueva libremente entre los diferentes sistemas de manejo de tierras privadas. Utilizamos cámaras trampa para muestrear mamíferos mayores asociados con 4 diferentes sistemas de manejo (santuarios de rinocerontes, sin ganado; zonas de conservación, nivel intermedio de ganado; ranchos cercados, nivel alto de ganado; y ranchos grupales, nivel alto de ganado, sin cercos, régimen de propiedad clan pastoril) para examinar si los niveles de manejo y de ganado afectan a la vida silvestre. Colocamos cámaras en 522 localidades en 8 propiedades de enero 2008 a octubre 2010 y utilizamos las fotografías obtenidas durante ese período para estimar la riqueza, la ocupación y la abundancia relativa de especies. La riqueza de especies fue mayor en las zonas de conservación y los santuarios y menor en los ranchos*

†*Address correspondence to Timothy G. O'Brien, email tobrien@wcs.org*
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cercados y grupales. Las estimaciones de ocupación fueron, en promedio, 2 y 5 veces mayor en los santuarios y las zonas de conservación que en ranchos cercados y grupales, respectivamente. Diecinueve especies en ranchos cercados y 25 especies en ranchos grupales fueron consideradas poco comunes (ocupación < 0.1). La abundancia relativa de la mayoría de las especies fue mayor o la segunda en importancia en santuarios y zonas de protección. La carencia de derechos para manejar y utilizar la vida silvestre y la incertidumbre en la tenencia de la tierra reducen los incentivos de muchos propietarios para tolerar la vida silvestre. Sugerimos que las estrategias nacionales de conservación consideren métodos a nivel de paisaje en la planificación del uso de suelo que incrementen las zonas protegidas proporcionando incentivos a los propietarios para que toleren la vida silvestre. Posibles incentivos incluyen la mejoría del acceso a los beneficios del ecoturismo, celebración de acuerdos para mantener hábitat y corredores para vida silvestre, resolución de conflictos de tenencia de la tierra, restauración de praderas, expansión de oportunidades para arrendamientos de pastoreo y permitir beneficios directos para los propietarios mediante la cosecha de vida silvestre.

Palabras Clave: Abundancia de especies, ganado, Kenia, Laikipia, mamíferos mayores, ocupación, riqueza de especies, tierras privadas, trampeo con cámaras

Introduction

The effectiveness of nationally mandated protected areas for conservation of wide-ranging wildlife species (by *wildlife* we mean large terrestrial mammals) is limited by the small size and insular nature of most protected areas relative to wildlife movement (Newmark 1995; Woodroffe & Ginsberg 1998). There is widespread belief that wildlife conservation on private lands is integral to the persistence of large mammals (United States, Hunt 1997; Latin America, Environmental Law Institute 2003; Australia, Figgis 2004). Many management options promote conservation on private lands, including conservation easements and leases, payments for ecosystem services, compensation for depredation of livestock, wildlife tourism, game ranching, and hunting (Woodroffe et al. 2005; Gitahi & Fitzgerald 2011). In most countries wildlife is considered a public resource, and management often falls to national governments rather than the private sector (Krug 2001). A key feature of successful wildlife management on private lands is national policies that extend user rights to property owners to manage wildlife on their lands (Smith 1981; Norton-Griffiths 1998).

In Africa growing human populations and rural poverty lead to increasing demands for land for agriculture (Krug 2001). Increasing human populations near protected-area boundaries (Harcourt et al. 2001) and elsewhere have resulted in land-use conversion that prevents free movement of wildlife (Newmark 2008) and leads to increased human–wildlife conflict (Ogutu et al. 2011). Between 1970 and 2005, wildlife abundance in African protected areas declined by 50% (Craigie et al. 2010), and many species' ranges are now restricted to protected areas (Newmark 2008).

Trends in abundance of wildlife across Africa, however, have not been uniform. In southern African countries, where protected areas are relatively well funded and user rights on private lands are recognized, wildlife abundance has increased slightly or remained stable since 1970 (Cousins et al. 2010; Craigie et al. 2010). In Kenya, a country economically reliant on wildlife tourism, wildlife abundance declined 45% outside and 41% inside protected areas from 1977 to 1997 (Western et al. 2009). Ogutu et al. (2011) attribute losses in Kenya's Maasai Mara National Reserve to increasing numbers of boundary settlements that have been accompanied by illegal wildlife harvesting and livestock grazing. Sixty-five percent of Kenya's wild animals now live outside national parks and reserves (Western et al. 2009), even though >50% of land that once supported wildlife is under agricultural production (Norton-Griffiths & Said 2010). Kenya's policy of strict public ownership of wildlife without private user rights means landowners bear the cost of wildlife on their property and can derive no direct value from wildlife unless they are associated with the ecotourism industry. Meanwhile, substantial indirect and nonuse values accrue at the national and global levels rather than locally (Krug 2001; Norton-Griffiths & Said 2010).

Laikipia County, central Kenya, is an exception to the national trend in wildlife decline and provides an example of an area where wildlife conservation is being conducted successfully on private lands. Properties are managed as wildlife conservancies, ecotourism operations, sanctuaries for black (*Diceros bicornis*) and white rhinoceros (*Ceratotherium simum*), private and government-owned livestock operations, group ranches (communally owned and managed by pastoralist clans), or small-holding agriculture (Georgiadis et al. 2007). Laikipia is predominantly unfenced, which allows wildlife to move freely between areas with different land uses. Four rhinoceros sanctuaries, an ecological research center, and >40 ecotourism facilities, including 6 community-owned lodges, generate income from wildlife. Members of group ranches benefit from wildlife through management of and employment by ecotourism operations, grazing leases, and investment by private landowners in infrastructure (schools, clinics, water) and other development activities (Kaye-Zwiebel 2011). From 1980 through 1995, wildlife abundance throughout Kenya decreased substantially, whereas in

Laikipia wildlife populations increased (Kinnaird et al. 2010). Although the abundance of some species has declined since 1995, Laikipia has the second largest abundance of wildlife in Kenya, after Maasai Mara National Reserve.

Georgiadis et al. (2007) used data from 21 years of aerial surveys across Laikipia to examine the effects of climate and land use on 9 large ungulate species and 3 livestock species. They found that livestock and ungulate species tend to segregate spatially and that land use is the primary factor associated with ungulate abundance. Rainfall patterns, particularly drought, affected only common zebra (*Equus quagga*) and cattle (*Bos taurus*). Their results suggest predators, the abundance of which was severely reduced by hunting in the 1970s and 1980s, recovered on wildlife-friendly ranches and may have contributed to declines of several ungulate species.

As land use in Laikipia and elsewhere in Africa intensifies, more properties are being fenced and livestock stocking levels, lethal control of wildlife, and human population are increasing. These factors may negatively affect wildlife. We used camera-trap sampling to expand on Georgiadis et al.'s (2007) examination of Laikipia livestock and wildlife. Camera-trap sampling avoids many biases inherent in aerial and ground sampling (Caughley 1977; Pollock & Kendall 1987) and data from camera traps can provide representative estimates of species richness, abundance, and distribution for most diurnal and nocturnal mammals (O'Brien et al. 2003, 2011). We sampled properties that managed livestock in different ways to test 3 hypotheses: (1) intensification of livestock management reduces species richness, distribution, and abundance; (2) livestock management intensification reduces abundance and distribution of large ungulates and large predators more than small ungulates and small predators; and (3) activity by livestock, humans, and dogs reduces wildlife abundance and distribution.

Methods

Study Area

In Laikipia County (9666 km^2), rainfall varies from 900 mm at the equator to 400 mm in the north. Consequently, humans and permanent agriculture are concentrated in the south and livestock ranching and wildlife are concentrated in the north (Fig. 1). Three vegetation types characterize the study area (Table 1): woodland dominated by whistling-thorn acacia (*Acacia drepanalobium*), which is the most common vegetation type (Young et al. 1997); savanna dominated by perennial grasses with widely spaced trees and shrubs; and bushland with a discontinuous layer of perennial grasses and >30% canopy cover dominated by wait-a-bit thorn (*Acacia mellifera)*, mgunga (*Acacia etbaica*), prickly thorn (*Acacia brevispica*), and white crossberry (*Grewia tenae*) (Augustine & McNaughton 2004).

We sampled 8 properties (approximately 10% of Laikipia), including 2 group ranches, 2 fenced ranches, 2 conservancies, and 2 rhinoceros sanctuaries (Fig. 1). Group ranches are owned by clans of Samburu and Maasai pastoralists. Stocking levels on group ranches are high, typically >25 total livestock units (TLU) per km^2 (a TLU is a common unit used to describe the amount of livestock present, irrespective of species). We used a cow as the basic unit. Group ranches had no property fences or guards. Livestock were owned privately, but land was owned and managed communally. Group-ranch members could move livestock outside ranch boundaries during dry seasons and droughts, but nomadic movements were limited (Kaye-Zwiebel 2011).

Fenced cattle ranches had stocking levels of >25 TLU/km^2, and fences on these ranches were used to exclude large wild herbivores. Owners employed 15–20 security guards, herders, and charcoal-production teams to manage expansion of bushes.

Conservancies were managed for livestock and wildlife and tourism or research. Stocking densities were moderate (10–20 TLU/km^2) and fencing was minimal. Most owners employed 15–30 security guards.

Sanctuaries were managed for black and white rhinoceroses. Perimeter fences were semipermeable to allow wildlife other than rhinoceroses to pass. Sanctuary owners employed >30 security guards.

Ranch owners managed livestock with traditional herding methods, employed pastoralist herders, and used thorn or metal corrals. Fenced ranches were subdivided into paddocks. Carnivore tolerance varied by property management, owner, and species. Lethal predator control has been widely practiced in Laikipia (Frank 2011) and continues today.

The properties were not a random sample because we based selection on whether we were allowed access. On the basis of extensive land-use databases for Laikipia maintained by Mpala Research Centre and a study of Laikipia group ranches (Kaye-Zwiebel 2011), however, we believe our property choices were representative of land management in arid and semiarid lands in Kenya where rainfall is <600 mm/year.

Data Collection and Analyses

On each property, we systematically deployed film (n = 216 locations) and digital (n = 306 locations) camera traps (see Supporting Information for detailed methods). We chose 1-km^2 sample units for properties <100 km^2 and 2-km^2 sample units for properties >100 km^2 (Table 1). We used ArcView 3.2 (ESRI, Redlands, CA, U.S.A.) to locate sample unit centroids and placed traps within 50 m of the centroid, typically on a game trail. Points were sampled 19–23 d during the dry seasons

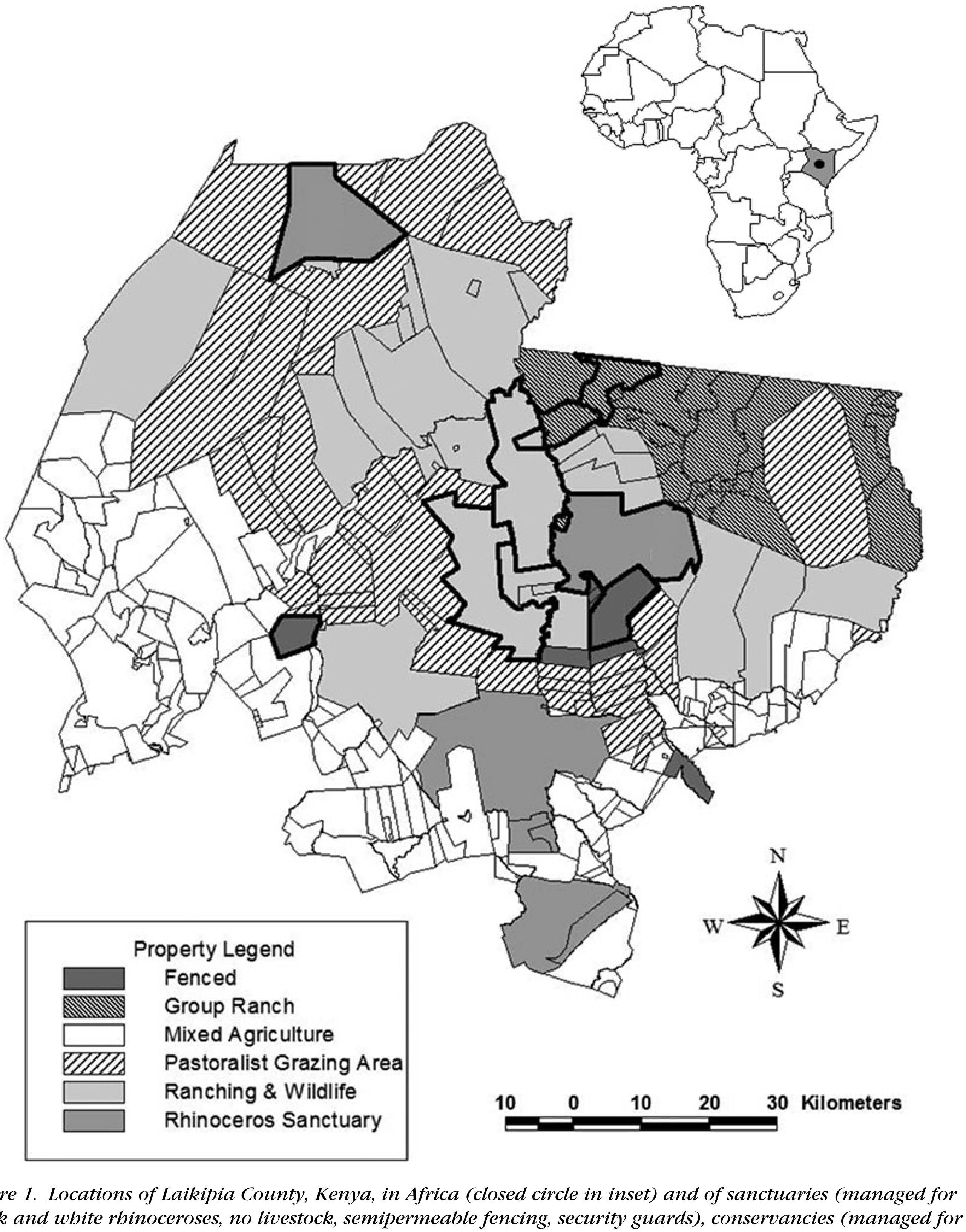

Figure 1. Locations of Laikipia County, Kenya, in Africa (closed circle in inset) and of sanctuaries (managed for black and white rhinoceroses, no livestock, semipermeable fencing, security guards), conservancies (managed for livestock, wildlife, and tourism or research, moderate stocking levels, no fencing, security guards), fenced (managed for livestock, high stocking levels, exclusion fences, security guards), and group ranches (owned by clans of Samburu and Maasai pastoralists, high stocking levels, no fences, no security guards) (bold boundaries) relative to other land uses in Laikipia County. Pastoralist grazing areas are a mix of government trust lands, private properties with absentee owners, and properties with contested ownership.

Table 1. Characteristics of 8 properties in 4 livestock-management types.

Management class[a]	Area (km^2)	Vegetation type (% of area)			Livestock		Humans/km^{2c}		Sampling[d]			
		savanna	*whistling-thorn acacia*	*bushland*	*density*[b]	*composition*	*security*	*other*	*points*	*start*	*stop*	*events/pt.*
Group ranch 1	38	19.0	73.9	7.1	25.2	sheep & goats>camel>cattle	0.00	1.71	37	21/05/08	05/07/08	88.0
Group ranch 2	54	14.9	62.0	23.1	29	sheep & goats>camel>cattle	0.00	1.67	45	14/06/08	16/09/08	61.8
Fenced ranch 1	65	2.9	68.3	28.8	25.2	cattle>sheep and goats	0.20	0.62	64	03/02/09	05/04/09	23.6
Fenced ranch 2	33	22.0	52.6	25.4	37.5	cattle	0.45	1.97	37	19/07/10	08/08/10	41.2
Conservancy 1	200	8.4	12.4	79.2	13.5	cattle>camel>sheep	0.16	0.23	97	08/01/08	12/04/08	44.3
Conservancy 2	200	3.4	44.5	52.1	12.5	cattle>sheep	0.15	0.19	99	07/07/09	22/09/09	79.9
Sanctuary 1	225	17.8	70.9	11.3	0	none	0.58	0.00	100	23/02/10	18/03/10	50.2
Sanctuary 2	92	3.9	92.6	3.5	0	none	0.39	0.00	43	15/09/10	08/10/10	51.8

[a]*Group ranches are owned by clans of Samburu or Maasai pastoralists; fenced ranches use exclusion fencing; conservancies manage for livestock, wildlife, and tourism or research; sanctuaries manage for black and white rhinoceros.*
[b]*Expressed as total livestock units (TLU) per square kilometer and scaled to the weight of a cow.*
[c]*Security refers to workers employed to patrol the property. Other includes herders, charcoal makers, and other ranch personnel and pastoralist community members working in the sampling area. Families living on a property are not included.*
[d]*Definitions: points, number of camera-trap sampling points; start, date sampling began (day/month/year); stop, date sampling ended (day/month/year); events/pt., average number of independent photographic events at a sampling point.*

(January 2008 to October 2010), when roads were passable (Table 1). We classified all animals in photographs to species and grouped photographic sequences into independent photographic events following O'Brien et al. (2003). We used the number of independent photographic events per 100 trap days as a relative abundance index (RAI).

We used single-season occupancy analyses to estimate relative species richness (φ) (Cam et al. 2000; O'Brien et al. 2011), probability of detecting a species if it was present (p), and effect of covariates on φ and p. Relative species richness is alpha diversity/gamma diversity (i.e., the proportion of a regional pool of species represented at a site). We assumed that 64 species of mammals (Supporting Information) represented regional species richness. Because mammal body size can affect detection by the camera sensor, we considered the z-score of body mass as a covariate for detection probability. We used z-scores of number of days camera traps were active as a covariate of sampling effort. We considered model hypotheses that related φ to livestock management type (management) and controlled for effects of vegetation type (vegetation), sampling effort (sampling), and body size (mass) on detection probability.

We used program PRESENCE 3.1 (Hines 2008) for all analyses of species richness. We analyzed management types separately because the combined model failed to converge numerically due to the large numbers of possible detection histories with very small probabilities (J. E. Hines, personal communication). For each management type, we evaluated the full set of candidate models from the no-covariate model, $\varphi_{\text{management}}(\cdot)$, $p(\cdot)$, to the full model, $\varphi_{\text{management}}$(vegetation, sampling), p(mass). We based model rank on the minimum Akaike information criterion (AIC) and deleted models with AIC weights $w_i \leq 0.05$. We used model averaging to estimate φ, p, and covariate coefficients (Burnham & Anderson 2002) when multiple models provided adequate descriptions of the data. We then compared results for management types across analyses.

We used single-season occupancy analyses (MacKenzie et al. 2006) to estimate the probability that a given site was occupied by a species (ψ) or the proportion of an area occupied within a management type for each species. Because management types included different distributions of vegetation types, we treated vegetation type as a covariate of occupancy. We also included covariates that measured activity at camera points: z-scores of RAI for cattle, sheep and goats, dogs, and humans. We refer to these covariates collectively as livestock-related activities. Finally, we included z-scores of date of camera activation as a covariate (start) to control for changes in detection probability over the 2.4 years of sampling.

Occupancy of each species was analyzed separately with program PRESENCE 3.1. We considered model hypotheses that related occupancy to livestock management type while controlling for the effects of vegetation type and livestock-related activity on occupancy. We treated detection probability as constant or a function of time. We evaluated all covariate combinations from $\psi(.)$, $p(.)$ to the full model ψ(management, vegetation, human, cattle, sheep and goats, dog), p(start) as candidate models. We ranked models by minimum AIC and deleted models with $w_i \leq 0.05$. We used model averaging to estimate ψ, p, and covariate coefficients (Burnham & Anderson 2002) when multiple models provided adequate descriptions of the data.

We evaluated livestock management effects on wildlife abundance with the RAI of independent photographs (O'Brien et al. 2003), calibrated to independently derived abundance estimates (Supporting Information). We normalized the RAI values within species on the basis of z-scores. We used multiple analyses of covariance (MANCOVA) to analyze RAI for groups of carnivores (large and small, $n = 11$), ungulates (large and small, $n = 19$), and other species (scrub hare [*Lepus saxatilis*], aardvark [*Orycteropus afer*], and crested porcupine [*Hystrix cristata*]). We evaluated each MANCOVA with Wilk's Λ test to evaluate simultaneously the effects of covariates on grouped RAIs and used analysis of covariance (ANCOVA) with multiple-means comparison tests to evaluate whether effects on each species were significant.

To characterize community structure we plotted species RAIs as a function of management type, body size, and trophic category. For each species, we obtained body sizes from Smith et al. (2003) and Kingdon (1997) and assigned each species a trophic category (carnivore, herbivore browser and grazer, insectivore, or omnivore) (Supporting Information).

Results

Photographs from 522 locations were usable (Table 1). Film and digital cameras provided a similar number of detections (average of 54.4 [SD 27.3] independent photographic events per point for film and 55.8 [SD 16] for digital cameras). We recorded 28,586 independent photographic events of 50 mammal species, 14 bird species, 5 livestock species, domestic dogs, and humans.

Species Richness

Model-averaged relative species richness was highest for conservancies ($\hat{\phi}$= 0.753, 48 species), followed by sanctuaries ($\hat{\phi} = 0.584$, 37 species), fenced ranches ($\hat{\phi} = 0.518$, 33 species), and group ranches ($\hat{\phi} = 0.408$, 26 species) (Table 2), consistent with our first hypothesis. Model $\varphi(\cdot)$, p(mass) was most strongly supported for sanctuaries ($w_i = 0.881$), conservancies ($w_i = 0.881$), and fenced ranches ($w_i = 0.732$) (Table 2). Model $\varphi(\cdot)$,

Table 2. Model selection for relative species richness (φ) and model-averaged parameter estimates.

Management type and model[a]	Model selection parameters[b]						Model-averaged parameter estimates[c]			
	AIC	*ΔAIC*	*AICwgt*	*no. par*	*−2LL*	*Observed occupancy*	*$\hat{\varphi}$ (SE)*	*95%CI*	*$\hat{p}$ (SE)*	*$\hat{N}$*
Sanctuary										
psi(.), p(mass)	509.30	0.00	0.8808	3	503.30	0.5781	0.5837 (0.0625)	0.459–0.699	0.528 (0.041)	37
psi(vegetation), p(mass)	513.30	4.00	0.1192	5	503.30					
Conservancy										
psi(.), p(mass)	614.12	0.00	0.8808	3	608.12	0.7344	0.7533 (0.0566)	0.627–0.847	0.557 (0.032)	48
psi(vegetation), p(mass)	618.12	4.00	0.1192	5	608.12					
Fenced ranch										
psi(.), p(mass)	499.07	0.00	0.7325	3	493.07					
psi(.), p(.)	502.01	2.94	0.1684	2	498.01	0.5156	0.5181 (0.0628)	0.396–0.638	0.473 (0.036)	33
psi(vegetation), p(mass)	503.07	4.00	0.0991	5	493.07					
Group ranch										
psi(.), p(.)	412.14	0.00	0.6460	2	408.14	0.4063	0.4082 (0.0617)	0.295–0.532	0.446 (0.028)	26
psi(.), p(mass)	413.91	1.77	0.2666	3	407.91					
psi(vegetation), p(.)	416.14	4.00	0.0874	4	408.14					

[a]*Management type defined in Table 1. Models are alternative relative species richness models, estimated for each management type. Covariates: vegetation, vegetation type; mass, body mass.*
[b]*Abbreviations: AIC, Aikaike information criterion; ΔAIC, difference between model AIC and lowest AIC; AICwgt, AIC weight; no. par, number of parameters in model; −2LL, negative value of twice the log likelihood.*
[c]*Definitions: $\hat{\varphi}$, estimated relative species richness; 95% CI, 95% confidence interval for relative species richness; $\hat{p}$, estimated detection probability; $\hat{N}$, estimated number of species.*

$p(\cdot)$ was most strongly supported for group ranches (w_i = 0.646). There was little support for effects of vegetation type on relative species richness ($w_i = 0.087$–0.119) (Table 2). Effects of body size on detection probability varied by management type ($w_i = 0.267$–1.0) (Table 2). For sanctuaries and conservancies, detection probability increased as body size increased, but for fenced ranches detection probability decreased as body size increased. For group ranches, detection probability was not associated with body size. Estimates of relative species richness were not significantly different from observed relative species richness, most likely due to high detection probabilities ($\hat{p} = 0.446$–0.528).

Species Distribution

We determined occupancy for 29 species and 2 additional species groups (3 small cats and 5 small carnivores) for which we had sufficient data (Table 3). Effects of management type were strongly supported in all occupancy models ($w_i = 1.0$), except white tailed mongoose (*Ichneumia albicauda*) and crested porcupine. Occupancies were highest for conservancies (0.272 [SD 0.183]) and sanctuaries (0.257 [SD 0.183]), compared with fenced (0.124 [SD 0.142]) and group ranches (0.055 [SD 0.082]). We considered species with $\hat{\psi} < 0.1$ uncommon within management types. Uncommon species occurred more often in group (25 species) and fenced (19 species) ranches than in sanctuaries (10 species) and conservancies (6 species). The small carnivores, white-tailed mongoose, and crested porcupine were uncommon on all properties. Black-backed jackal (*Canis mesomelas*), bushbuck (*Tragelaphus scriptus*), bush duiker (*Sylvicapra grimmia*), and Thompson's gazelle (*Gazella rufifrons*) were uncommon on sanctuaries and fenced and group ranches (Table 3).

Occupancy of large mammals was more strongly associated with management type than smaller mammals, consistent with hypothesis 2 (Table 3). Large-carnivore occupancy was higher on conservancies and sanctuaries (0.325 [SD 0.155]) than on fenced and group ranches (0.066 [SD 0.088]). Occupancy of smaller carnivores was similar for sanctuaries and conservancies (0.121 [SD 0.189]) and fenced and group ranches (0.064 [SD 0.124]). Large-ungulate (>100 kg) occupancy was higher for sanctuaries and conservancies (0.347 [SD 0.206]) than for fenced and group ranches (0.032 [SD 0.054]), whereas occupancy for smaller ungulates was similar for sanctuaries and conservancies (0.208 [SD 0.190]) and fenced and group ranches (0.171 [SD 0.165]).

Effects of livestock-related activity during sampling on occupancy of species were highly variable (Table 3). At least one livestock-related activity was associated with occupancy of 16 species ($w_i \geq 0.6$; 11 negative and 8 positive associations). Occupancy of carnivores was least associated with livestock-related activity, perhaps because carnivores tend to be nocturnal, whereas most activity was diurnal. Cattle abundance was associated with occupancy of 6 ungulate species (3 negative, 3 positive). Sheep and goat abundance was associated with occupancy of 2 carnivores (both negative) and 2 ungulates (1 positive and 1 negative). Dog abundance was associated with occupancy of 3 ungulates (1 negative and 2 positive) and 1 carnivore (positive). Finally, human abundance was associated with occupancy of 3 ungulates (2 negative and 1 positive) and 1 carnivore (negative).

Vegetation type was strongly associated with occupancy ($w_i \geq 0.85$) of 17 species (Table 3). Occupancy for Olive baboon (*Papio anubis*) and 6 ungulate species was significantly higher in whistling-thorn acacia woodland. Occupancy was significantly higher in savanna for 13 species and significantly higher in acacia bushland for 7 species (Table 3). Seven ungulates and 2 carnivores were significantly associated with one vegetation type. Seven ungulates and 2 carnivores were significantly associated with savanna and one other vegetation type.

Sampling start date was a significant covariate of detection in 20 species models, but the effect varied by species (Table 3). Detection declined over time for 8 species and increased for 12 species.

Species Abundance

Camera trap RAIs were highly correlated with independent estimates of carnivore and ungulate abundance (Supporting Information). Carnivore abundance explained 96% of variance in carnivore RAI. Removal of an apparent outlier reduced the regression fit ($r^2 = 0.74$) but did not significantly change the regression intercept ($t_{\text{intercept}} = 2.06$, df = 14, $p = 0.058$) or slope ($t_{\text{slope}} = 2.08$, df = 14, $p = 0.056$). Ungulate abundance explained 89% and 76% of variation in ungulate RAIs for conservancies I and II, respectively. Regression slopes and intercepts were not significantly different ($t_{\text{intercept}} = 1.25$, df = 20, $p = 0.22$; $t_{\text{slope}} = 0.11$, df = 19, $p = 0.91$). Therefore we used RAIs as surrogates for species-specific abundances.

Management type significantly affected RAIs for carnivores ($p < 0.001$) and ungulates ($p < 0.001$) (Table 4). Vegetation type significantly affected RAI of carnivores ($p = 0.029$), as did an interaction between management type and vegetation type ($p = 0.032$). Among the livestock-related activities, human activity significantly affected ungulates ($p < 0.001$) (Table 4). As predicted in hypotheses 1 and 2, large-carnivore RAIs were higher for sanctuaries and conservancies ($\bar{z} = 0.299$) than for fenced and group ranches ($\bar{z} = -0.43$) (Table 5). Smaller carnivores were generally uncommon, but they were more abundant on sanctuaries ($\bar{z} = -0.006$) and conservancies ($\bar{z} = -0.023$). The RAIs for caracals (*Felis caracal*) and servals (*Felis serval*) were highest on fenced ranches. Vegetation effects on carnivore RAIs were significant (Tables 4 & 5) only for leopards (*Panthera pardus*),

Table 3. Model-averaged occupancy analyses for 29 species and 2 species groups.

			Model-averaged weights for independent variables[c]								Model-averaged occupancy[d]						
Species	Guild (size class)[a]	No. models[b]	manage-ment	vegeta-tion	cow	sheep and goats	dog	human	start	Observed occupancy	sanc-tuary	conser-vancy	fenced	group	whistling-thorn	savanna	bushland
Guenther's dikdik, *Madoquoa guentheri*	browser (S)	1	1.0*	1.0*	1.0 (−*)	0.0	0.0	0.0	1.0 (−*)	0.389	0.369	0.469	0.408	0.342	0.218	0.432	0.668*
Steinbuck, *Raphicerus campestris*	browser (S)	5	1.0*	1.0*	0.08 (+)	0.0	0.051 (−)	0.756 (−)	0.819 (+*)	0.151	0.032	0.233	0.302	0.014	0.239*	0.070	0.097
Gerenuk, *Litocranius walleri*	browser (S)	5	1.0*	1.0*	0.0	0.0	0.767 (+*)	0.061 (−)	0.602 (+*)	0.123	0.368	0.000	0.043	0.153	0.076	0.272*	0.123*
Reticulated giraffe, *Giraffa camelopardis*	browser (L)	6	1.0*	0.908*	0.314 (+)	0.093 (−)	0.124 (−)	0.141 (+)	1.0 (+*)	0.399	0.693	0.638	0.064	0.000	0.461	0.52*	0.361
Black−backed jackal, *Canis mesomelas*	carnivore (S)	2	1.0*	1.0*	0.776 (−)	0.224 (−)	0.0	0.0	0.771 (+)	0.077	0.026	0.581	0.000	0.000	0.382*	0.117	0.072
Small cats, *Felis* spp. ($n = 3$)	carnivore (S)	2	1.0*	0.0	0.0	0.0	0.0	0.0	0.674 (−)	0.046	0.029	0.131	0.367	0.000	0.129	0.092	0.151
Small carnivores ($n = 5$)	carnivore (S)	8	1.0*	0.0605	0.106 (+)	0.371 (−*)	0.081 (−)	0.08 (+)	0.108 (+)	0.036	0.022	0.063	0.020	0.025	0.040	0.032	0.038
White−tailed mongoose, *Ichneumia albicauda*	carnivore (S)	6	0.477*	0.0	0.108 (−)	0.0	0.0	0.601 (−)	0.076 (−)	0.050	0.040	0.074	0.049	0.051	0.057	0.050	0.059
Leopard, *Panthera pardus*	carnivore (L)	5	1.0*	0.914*	0.0	0.088 (+)	0.489 (+*)	0.121 (−)	1.0 (−*)	0.115	0.251	0.135	0.038	0.000	0.099	0.187*	0.126*
Lion, *Panthera leo*	carnivore (L)	6	1.0*	0.0	0.111 (−)	0.103 (+)	0.117 (−)	0.236 (−)	0.186 (−)	0.069	0.286	0.129	0.019	0.000	0.140	0.153	0.102
Aardwolf, *Proteles cristata*	carnivore (L)	2	1.0*	0.893*	0.0	0.893 (−)	0.0	0.0	1.0 (−*)	0.077	0.409	0.167	0.025	0.018	0.128	0.249*	0.218*
Spotted hyena, *Crocuta crocuta*	carnivore (L)	4	1.0*	0.0	0.0	0.868 (−)	0.879 (+)	0.0	1.0 (+*)	0.318	0.559	0.517	0.193	0.050	0.420	0.390	0.354
Striped hyena, *Hyaena hyaena*	carnivore (L)	6	1.0*	0.852*	0.119 (−)	0.114 (+)	0.109 (+)	0.304 (−)	1.0 (−*)	0.203	0.376	0.420	0.258	0.062	0.304	0.281	0.369*
Scrub hare, *Lepus saxatilis*	grazer (S)	6	1.0*	1.0*	0.244 (+)	0.111 (−)	0.351 (+)	0.121 (+)	1.0 (−*)	0.169	0.139	0.244	0.208	0.190	0.122	0.318*	0.233
Warthog, *Phacochoerus africanus*	grazer (S)	1	1.0*	0.0	0.0	1.0 (−)	1.0 (+)	0.0	0.0	0.182	0.322	0.359	0.069	0.101	0.268	0.250	0.232
Thompson's gazelle, *Gazella rufifrons*	grazer (S)	6	1.0*	1.0*	0.124 (+)	0.342 (−)	0.338 (−)	0.109 (−)	1.0 (+*)	0.098	0.057	0.357	0.000	0.040	0.212*	0.217*	0.036
Grant's gazelle, *Gazella granti*	grazer (S)	4	1.0*	1.0*	0.613 (+*)	0.0	0.0	0.495 (+)	1.0 (+*)	0.211	0.327	0.344	0.016	0.012	0.388*	0.193*	0.072
Hartebeest, *Alcelaphus buselaphus*	grazer (L)	7	1.0*	0.176	0.275 (+)	0.0	0.161 (+)	0.169 (−)	0.571 (+)	0.046	0.111	0.229	0.000	0.000	0.136	0.096	0.102
Beisa oryx, *Oryx beisa*	grazer (L)	5	1.0*	1.0*	0.066 (+)	0.085 (−*)	0.0	0.675 (+)	0.546 (+)	0.115	0.362	0.123	0.013	0.000	0.203*	0.202*	0.034
Waterbuck, *Kobus ellipsiprymnus*	grazer (L)	8	1.0*	0.0824	0.122 (−)	0.108 (−)	0.062 (+)	0.466 (−)	0.215 (−)	0.090	0.126	0.179	0.224	0.000	0.153	0.120	0.150
Common zebra, *Equus quagga*	grazer (L)	1	1.0*	1.0*	1.0 (+*)	0.0	1.0 (−*)	0.0	1.0 (−*)	0.324	0.789	0.480	0.000	0.000	0.551*	0.419*	0.109
Grevy's zebra, *Equus grevyi*	grazer (L)	3	1.0*	1.0*	0.213 (+)	0.214 (-)	0.0	0.0	1.0 (+*)	0.086	0.296	0.102	0.000	0.000	0.063	0.265*	0.104
Cape buffalo, *Syncerus caffer*	grazer (L)	2	1.0*	0.151	0.0	0.0	0.0	1.0 (−*)	1.0 (+*)	0.157	0.318	0.366	0.056	0.025	0.259	0.226	0.220
Bush duiker, *Sylvicapra grimmia*	grazer/browser (S)	2	1.0*	0.188	0.0	1.0 (+*)	0.0	0.0	1.0 (−*)	0.123	0.057	0.066	0.516	0.094	0.145	0.125	0.189
Impala, *Aepyceros melampus*	grazer/browser (S)	5	1.0*	1.0*	0.094 (−)	0.534 (−)	0.120 (−)	0.088 (−)	1.0 (−*)	0.402	0.426	0.458	0.240	0.092	0.280	0.454*	0.382*
Bushbuck, *Tragelaphus scriptus*	grazer/browser (S)	5	1.0*	0.087	0.864 (−*)	0.0	0.0	0.062 (+)	0.306 (−)	0.038	0.000	0.020	0.154	0.000	0.036	0.022	0.049
Elephant, *Loxondonta africana*	grazer/browser (L)	7	1.0*	0.345*	0.826 (+*)	0.078 (+)	0.052 (−)	0.0	0.867 (+*)	0.255	0.345	0.500	0.012	0.123	0.354*	0.294	0.249
Eland, *Taurotragus oryx*	grazer/browser (L)	7	1.0*	1.0*	0.255 (−)	0.102 (−)	0.063 (−)	0.181 (−)	0.873 (+*)	0.144	0.377	0.208	0.053	0.000	0.189	0.150	0.224*
Olive baboon, *Papio anubis*	omnivore (S)	8	1.0*	1.0*	0.268 (-)	0.104 (−)	0.127 (−)	0.211 (−)	0.055(+)	0.276	0.323	0.449	0.311	0.015	0.334*	0.392*	0.251
Aardvark, *Orycteropus afer*	other (L)	7	1.0*	0.0	0.129 (+)	0.104 (+)	0.098 (−)	0.249 (+*)	0.933 (+*)	0.075	0.082	0.368	0.146	0.254	0.243	0.196	0.231
Crested porcupine, *Hystrix cristata*	other (S)	5	0.0	0.092	0.635 (-)	0.0	0.0	0.133 (+)	0.881 (+*)	0.036	0.049	0.038	0.033	0.053	0.041	0.044	0.043

[a] *Feeding-guild classifications and size class (L, large body size; S, small body size).*
[b] *Abbreviation: No. models, number of models with AIC weight > 0.05. These models are included in model averaging for final parameter estimates.*
[c] *Covariates: management, management type, defined in Table 1; vegetation, vegetation type; cow, sheep and goats, dog, and human, relative abundance index for these variables; start, Julien date for start of survey; +, positive coefficient; –, negative coefficient; *, $p < 0.05$).*
[d] *Model-averaged estimates of occupancy by management type (sanctuary, conservancy, fenced, group) and by vegetation type (whistling-thorn acacia woodland, savanna, acacia bushland) (*, values significantly different [$p < 0.05$] from other values).*

Table 4. Multiple analysis of covariance results for tests of effects of management type and covariates[a] on grouped relative abundance indices for carnivores, ungulates, and other mammals.

Species group and model	*Wilk's lambda*	*F*	*Hypothesis df*	*Error df*	*p*
Carnivores					
intercept	0.975	0.229	11	99	0.995
management	0.222	0.598	33	292.4	0.000
vegetation	0.706	1.710	22	198	0.029
management* vegetation	0.432	1.377	66	535	0.032
Ungulates					
intercept	0.924	0.391	19	90	0.989
management	0.169	3.845	57	269.2	0.000
vegetation	0.589	1.437	38	180	0.061
management* vegetation	0.346	0.934	114	525.5	0.667
human	0.568	3.601	19	90	0.000
Other mammals					
intercept	0.986	0.517	3	107	0.671
management	0.892	1.388	9	260.5	0.194
vegetation	0.915	1.62	6	214	0.143
management* vegetation	0.868	0.868	18	303.1	0.618

[a]*Abbreviations: management, management type; vegetation, vegetation type; human, relative abundance index for humans.*

which had lower RAI in whistling-thorn acacia woodland. Management type by vegetation type interactions had a significant effect on RAI of African wild dogs (*Lycaon pictus*), leopards, and striped hyenas (*Hyena hyena*). African wild dogs were observed only in acacia bushland on conservancies. Leopards were more abundant in conservancy acacia bushland and sanctuary and group-ranch savanna. Striped hyenas were more abundant in conservancy and group-ranch acacia bushland and in sanctuary and fenced-ranch savanna.

Among 19 ungulate species (Table 5), RAIs were highest on sanctuaries ($\bar{z} = 0.305$), followed by conservancies ($\bar{z} = -0.071$), fenced ranches ($\bar{z} = -0.017$), and group ranches ($\bar{z} = -0.289$), consistent with hypothesis 1. Sanctuaries had the highest RAI for 13 ungulate species. Conservancies had highest RAI for 2 species and second highest for 12 species, whereas fenced ranches had highest RAI for 4 species and second highest RAI for 3 species (Table 5). Abundance of large ungulates was highest in sanctuaries and second highest in conservancies, whereas smaller ungulates had similar abundance across management types, consistent with hypothesis 2. Contrary to expectation, human abundance positively affected RAIs of 3 small and 5 large ungulates. Although human abundance was highest on group ranches, most of the 8 species positively affected by human abundance attained highest RAI on sanctuaries and conservancies, where human activity included security patrols.

Community Structure

Community structure of mammals differed substantially among management types (Fig. 2). Within trophic levels, species abundance and average body size declined as livestock management intensified, and many species were absent from fenced and group ranches. Sanctuaries and conservancies had similar proportions and diversity of grazers and browsers and mixed feeders (i.e., ungulates capable of switching between grazing and browsing). On fenced and group ranches, abundance and diversity of grazers and mixed feeders was low and small browsers were dominant. As management intensified, abundance and diversity of carnivores and insectivores decreased and the size distribution shifted to smaller species. Omnivores were relatively unaffected by management type. In general, mammal communities in conservancies filled the functional space more completely than other communities due to high species richness and high RAI. On group and fenced ranches wildlife biomass was substantially lower than in conservancies and sanctuaries, due to lower species richness and abundance and smaller body sizes of species.

Discussion

Management types characterized by high stocking levels had detrimental effects across a broad range of Laikipia's mammal species. Wildlife appeared unaffected by moderate stocking levels in conservancies, but as stocking levels increased, species richness, abundance, and distributions declined. Species richness was highest in conservancies and sanctuaries. Occupancy was twice as high in sanctuaries and conservancies as on fenced ranches and 5 times higher than on group ranches. Most species on group and fenced properties were uncommon; RAI values of 31 of 32 species were highest or second highest in sanctuaries or conservancies. Distributions and abundances of large carnivores and ungulates were more adversely affected by management type than were smaller species. Only bush duikers, bushbuck, bush pigs, and serval were

Table 5. Univariate analysis of co-variance significance levels for tests of independent effects on relative abundance indices for each species in the species groups in Table 4.

Species group and species[a]	*Corrected model p*	*Management p*	*Vegetation p*	*Management x vegetation p*	*Human-activity covariate p*	*Ranked management effect*[b]	*Ranked vegetation effect*[c]	*Human- activity covariate effect*
Carnivores								
sm. carnivores (s)	0.897	0.823	0.523	0.910	no human activity			
wild dog (s)	0.003	0.096	0.138	0.023				
black-backed jackal (s)	0.009	0.002	0.844	0.849		C>S = F = G		
caracal (s)	0.076	0.016	0.149	0.165		F = C = S, F>G		
serval (s)	0.031	0.000	0.909	0.999		F>C = S = G		
aardwolf (l)	0.024	0.029	0.254	0.199		S = C = F, S = C>G		
striped hyena (l)	0.000	0.000	0.078	0.002		S>C>F = G		
spotted hyena (l)	0.067	0.003	0.726	0.642		S = C, S>F = G		
cheetah (l)	0.106	0.051	0.073	0.130				
leopard (l)	0.000	0.000	0.004	0.020		C = S>F = G	S = B>W	
lion (l)	0.008	0.000	0.569	0.953		S>C = F = G		
Ungulates					human activity			
Guenther's dik dik (S)	0.000	0.000			0.254	C>F>G = S		
steinbuck (S)	0.021	0.738			0.000	F>S = C>G		0.388
bush duiker (S)	0.000	0.000			0.484	F>G>S>C		
bushbuck (s)	0.004	0.000			0.894	F>C = G = S		
impala (s)	0.000	0.000			0.121	S>C = F, C>G		
Grant's gazelle (S)	0.000	0.000			0.266	S>C = F = G		
Thompson's gazelle (S)	0.232	0.775			0.008			0.298
warthog (s)	0.122	0.985			0.002			0.343
bushpig (s)	0.070	0.002			0.944			
Cape buffalo (L)	0.015	0.004			0.113	S = C, S>F = G		
common zebra (L)	0.464	0.445			0.050			0.221
Grevy's zebra (L)	0.000	0.484			0.000	S>C = F = G		0.434
eland (L)	0.018	0.001			0.078	S>C = F = G		
greater kudu (l)	0.434	0.741			0.412			
hartebeest (l)	0.235	0.180			0.497			
Beisa oryx (L)	0.000	0.304			0.000	S>C = F = G		0.515
waterbuck (L)	0.247	0.599			0.004			0.325
elephant (L)	0.188	0.075			0.574			
reticulated giraffe (L)	0.000	0.000			0.000	S>C>F = G		0.301

[a]*Abbreviations: L, large mammal; S, small mammal.*
[b]*Abbreviations: S, sanctuary; C, conservancy; F, fenced ranch; G, group ranch.*
[c]*Abbreviations: S, savanna; B, acacia bushland; W, whistling-thorn acacia woodland.*

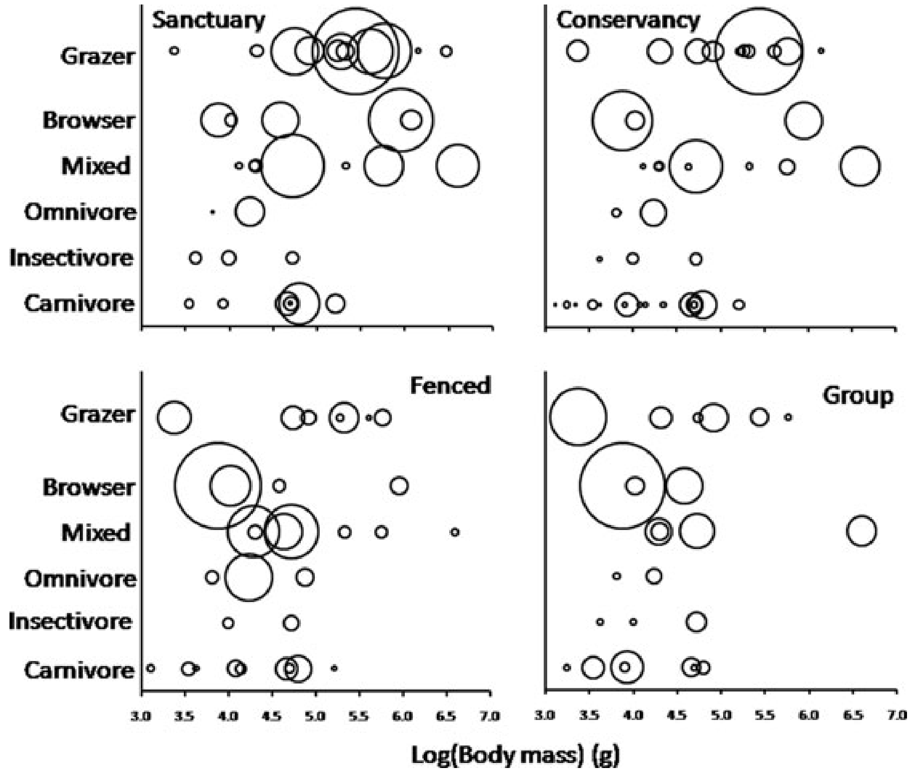

Figure 2. Distribution of mammal species in 4 livestock-management types in Laikipia County, Kenya, on the basis of body size and trophic category (management type: sanctuary, managed for black and white rhinoceroses, no livestock, semipermeable fencing, security guards; conservancy, managed for livestock, wildlife, and tourism or research, moderate stocking levels, no fencing, security guards; fenced ranch, managed for livestock, high stocking levels, exclusion fences, security guards; group ranch, owned by clans of Samburu and Maasai pastoralists, high stocking levels, no fences, no security guards; each circle represents a species in functional space; size of the circle proportional to the relative abundance index for that species).

significantly more abundant on fenced ranches than in sanctuaries and conservancies.

Because we focused explicitly on livestock management on private properties, our work has limitations. First, some properties classified as pastoralist grazing areas (Fig. 1) are government owned or have absentee owners or contested ownership (Kaye-Zwiebel 2011). These lands are used as common grazing areas and cannot be considered private property. We were unable to sample these areas due to security risks. Second, use of TLU to characterize stocking levels may imply the equivalent effect on rangeland of a cow TLU relative to a goat or sheep TLU. This may not be true. Finally, we assumed livestock management types incorporated unmeasured variables such as household density, security, and rangeland quality, but we did not test this assumption. Given these caveats, several factors may explain our results, and although none are mutually exclusive, all relate to styles of livestock management and levels of human tolerance of wildlife. These factors include fencing, livestock type and stocking levels, human activity, lethal measures used to control wildlife, and the economics of human tolerance of wildlife.

Fencing has been used to restrict access of large wild herbivores, especially those that presumably compete with livestock, to agricultural fields and cattle pastures (Young et al. 2005, but see Odadi et al. 2011). In the 1960s, most Laikipia ranches had perimeter fences (2325 km total) and interior paddock fences (Denney 1972). Today there are approximately 766 km of fences, primarily in agricultural areas of south Laikipia, around rhinoceros sanctuaries, and where wildlife or livestock movements are discouraged (e.g., 120 km Laikipia West Elephant Fence). One fenced ranch had twice as many species as the other; most of this disparity was due to the detection of many species near a semipermeable fence shared with one of the sanctuaries. In general, fencing constrains movement, but relatively few Laikipia properties are completely fenced and sanctuary fences are permeable to all species except rhinoceroses. Therefore wildlife moves largely unfettered across northern Laikipia (Georgiadis et al. 2007).

Semiarid rangelands have a maximum stocking capacity of 10–20 TLU/km^2, equivalent to 2–4 t/km^2 (Denney 1972; Hein & Weikard 2008). If one assumes combined livestock–herbivore biomass on conservancies approximates maximum stocking capacity of north Laikipia rangeland (4.6 t/km^2, excluding elephants) (Georgiadis et al. 2007), then stocking levels on fenced properties (>5 t/km^2) and group ranches (4.5 t/km^2) could be maintained only through exclusion of wildlife. Otherwise, vegetation may be negatively affected by browsing and grazing (Du Toit & Cummings 1999). Elimination of large grazers and browsers combined with rotational grazing on fenced ranches did not appear to degrade paddocks despite high stocking levels. On group ranches, high livestock densities were associated with sheep and goats (1 TLU = 8 sheep or goats) and little opportunity to allow livestock to graze larger areas. The combination of high densities of close-cropping grazers and low- to mid-level browsers, limited mobility, and lack of rotational grazing led to vegetation degradation on group ranches (Kaye-Zwiebel 2011). The observed trophic shifts in wildlife from many large grazers and browsers to few small browsers are, in part, a consequence of vegetation degradation on group ranches and exclusion of large wildlife on fenced ranches.

Harassment of wildlife may lead to their displacement, especially on group ranches. Multiple, large livestock herds moving daily (>2 herds/km^2) on group ranches may increase the likelihood of wildlife encounters with livestock, people, and dogs. Human and dog RAIs were 5 times higher on group ranches than in conservancies. Although some species can move in response to this activity (i.e., common zebra, elephant), territorial species or habitat specialists cannot. Wildlife distribution tended to decline in response to livestock-related activity. As livestock-related activities increased, occupancy decreased for 8 species and increased for 5 species. Species whose distribution benefited from livestock and humans were uncommon or absent on group ranches. We attributed positive effects on distribution on other properties to security staff and wildlife-tolerant policies. Species abundances were less sensitive to livestock-related activity than to management type because wildlife tended to vacate an area when livestock arrived (personal observation). On conservancies and sanctuaries the effect of livestock-related activities was minimal, but on group ranches resulted in displacement and disappearance of large grazers and browsers.

Woodroffe and Frank (2005) showed that Laikipia's lion (*Panthera leo*) population is regulated by lethal control and that activities on a single ranch can affect lions across the landscape. Whereas most ranch owners are tolerant of predators, owners of fenced ranches and members of group ranches have negative attitudes toward predators unless they benefit from ecotourism (Kaye-Zwiebel 2011). Lions are consistently identified as problem animals and are the most likely carnivore to be killed. Frank (2011) confirmed that lions respond to being hunted by avoiding group ranches, where all incidents of poisoning in Laikipia occurred (Frank et al. 2011). Use of nonselective lethal control (poisons and snares) on group ranches may explain the rarity of medium and large carnivores.

Retribution killing of crop-raiding animals and bushmeat hunting for trade are often linked and hard to document. Kiringe et al. (2007) found protected area managers in Kenya rank bushmeat hunting and retaliatory killing for crop damage as the greatest threats to wildlife. We assumed these threats are present outside protected areas, where most wildlife reside. We documented one poaching incident (Guenther's dikdik) and observed snare traplines for ungulates and human removal of meat from giraffe and hippopotamus carcasses. Wildlife disappearances from group ranches and countrywide declines over 20 years indicate that some species are being eradicated rather than displaced (Norton-Griffiths & Said 2010). However, the relative roles of retribution killing and bushmeat trade in declines in abundance and shifts in distribution of wildlife across Laikipia are unclear. The exception is the role of illegal killing of elephants for retribution and ivory. Between 2002 and 2008, poaching and retribution killing were the dominant forms of elephant mortality on group ranches and government lands (31% and 17%, respectively), whereas natural mortality was most common on other ranches (Douglas-Hamilton et al. 2010). Illegal killing of elephants is currently at the highest levels recorded since the 1970s (I. Douglas-Hamilton, personal communication).

Norton-Griffiths and Said (2010) attribute wildlife population declines to Kenya's ban on consumptive use. They argue that costs of wildlife to pastoral communities and ranches are so high that only properties with supplemental income can afford to tolerate wildlife. In Laikipia many owners who tolerate wildlife engage in tourism businesses or augment their income by leasing property for British army-training exercises. Members of group ranches are increasingly turning to tourism, bioenterprise schemes (e.g., honey, cultivation of medicinal plants), outside employment, and small-scale agriculture to supplement their incomes. Between one-third and two-thirds of households on group ranches have at least one wage-earning member (Kaye-Zwiebel 2011).

Our study underscores the importance of private lands in semiarid regions to wildlife conservation. In Laikipia creation of a larger network of wildlife-tolerant properties would further benefit wildlife but will occur only if members of group ranches and pastoral grazing areas (Fig. 1) benefit directly from wildlife through a range of activities (Norton-Griffiths & Said 2010). Incentives to conserve wildlife include further development of ecotourism ventures that benefit local communities, agreements (e.g., conservation easements) to maintain wildlife habitat and corridors, resolution of land-ownership conflicts, equitable and effective compensation schemes for loss of life and property, assistance in restoration of degraded rangelands, creation of fair systems of leased grazing, and wildlife harvesting schemes that provide direct benefits to local people. Such policies would allow a wider range of options for landholders to capitalize on benefits from wildlife. Key elements of Kenya's Draft Wildlife Policy, although controversial, include decentralization of wildlife conservation planning, a focus on local-level decision making and implementation, increased community participation in wildlife conservation through establishment of community wildlife-conservation areas, incentives and user rights to promote sustainable management, and compensation for wildlife damage on private properties. We think this policy could provide a framework for continued, successful wildlife conservation throughout Kenya and serve as a model for other parts of Africa.

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Supporting Information

Detailed methods (Appendix S1), list of large mammal species in Laikipia County (Appendix S2), and calibration of relative abundance indices (RAIs) to abundance estimates of carnivores and ungulates (Appendix S3) are available online. Authors are responsible for content and functionality of these materials. Queries (other than absence of material) should be directed to corresponding author.

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