Response of native ungulates to drought in semi-arid Kenyan rangeland

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Abstract

The distribution and abundance of native ungulates were measured on commercially managed, semi-arid rangeland in central Kenya over a 3-year period that encompassed severe drought and above-average rainfall. Native ungulate biomass density averaged 5282 kg km^{-2} over the study and was dominated by elephant (*Loxodonta africana*), impala (*Aepyceros melampus*) and dik-dik (*Madoqua kirkii*). Biomass density of domestic cattle (*Bos taurus*) averaged 2280 kg km^{-2} during the study. Responses of native ungulates to severe drought were variable. Impala densities were similar to or greater than densities for similar habitat in protected areas, and varied from 12 to 16 km^{-2} during and following the drought to 24–29 km^{-2} following above-average rainfall. Dik-dik densities were also greater than densities reported for protected areas and were surprisingly stable throughout the study despite the wide annual fluctuations in rainfall. Elephant migrated out of the region during drought but were present at high densities (2.9–5.2 km^{-2}) during wet seasons, consistent with telemetry studies emphasizing the importance of *Acacia* bushland habitat on commercial rangelands for the migratory portion of the Laikipia–Samburu elephant population. Results show that substantial densities of native browsing and mixed-feeding ungulates can occur on rangeland managed for commercial beef production and suggest that the capacity for ungulates to move over large spatial scales (>100 km^2) and to shift distributions in response to locally variable thunderstorms may be important for sustaining these populations.

Key words: cattle, dik-dik, DISTANCE, eland, elephant, impala, migration, nomadism, zebra

Résumé

Pendant trois ans, on a mesuré la distribution et l'abondance d'ongulés indigènes dans une propriété semi-aride, gérée de façon commerciale, située au centre du Kenya. Cette période a inclus de graves sécheresses et aussi des chutes de pluies au-dessus de la moyenne. La biomasse des ongulés natifs fut en moyenne de 5282 kg km^{-2} pendant cette période; elle était dominée par les éléphants *Loxodonta africana*, les impalas *Aepyceros melampus* et les dik-diks *Madoqua kirkii*. La biomasse du bétail domestique *Bos taurus* était en moyenne de 2280 kg m^{-2} pendant cette étude. Les réponses des ongulés indigènes face à la sécheresse prononcée furent variables. La densité des impalas fut la même, voire supérieure à celle des habitats similaires dans des aires protégées et elle a varié de 12–16 per km^2 pendant et juste après la sécheresse à 24–29 km^{-2} suite à des pluies exceptionnellement abondantes. La densité des dik-diks fut aussi supérieure à celle qui fut rapportée pour les aires protégées, et elle est restée étonnamment stable durant toute la durée de l'étude malgré les amples fluctuations des pluies annuelles. Les éléphants ont migré hors de la région pendant la sécheresse mais ils étaient là en forte densité (2.9–5.3 per km^2) pendant les saisons des pluies, ce qui conforte les études télémétriques qui insistent sur l'importance de la brousse à acacias dans les exploitations commerciales pour la partie de la population d'éléphants de Laikipia-Samburu qui fait des migrations. Les résultats montrent que l'on peut observer des densités importantes d'ongulés indigènes herbivores et mixtes sur des propriétés gérées en vue de la production commerciale de boeuf, et ils suggèrent que le fait que des ongulés puissent migrer sur de longues distances (>100 km) et que leur distribution puisse ainsi évoluer en réponse à des tempêtes locales de force variable pourrait être très important pour le maintien de ces populations.

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Introduction

In East Africa, most native ungulates still occur on managed rangeland, such that long-term coexistence of livestock and native species outside protected areas is central to wildlife conservation (Western, 1989, 1994; Lewis, 1993). In semi-arid pastoral rangeland of northern Kenya, wildlife and livestock abundance are inversely correlated, with livestock concentrated around permanent water sources and wildlife density and diversity increasing much further from water points (de Leeuw *et al.*, 2001). This inverse correlation between livestock and wildlife abundance has been attributed to indirect interference from humans associated with livestock, most likely because of poaching and harassment, rather than direct competition for forage (de Leeuw *et al.*, 2001). In contrast, less is known about the abundance and distribution of native ungulates on commercially managed rangeland, where greater control over wildlife poaching and harassment combined with lower long-term cattle stocking rates potentially contributes to increased abundance of the native ungulate community (Georgiadis *et al.*, 2007).

Semi-arid rangelands are characterized by substantial seasonal and inter-annual fluctuations in precipitation, including periodic drought. Competitive interactions between native ungulates and domestic livestock are likely to be most severe during droughts, but few studies have examined how native ungulates respond to droughts in regions where they coexist with domestic livestock. In the Laikipia district of central Kenya, approximately 6500 km^2 of savannah are managed primarily for commercial livestock production. No formally protected natural areas exist in the district, but management to increase or maintain wildlife on private lands could contribute significantly to the local economy through wildlife consumption and ecotourism.

One of the few studies examining ungulate responses to drought on commercial rangelands focused on plains zebra (*Equus burchelli*) in Laikipia, which primarily occur in open grassland habitats (Georgiadis, Hack & Turpin, 2003). Long-term aerial survey trends and population modelling showed that fluctuations in zebra numbers are strongly influenced by precipitation, a finding that has assisted in managing annual zebra harvest in the district (Georgiadis, Hack & Turpin, 2003). In contrast, little is known about wildlife in low-visibility, bushland habitats, where the accuracy of aerial counts for abundant native species is unknown, and aerial counts of smaller species such as dik-dik are not possible. Dense bushland habitats dominate the red, sandy soils distributed across much of central and northern Laikipia as well as adjacent regions of Samburu district (Taiti, 1992). Improved understanding of the distribution and abundance of native ungulates in semi-arid bushland habitat and their responses to drought could help refine wildlife management strategies on commercial rangeland.

I examined the distribution and abundance of native ungulates within *Acacia*-dominated bushland at the Mpala Ranch and Research Centre (MRC), which encompasses 190 km^2 of semi-arid savannah in central Laikipia managed for beef production. My objectives were to (i) measure seasonal ungulate densities using line-transect sampling, which overcomes uncertainty associated with aerial count visibility in bushland habitats (Buckland *et al.*, 2001; Jachmann, 2002), and (ii) examine changes in abundance of the most common species in response to a severe drought. Native ungulates were not harvested on this property during the study, and poaching is minimal. Therefore, estimates provide an indication of densities that can be achieved in the absence of mortality caused by humans. Measurements were initiated prior to and continued for 1 year after one of the most severe droughts on record in the region, providing an opportunity to examine variation among ungulate species in their response to drought.

Methods

Study Area

All research were conducted at the Mpala Research Centre and associated Mpala Ranch (0° 17′ N, 37° 53′ E) within *Acacia* bushland habitat occurring on well-drained, red sandy loam soils. The shrub layer is dominated by *Acacia mellifera* Benth., *A. etbaica* Schweinf. and *A. brevispica* Harms (mean shrub cover = 28%), and the understory is dominated by patchily distributed perennial grasses (Augustine, 2003a). Permanent rivers occur along the northern and eastern borders of MRC, and dams are well distributed throughout the ranch. Mean annual rainfall measured at the Mpala Ranch headquarters during 1972–2000 (K. Wreford-Smith, pers. Comm.) was 508 mm (CV = 0.44). Rainfall is trimodal with 'long rains' during April–June, and smaller precipitation pulses in August and October. A predictable dry season occurs during January and February. Rainfall recorded at the Mpala Ranch

headquarters rainfall data showed that 2000 was the second-driest year during 1972–2000. Analysis of five long-term (1965–2005) rain gauges distributed across central Laikipia (did not include the Mpala Ranch headquarters gauge) showed that during this 40-year period, the two most severe droughts, which were of equal severity, occurred in 1984 and 2000 (Georgiadis *et al.*, 2007). From January of 1999 until March of 2002, I maintained three rain gauges distributed across my study area. Based on the average of these three gauges, my ungulate surveys were initiated after a below-average rainfall year in 1999 (410 mm) and encompassed the severe drought in 2000 (296 mm) and an above-average year in 2001 (658 mm). MRC supports cattle managed for market production using traditional Maasai herding methods. All cattle are contained overnight in bomas. Predators occurring in the area include spotted hyaena (*Crocuta crocuta*), lion (*Panthera leo*), leopard (*Panthera pardus*) and wild dog (*Lycaon pictus*).

Ungulate density estimation

Line-transect sampling (Buckland *et al.*, 2001) was used to estimate densities of native ungulates during 2000–2002. Five surveys were conducted in March 2000 (dry season), August 2000 (wet season), March 2001 (dry), August 2001 (wet) and March/April 2002 (dry–wet transition). Four transects were surveyed along ranch tracks in 2000 and six transects in 2001 and 2002. Each transect was surveyed four times in March 2000, and six times in each survey month thereafter, giving a total transect length of 35.9 km in March 2000, 63.6 km each in May and August 2000 and 92.8 km each in 2001 and 2002. Sampling intensity was increased in 2001 and 2002 to improve precision of the density estimates, after examining the results from 2000. Transects were selected in a stratified, random manner from available tracks within an 82 km^2 study area, and only used tracks that (i) experienced minimal use by other ranch and research vehicles and (ii) ran across topographical features (ridgelines and drainages) rather than following a single topographic position.

The presence of cape buffalo (*Syncerus caffer*) and elephant prohibited us from using walking transects as a standard method. To test for possible bias associated with using established tracks, we walked six replicate 1-km track transect counts that were paired to 6, 1-km transects running parallel to but at least 300 m away from the

track. Group observation rates were similar on both transect types for dik-dik (X_{tracks} = 3.2 ± 1.0 groups km^{-1}, $X_{bushland}$ = 3.7 ± 2.5 groups km^{-1}; Paired t = 0.44, P = 0.67) and impala (X_{tracks} = 0.33 groups km^{-1}, $X_{bushland}$ = 0.67 groups km^{-1}; Paired t = 0.58, P = 0.18). In addition, recent comparisons of distance sampling versus fixed strip width sampling for ungulates in these habitats found that distance sampling provided the best balance between accuracy and precision (Shorrocks, Cristescu & Magane, 2008).

Counts were conducted from a Land Rover driven ~10 km hr^{-1} with two seated observers (with views beneath shrub canopies) and two standing observers (searching above and beyond shrubs close to the transect). Counts were conducted during the hour following sunrise or the hour prior to sunset. For each ungulate group observed, we recorded the species, group size, distance to the transect (measured with a laser rangefinder) and angle of the distance measurement to the transect.

Densities of each species were calculated using DISTANCE 3.5 (Thomas *et al.*, 1998; Buckland *et al.*, 2001). For dik-dik and impala, densities were calculated using a detection function that pooled group observations for each species across all surveys. For other species, observations were less frequent, so the detection function was estimated for two species groups: medium to large ungulates [zebra, eland (*Taurotragus oryx*), cape buffalo (*Syncerus caffer*), waterbuck (*Kobus ellipsiprymnus*), warthog (*Phacochoerus africanus*), bushbuck (*Tragelaphus scriptus*) and steenbuck (*Raphicerus campestris*)] and megaherbivores (elephant and giraffe [*Giraffa camelopardalis*]). For fitting of detection functions, observations were truncated at a distance of 150 m from the transect based on recommendation of Buckland *et al.* (2001). Densities were estimated for each species and month separately, but were based on a global detection function. This assumes detection is similar across all species within a given category; inspection of mean observation distances for each species indicated this assumption was met. In addition, the distribution of group observation distances was nearly identical for impala and 'medium and large ungulates', supporting the assumption of a consistent detection distance for different species of similar size. Selection of models to describe the detection function was based on Akaike's Information Criterion. When estimating ungulate density means and variances, replicate counts along the same transect within a given month were averaged (i.e. I included all observations and summed the transect length of replicate counts), such that

confidence intervals are based on among-transect variance.

Emergency feeding of cattle occurred during the drought, so the density of cattle that could have been supported without importing emergency feed (reported as both mean and −95% CI) was conservatively estimated assuming 100% cattle mortality/emigration during April 2000–April 2001, averaged with actual monthly stocking rates predrought and postdrought. Maximum cattle density (+95% CI) is the actual density calculated from monthly ranch records for the entire study period (K. Wreford-Smith, pers. comm.).

Biomass densities of ungulates were calculated from species body weights reported by Coe, Cumming & Phillipson (1976). Responses of dik-dik and impala densities to drought were examined with paired, two-tailed t-tests comparing transect counts for March versus August 2000 (response to failure of long rains) and March 2001 versus March 2002 (response to above-average rainfall) as recommended by Plumptre (2000). I report exact P values for these test, and because of the limited degrees of freedom, I considered differences to be significant at the $\alpha < 0.1$ level.

Native ungulate biomass density was summarized according to feeding guilds, for comparison to cattle density. Previous analyses of dung ^{13}C content showed that elephant, eland and dik-dik within this particular study area are predominately browsers year-round, impala are mixed feeders (grazing in wet seasons and browsing in dry seasons), and cattle are grazers year-round (Augustine & McNaughton, 2004a). This previous analysis was based on limited sample sizes and did not include eland, which is sometimes classified as a mixed-feeding antelope (Hofmann, 1973). Because impala, eland and elephant can vary in their use of grass versus shrub foliage among different regions of Africa, I report here on a larger dataset of dung samples collected from impala, eland and elephant within my study area during 1999–2001. For each of these three species, no more than eight dung samples were collected within a given month and year, and collections were widely distributed throughout the study area. I collected at least 25 samples for each species and season, with the exception of elephant in the dry season (because so few elephant used the study area in dry seasons). Dung was oven-dried at 70°C for 3 days and analysed for ^{13}C content by the Staple Isotope Laboratory at the University of California at Davis. Because of major differences in the ^{13}C signature of C_4 grasses versus C_3 dicots and the fact that all grasses at MRC have the C_4 photosynthetic pathway, this measurement provides an index of the degree to which grasses contribute to a given ungulate's diet (Cerling, Harris & Passey, 2003). Analyses of plants from East African savannahs (including MRC) showed that C_3 dicots have a $\delta^{13}C$ signature of −25 to −29, while C_4 grasses have a $\delta^{13}C$ signature of −11 to −14 (Cerling, Harris & Passey, 2003). Results were compared with the previously published measurements of ^{13}C for dung from cattle (pure grazer) and dik-dik (pure browser; Augustine & McNaughton, 2004a). Based on the literature (Hofmann, 1973; Kingdon, 1997) and my observations, I assumed that zebra, waterbuck, cape buffalo and warthog are grazers and that giraffe, steenbuck and bushbuck are browsers.

Native ungulate biomass density was also summarized according to the spatial scale of movement patterns of the different species (nomadic versus resident), for comparison to cattle density. Nomadic species were defined as those species, which exhibit movements at spatial scales larger than the study area in response to seasonal and inter-annual variation in vegetation conditions. Based on findings from the transect surveys (see Results), direct observations of animal movements, and previous research in the study area (Thouless, 1996; Georgiadis, Hack & Turpin, 2003; Georgiadis *et al.*, 2007; Sundaresan *et al.*, 2007), I classified elephant, giraffe, eland, plains zebra and grevy's zebra as nomadic species, and the remainder of the species as resident species.

Spatial responses of ungulates to drought

The drought in 2000 was characterized by minimal rainfall during the typical April–June wet season, but some small, spatially isolated thunderstorms occurred in May of 2000. These thunderstorms only affected two areas of the ranch, each approximately 5 km in diameter, while the remainder of the ranch received no rainfall at this time. In addition to the regular surveys conducted in March and August each year, we conducted an additional survey in late May of 2000 to examine ungulate distributions in response to these two small, spatially isolated thunderstorms. Although most of MRC was extremely dry at this time, two of the transects (one in the north and one in the south of the study area) received rain from these isolated thunderstorms and two transects (one north and one south) lacked sufficient rainfall to initiate any grass growth. In the south, dry and wet transects were separated by 3 km; in the north they were separated by 5 km. The

May survey was only used to examine local shifts in ungulate densities and was not used in estimates of overall ungulate densities.

Results

Dik-dik, impala and elephant dominate the native ungulate community in terms of both abundance and biomass (Table 1). For cattle, the estimated ecological density, which assumed 100% drought mortality followed by restocking, still comprised 21% of total ungulate biomass and was at least double the biomass of all native species except elephant (Table 1). Total ungulate biomass supported by this ecosystem was 7563 kg km^{-2}, and total native ungulate biomass (excluding cattle) was 5282 kg km^{-2}.

Analyses of $\delta^{13}C$ in dung samples from impala and elephant within the study area showed that (i) impala are predominantly browsers in dry seasons, (ii) impala substantially increase grass consumption in wet seasons, (iii) elephants are pure browsers in dry seasons and (iv) elephants remain predominantly browsers in wet seasons (Fig. 1), which corroborates previous findings reported by Augustine & McNaughton (2004a). In addition, dung ^{13}C analyses for eland showed that they are pure browsers in the dry season and remain predominantly browsers in the wet season (Fig. 1). Native ungulates within the study area
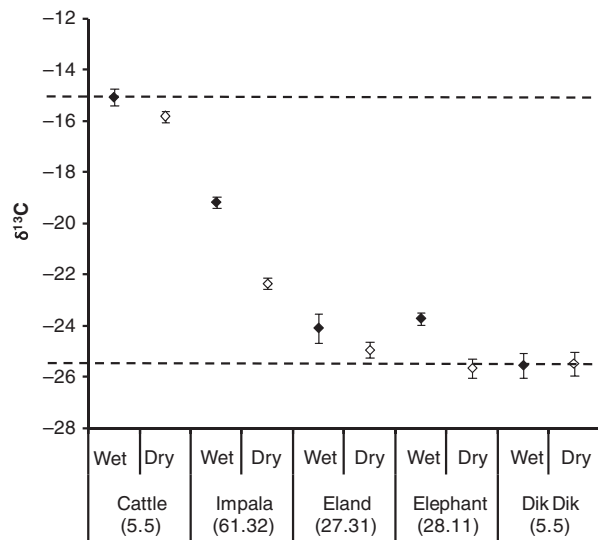

Fig 1 Variation in the $\delta^{13}C$ content of dung samples collected during wet seasons (solid symbols) and dry seasons (open symbols) for each of five species within the *Acacia* bushland habitat at Mpala Research Centre in central Kenya. Numbers in parentheses beneath each species show samples sizes for wet and dry seasons, respectively. Data for cattle and dik-dik are from Augustine and McNaughton (2004). Dashed lines indicate wet-season values for pure grazers based on cattle dung measurements and for pure browsers based on dik-dik dung measurements. Error bars show 1 SE around the means

Table 1 Density (# per km^2), coefficient of variation in the density estimate (CV), 95% confidence intervals for the density estimate, mean biomass per individual (kg per animal), biomass density (kg per km^2), and 95% confidence intervals for the biomass density estimate for 13 ungulate species inhabiting *Acacia* bushland habitat at Mpala Research Centre in central Kenya. Wildlife densities are averaged across five surveys during 2000–2002. See text for details on the calculation of cattle density. Greater kudu and common duiker were also encountered within the study area, but were too infrequent to estimate density

Species	# per km^2	CV (%)	−95% CI	+95% CI	kg per animal	kg per km^2	−95% CI	+95% CI
Cattle	7.1		7.1	12.2	322	2280	2280	3941
Elephant	1.7	36.1	0.8	3.4	1725	2882	1420	5858
Impala	20.3	17.6	14.3	29.0	40	813	572	1158
Dik-dik	138.7	5.6	123.6	155.6	5	693	618	778
Plains zebra	1.3	37.9	0.6	2.8	200	263	125	551
Giraffe	0.33	46.1	0.13	0.79	750	244	101	593
Eland	0.37	45.3	0.15	0.88	340	125	52	300
Grevys zebra	0.28	54.6	0.10	0.81	375	104	36	304
Waterbuck	0.54	53.2	0.20	1.50	160	87	32	240
Buffalo	0.11	57.74	0.04	0.34	450	51	17	153
Warthog	0.19	29.27	0.62	0.58	45	9	28	26
Bushbuck	0.20	58.6	0.07	0.62	30	6	2	18
Steenbuck	0.52	26.61	0.31	0.88	10	5	3	9

Table 2 Distribution of ungulate biomass within *Acacia* bushland habitat at Mpala Research Centre in central Kenya in terms of ungulate species feeding type and movement patterns. All values are kg per km^2. See Table 1 for individual species densities

	Mean	−95% CI	+95% CI
Total ungulate biomass	7563	5284	13930
Summarized by feeding guild			
Cattle	2280	2280	3941
Native browsers	3956	2195	7557
Native mixed feeders	813	572	1158
Native grazers	514	237	1275
Summarized by movement patterns			
Cattle	2280	2280	3941
Nomadic wildlife	3618	1733	7606
Resident wildlife	1665	1271	2383

therefore include five browsers (elephant, dik-dik, eland, giraffe, bushbuck and steenbuck), one mixed feeder (impala) and five grazers (plains zebra, grevy's zebra, waterbuck, cape buffalo and warthog). Greater kudu (*Tragelaphus strepsiceros*) and common duiker (*Sylvicapra grimmia*) were also encountered infrequently during the study, giving a total of 13 native species. Browsers dominate the native ungulate biomass, primarily because of elephant, while all native grazers occur at low density (Table 2).

Short-term fluctuations in densities suggest elephant, eland, zebra and giraffe move over far larger areas than MRC. Variation in zebra densities among the five surveys compared with measurements of seasonal variation in grass biomass (Augustine & McNaughton, 2004b) indicates that plains zebra were rare within the study area during dry seasons (X = 0 and 0.4 zebra km^{-2}) and

infrequent when grass biomass was low in August of 2001 (0.8 zebra km^{-2}), but migrated into the area in August of 2000 when grass biomass was increasing (5.3 zebra km^{-2}). Densities of eland and buffalo were greatest in 2000 and extremely low (eland) or zero (buffalo) after the drought. Buffalo carcasses were regularly encountered throughout the study area in June–August 2000, suggesting a die-off within MRC. Eland carcasses were rare, consistent with observations of movement outside the study area. Elephant densities were extremely high on MRC during wet seasons (5.2 and 2.9 km^{-2} in August 2000 and 2001), minimal during dry seasons (0 and 0.05 km^{-2} in March 2000 and 2001) and intermediate during the dry–wet transition in 2002 (0.32 km^{-2}). Combined biomass density of nonresident species (elephant, eland, zebras and giraffe) far exceeds that of resident species (Table 2).

The two most common native ungulates showed disparate responses to the severe drought in 2000. Dik-dik densities remained constant throughout the study with no changes in response to failure of the long rains (March versus August 2000; Paired t_2 = 1.51, df = 3, P = 0.23) or above-average rainfall (March 2001 – March 2002, Paired t_2 = 0.24, df = 5, P = 0.82; Table 3). Mean dik-dik density estimates were relatively stable across all five surveys and were not correlated with the amount of rainfall received during the previous 6 months (P = 0.34; Table 3). I also used the percent of dik-dik groups with >2 individuals as an index of pairs with calves. This index did not decline between March and August of 2000 in spite of the limited rainfall between those two surveys. Across all five surveys, this index was not correlated with the amount

Table 3 Variation in the amount of precipitation occurring during the previous 6 months, dik-dik density, dik-dik calf index (percent of dik-dik groups with >2 individuals) and densities of impala, elephant and plains zebra for five surveys conducted at Mpala Research Centre in central Kenya during 2000–2002. Note that although August surveys in 2000 and 2001 were both conducted when vegetation was green, they differed in that the August 2000 survey was preceded by failure of the typical rainy season during April–July, while the August 2001 survey was preceded by above-average April–July precipitation

Date	Season	6-month Rainfall (mm)	Dik-dik # km^{-2} Mean (95% CI)	Dik-dik % of groups >2 Mean (95% CI)	Impala # km^{-2} Mean (95% CI)	Elephant # km^{-2} Mean (95% CI)	Plains zebra # km^{-2} Mean (95% CI)
March 2000	Dry	122	130 (90,188)	14.0 (4.4, 23.6)	20.5 (8.5, 49.8)	0.0 (0.0, 0.0)	0.0 (0.0, 0.0)
August 2000	Wet	109	140 (93, 212)	17.4 (6.4, 28.3)	11.9 (5.6, 25.2)	5.2 (1.4, 19.8)	5.3 (2.4, 11.8)
March 2001	Dry	146	139 (99, 195)	18.8 (9.2, 28.3)	16.0 (8.7, 29.4)	0.04 (0.01, 0.4)	0.2 (0.01, 1.3)
August 2001	Wet	372	139 (114, 170)	23.8 (14.7, 32.9)	28.8 (12.5, 66.2)	2.9 (1.3, 6.4)	0.8 (0.2, 3.8)
March 2002	Dry	346	145 (116, 181)	14.3 (6.8, 21.8)	24.5 (11.8, 50.9)	0.3 (0.1, 1.7)	0.4 (0.8, 2.3)

of rainfall received in the previous 6 months ($P = 0.51$; Table 3).

In contrast, impala density declined following the failure of the long rains in 2000 (March versus August 2000; Paired $t_2 = 2.46$, df = 3, $P = 0.091$) then increased following above-average rainfall throughout 2001 (March 2001 versus March 2002; Paired $t_2 = 2.015$, df = 5, $P = 0.073$). Across all five surveys, impala density was significantly correlated with rainfall during the previous 6 months ($r^2 = 0.78$, $P = 0.046$; Table 3). Fluctuations in impala density were strongly correlated with changes in mean group size ($r^2 = 0.93$, $P = 0.008$) but unrelated to herd detection rate ($P = 0.89$; Fig. 2). Observations of impala calves were rare during the survey in March of 2001, while the subsequent increase in impala group size by August of 2001 was associated with a notable presence of calves in female herds during that survey.

Transect counts in May 2000, indicated spatial shifts in the ranges of impala, but not dik-dik, in response to small, isolated thunderstorms. Compared to the March survey (all transects dry) and August survey (all transects green), dik-dik densities were locally constant over time (Fig. 3a). In contrast, impala virtually abandoned dry regions while densities of 40–54 km^{-2} were documented in the areas
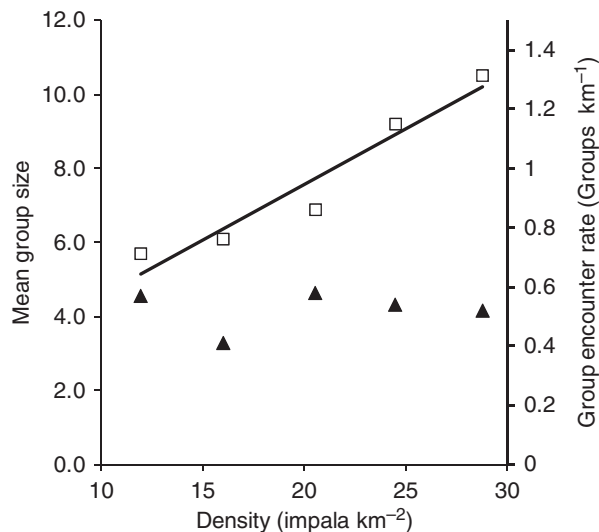

Fig 2 Variation in mean impala group size (open squares) and impala group detection rate (solid triangles) in relation to mean impala density for five surveys conducted at the Mpala Research Centre in central Kenya during 2000–2002. Impala group size increased significantly with increasing impala density ($r^2 = 0.93$, $P = 0.008$) while group detection rates were not correlated with impala density ($P = 0.89$)

that received isolated thunderstorms (Fig. 3b). Elephants responded to drought primarily by migrating out of the region, although a few herds were attracted to the isolated thunderstorms in May (Fig. 3c).

Discussion

Ungulate abundance on managed rangeland

Results show that an abundant and diverse community of native ungulates occurs on semi-arid, commercial rangeland in central Kenya. The native ungulate community at MRC is dominated by nomadic species (Table 2) suggesting that large-scale movements between ranches may play an important role in maintaining wildlife abundance. At the same time, resident populations of dik-dik and impala occur at densities similar to levels reported for bushland habitat in national parks and other protected game reserves (Lamprey, 1964; Barnes & Douglas-Hamilton, 1982; Walker *et al.*, 1987; Komers & Brotherton, 1997). In contrast to the inverse relationship between cattle and wildlife documented on northern Kenyan pastoral rangeland (de Leeuw *et al.*, 2001), results for MRC indicate that substantial densities of native browsing and mixed-feeding ungulates can coexist with cattle within *Acacia* bushland habitats on commercial rangeland. The total native ungulate biomass estimate of 5282 kg km^{-2} substantially exceeds predictions based on rainfall for both low-fertility (1785 kg km^{-2}) and moderate-fertility (3060 kg km^{-2}) African savannahs (Fritz & Duncan, 1994), which may be related to several factors. First, control of poaching and minimal harassment of wildlife by herders are likely to be important. In addition, the high biomass density of elephant, which is related to their ability to migrate in response to rainfall patterns in the region, and the high dik-dik density [a species too small to be included in datasets analysed by Fritz & Duncan (1994)] are key contributors. Removal of elephant and dik-dik from the study area would give an overall native ungulate biomass density of 1701 kg km^{-2}, which is similar to the rainfall-based prediction for nutrient-poor savannahs (Fritz & Duncan, 1994).

Sustainable management of wildlife on semi-arid rangeland requires an understanding of how different species respond to periodic drought. Responses of different species at MRC were extremely variable and related to body size and feeding pattern. Mortality of grazers was widespread, as has been reported in many African
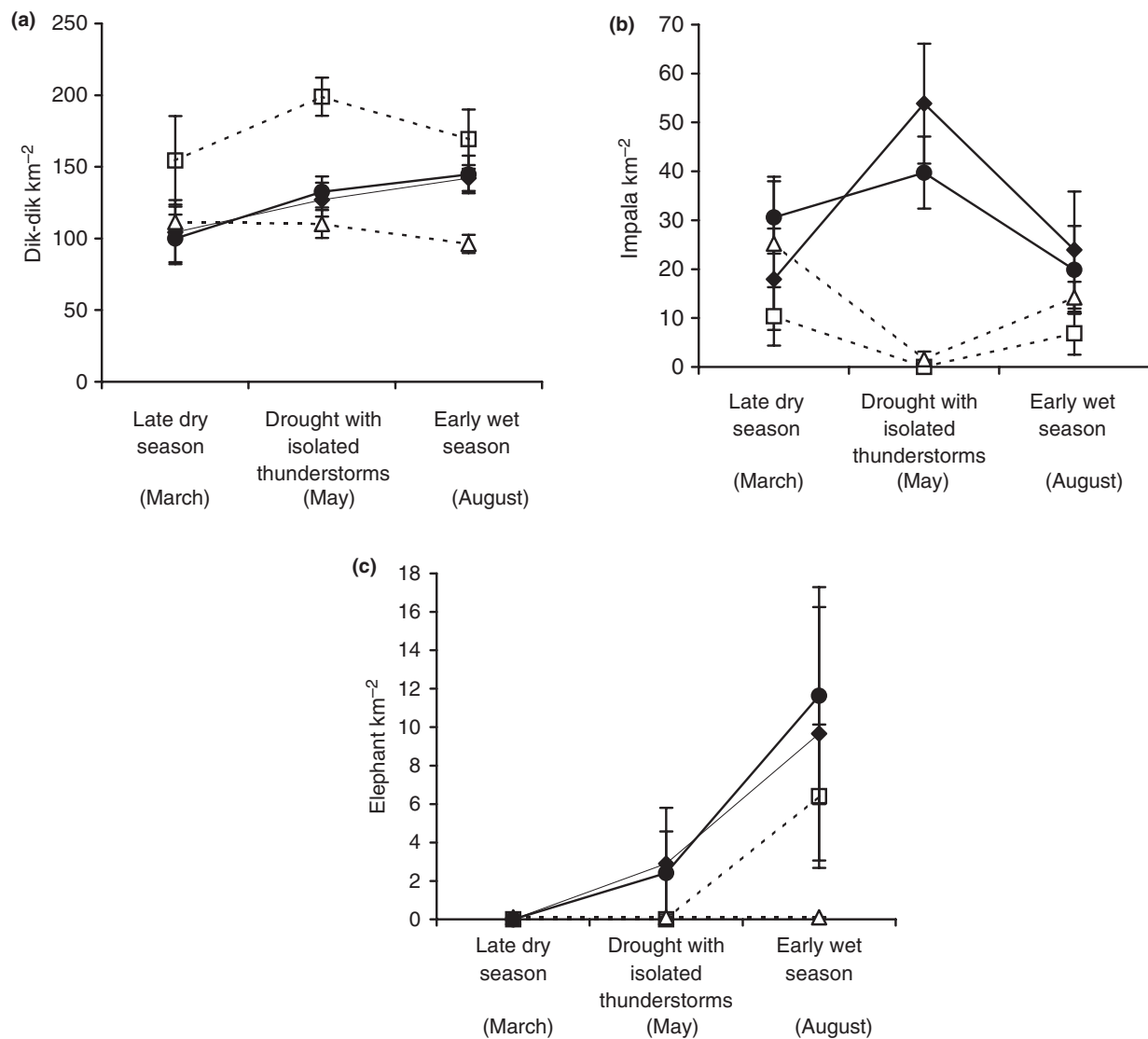
Fig 3 Variation in local densities of dik-dik (a), impala (b) and elephant (c) during 2000 at the Mpala Research Centre in central Kenya. Different symbol shapes are used for each of the four transects surveyed. Solid symbols show the two transects that experienced isolated thunderstorms in May of 2000, and open symbols show transects that received no rainfall in May of 2000. In contrast to the relatively similar distribution of impala and vegetation conditions across the four transects in that late dry season (March 2000; all transect dry) and early wet season (August 2000; all transects green), impala densities were extremely high on transects that received isolated thunderstorms in May of 2000 (solid symbols, panel b) and nearly zero on transects 3–5 km distant that received no rainfall in May (open symbols; panel b). In contrast, local dik-dik densities were relatively constant across seasons (panel a), and elephants were largely absent from the study area until widespread rains began (early wet season; panel c). Error bars show 1 SE around the mean based on replicate counts of each transect within each season

savannahs (Walker *et al.*, 1987; Knight, 1995; Georgiadis, Hack & Turpin, 2003). Although emergency feed was imported to MRC in 2000, cattle numbers declined from 3100 (16.4 km^{-2}) in November 1999 to 1350 (7.1 km^{-2}) in March 2001 because of mortality and movement to distant ranches with greater rainfall (K. Wreford-Smith, pers. comm.). Observations of carcasses indicated buffalo suffered significant mortality within the study area. Zebra emigrated from the study area, but mortality occurred elsewhere in the district (Georgiadis, Hack & Turpin,

2003). In addition, overall native grazer densities in the area are low (Table 2), which may reflect competition with cattle for forage (Young, Palmer & Gadd, 2005).

The larger browsers (elephant, giraffe and eland) also emigrated from the study area during dry seasons. Long-term viability of populations of these mobile species in Laikipia will likely depend on management at scales far larger than individual ranches (>100 km^2). Although little is known about movements of giraffe and eland in the region, long-term studies initiated in the early 1990s have examined the Laikipia–Samburu elephant population. The overall population numbers approximately 5400 animals (Omondi *et al.*, 2002) and consists of several overlapping subpopulations that can be defined based on different migration patterns (Thouless, 1996). Both radio and global positioning system telemetry studies have identified individuals that move >100 km between MRC and pastoralist areas of Samburu district to the northeast (Thouless, 1995; Douglas-Hamilton, Krink & Vollrath, 2005). My surveys documenting wet-season elephant densities of 2.9–5.2 km^{-2} (August 2001 and 2000, respectively) at MRC are consistent with the telemetry results suggesting a regular migration into commercial rangelands of north central Laikipia during June–October each year (Thouless, 1995, 1996) and highlight the importance of *Acacia* bushland habitat in this region as wet-season habitat for the Samburu–Laikipia elephant population. Conversely, elephant numbers increase in protected areas such as the Samburu and Buffalo Springs National Reserves during dry seasons (Wittemyer, 2001). Similar elephant migration patterns have also been documented in the Marsabit region of Kenya, where some elephants utilizing protected forests during the dry season migrate long distances to *Acacia*-dominated bushland during the wet season (Ngene *et al.*, 2009). Despite the presence of two permanent rivers at MRC, this area does not appear to provide optimal dry-season habitat, and determinants of the elephant migration to and from Samburu district require further research.

In contrast to the consistent effects of drought on grazers, the reported effects of drought on resident populations of mixed feeders and browsers have been variable. In South Africa, declines in impala density of 36–75% during a 2-year drought occurred in Kruger and Klaserie conservation areas, but impala densities remained at 24–28 km^{-2} through the same drought in the Tuli reserve (Walker *et al.*, 1987). In southern Kenya, Ottichillo *et al.* (2000) reported no response of impala densities to periodic drought over two decades (1977–1997), and Lamprey (1964) observed seasonal movements but no annual density fluctuations for impala in central Tanzania.

At MRC, mean impala density (20.3 km^{-2}) was similar to or greater than levels reported for bushland habitats in protected areas (20.7 km^{-2} in Tarangire NP, Tanzania, Lamprey, 1964; 6.1; per km^{-2} in Ruaha NP, Tanzania, Barnes & Douglas-Hamilton, 1982; 9–30; km^{-2} in South African reserves, Walker *et al.*, 1987) and fluctuated in response to annual rainfall. Densities declined from 20.5 km^{-2} predrought to 12–16 km^{-2} during the drought and recovered rapidly to 24–29 km^{-2} after above-average rainfall in 2001 (Fig. 3). Observations of impala calves were extremely rare in August 2000 and March 2001 at MRC, while calves < 1 year of age clearly represented a major component of female herds in August 2001. In addition, the impala herd detection rate was relatively constant across all surveys, while mean herd size fluctuated substantially among years. These findings plus the rarity of impala carcasses during the drought suggest variation in birth rates and calf survival, rather than adult survivorship, played an important role in annual density fluctuations. Carcasses from starvation-induced mortality in adults in South Africa were only observed in the second year of sustained drought (Walker *et al.*, 1987). Clearly, reproduction alone cannot account for the estimated increase in impala density during 2001. However, significant movement across ranch boundaries is an unlikely explanation as similar habitat types and rainfall conditions occurred to the north, east and south of the study area, and unsuitable habitat occurred to the west. Local shifts in impala distribution and sampling error likely influenced the highest impala density estimate in August 2001 (CV = 38%), but results indicate that impala numbers are influenced at least in part by drought.

Impala are relatively sedentary ungulates with year-round home ranges varying from 50 ha (Murray, 1982) to 581 ha (Du Toit, 1990), which corresponds to home range diameters on the order of only 0.25–0.86 km assuming relatively circular home ranges. Shifts in impala diet from grass to browse during dry seasons (Klein & Fairall, 1986; Meissner, Pieterse & Potgieter, 1996) minimize fluctuations in available food for this sedentary species. However, shifts in impala distribution during the drought in 2000 (Fig. 3) suggest impala may abandon typical home ranges and undertake movements on the order of 3–5 km during periods of severe food shortage. Movements at this spatial scale were also reported during a drought in Serengeti,

Tanzania (Jarman, 1970). The ability of impala to shift local distributions may be an important buffer against variable weather patterns in semi-arid regions (Hobbs *et al.*, 2008). In addition, the way in which cattle corrals (bomas) are established and abandoned over time at MRC has created localized patches of nutrient-rich soils (from the inputs of cattle manure; $\sim$1 ha per patch occurring at a mean density of $\sim$1 per km^2) throughout the landscape (Augustine, 2003b). For >40 years after a boma is abandoned, the nutrient-rich soils in these patches support grasses that are enriched in mineral elements, and provide a key wet-season forage resource for impala (Augustine, 2004). The continual creation of these patches in the landscape through cattle management practices may be one important factor maintaining such high densities of impala in this area.

In contrast to impala, dik-dik densities remained high and surprisingly stable regardless of precipitation patterns. Dik-dik live as pairs of adults that defend an exclusive territory (Boshe, 1984). Both territoriality and predation could be related to the lack of response to major fluctuations in food availability. Predation may be a factor if predators maintain herbivores at sufficiently low densities that minimize food limitation. Dik-dik can be an important component of the diet of predators at MRC, such as the African wild dog (Woodroffe *et al.*, 2007). However, dik-dik density at MRC (138 km^{-2}) is extremely high, even exceeding densities reported for bushland habitat in Tsavo National Park (107–112 km^{-2}, Komers & Brotherton, 1997). Such high densities suggest territoriality may play a role in population stability of this species and support Boshe's (1984) conclusion that dik-diks defend year-round territories large enough to meet their needs during periods of food scarcity.

Conclusions

Overall, my results show that substantial densities of native ungulates can be sustained on rangeland managed for commercial beef production. However, the native ungulate community was dominated by mixed feeding and browsing species, while native grazers occurred at low densities and were rare after the drought. As recently suggested by Hobbs *et al.* (2008), my findings indicate that the capacity for native grazers, as well as native browsers of large body size, to move over large spatial scales (>100 km^2) may be important for sustaining these populations. At smaller spatial scales (within an individual ranch, or <100 km^2), relatively high densities of smaller browsing and mixed-feeding ungulates can be sustained through droughts. The ability of impala to shift distributions in response to locally variable thunderstorms (Fig. 3) and the presence of nutrient-rich forage patches derived from abandoned cattle bomas (Augustine, 2003b, 2004) may be two factors contributing to high impala densities in the region. In addition, impala densities fluctuated significantly in response to the amount of rainfall received during the preceding 6 months, indicating that incorporation of rainfall variability into population models and annual adjustments of harvest quotas for impala could improve management for this species in the region.

Acknowledgements

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