

## Energy Availability and Density Estimates in African Ungulates

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**ABSTRACT:** While many studies have investigated the link between primary productivity and species richness, the link between primary productivity and species abundance is still poorly understood. We explored how primary productivity, assessed by the satellite-based normalized difference vegetation index, influenced density estimates in 13 African ungulate species. We found that primary productivity generally correlated positively with density estimates. However, this link was more pronounced for some species than for others, and information regarding the area surveyed needed to be taken into account to highlight this functional relationship. Detailed consideration of measurements of productivity in broadscale studies identify a general link between primary productivity and abundance of African ungulates and highlight remote-sensing-based analyses as a potentially crucial tool in assessing the population consequences of future changes in primary productivity on this continent.

**Keywords:** Africa, ungulate abundance, remote sensing, NDVI.

### Introduction

The amount of energy available in a system is thought to be one of the major determinants of species diversity and richness (Currie 1991; Mittelbach et al. 2001; Hurlbert and Haskell 2003; Bailey et al. 2004; Bonn et al. 2004) as well as species abundance and biomass (Coe et al. 1976; Verlinden and Masogo 1997; Blackburn and Gaston 2001; Carbone and Gittleman 2002; Tveraa et al. 2007). Interestingly, the former relationship has received considerably more attention than the latter (Latham and Ricklefs 1993; Abrams 1995; Leibold 1999; Waide et al. 1999; Lennon et al. 2000; Bailey et al. 2004), and few studies have explored how animal biomass/abundance relates to energy availability at large scales (but see Coe et al. 1976; Carbone and Gittleman 2002; Currie et al. 2004). However, energy has been hypothesized to determine species richness through its effects on total species biomass or abundance. For example, higher primary productivity may allow more individual animals in total to persist in an area. This in turn may enable individual species to obtain

higher population densities, reducing their risk of extinction and consequently increasing the species richness of the area (Hurlbert 2004; Evans et al. 2005, 2006). To validate such links, broadscale studies exploring the relationship between energy and abundance are critically needed.

There are several possible reasons for the scarcity of studies addressing the relationship between energy and abundance. One explanation may lie in the difficulty of measuring energy. However, satellite imagery has recently provided a wealth of such information for ecologists, and several ecological studies have pointed out the utility of the NDVI (normalized difference vegetation index) as an index of primary productivity (Running 1990; Kerr and Ostrovsky 2003; Turner et al. 2003; Pettorelli et al. 2005). Another explanation lies in the difficulty of monitoring abundance, as compared to species presence or species richness (Caughley 1977; Seber 1982, 1992; Rabe et al. 2002; Walter and Hone 2003; Bart et al. 2004; Roberts and Schnell 2006). Ideally, analyses linking energy and abundance would use data collected for a large number of populations across a wide range of habitats and for a large number of species (Carbone and Gittleman 2002).

In this study, making use of a well-established and extensive database compiled by the International Union for Conservation of Nature (East 1999), we explore how NDVI-based estimates of primary productivity relate to density estimates of ungulates in Africa. We expected a positive relationship between NDVI and species density estimates and focused our analysis on 13 herbivorous ungulate species for which a reasonable number of population estimates were available. Species characteristics, such as diet (Jarman 1974) and body mass (Damuth 1981), were expected to affect the relationship between primary productivity and density estimates, with species with different diet types or body masses possibly reacting differently to variation in primary productivity.

### Material and Methods

#### *Ungulate Data*

Data on the population densities of individual herbivore species were based on the compilation by East (1999),

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which encompasses data for African antelopes, giraffes, and buffaloes. We limited our analysis of this data set to 13 different species that were the best represented in the database (setting a minimum of 10 population estimates). In total we used 290 density estimates of these species from 23 different countries and 77 different national parks, collected between 1986 and 1998 (table 1). For each species' density reported in this data set, the location, the size of the sampled area, and the survey method were provided. The data set included estimates from several census methods, but we considered only the two most rigorous and common methods: aerial surveys, which combined the total count survey and aerial survey categories defined by East (1999), and ground surveys. On various occasions, different census methods were used in the same location. The size of the sampled area varied from 60 km<sup>2</sup> to >60,000 km<sup>2</sup> (East 1999). Species' diet was indexed as the average percentage of grass eaten: this information was compiled from several sources (e.g., Funioli and Simonetta 1962; Estes 1991; Perez-Barberia and Gordon 2005). From this, three categories were defined: browsers (<20% grass in diet), mixed feeders (20%–80% grass in diet), and grazers (>80% grass in diet). From the literature, we also compiled information on species' average body mass, which ranged from 15 to 1,555 kg (table 1).

### NDVI

We used NDVI data collected by National Oceanic and Atmospheric Administration (NOAA) satellites equipped with

the advanced very high resolution radiometer (AVHRR) and processed by the Global Inventory Modeling and Mapping Studies (GIMMS) group (Tucker et al. 2005). NDVI is a satellite-based vegetation index that is derived from the red : near-infrared reflectance ratio ( $NDVI = [NIR - RED] / [NIR + RED]$ ), where NIR and RED are the amounts of near-infrared and red light, respectively, reflected by the vegetation and captured by the sensor of the satellite). Different AVHRR-based NDVI data sets are available, with differences in corrections applied or in the spatial and temporal resolutions available. However, they are all derived from the daily data collected by the NOAA satellites: over the past 20 years, five satellites have been launched, and data have been intercalibrated across the NOAA-7, -9, -11, -14, and -16 satellites. Nowadays, AVHRR-based NDVI data compose the only freely available data set that gives coverage over an extensive time period (from July 1981 to present), and the data produced by the GIMMS group show good correlation with data from higher-quality sensors (Tucker et al. 2005). The spatial scale of resolution of the GIMMS data set is 64 km<sup>2</sup>, and an NDVI value is available on a bimonthly basis. We were interested in indexing annual primary productivity in each national park where ungulate density was available: we therefore determined the annual integrated NDVI (INDVI) for that national park, during the year the survey was performed. All the surveys considered were performed between 1986 and 1998. The INDVI, representing the sum of NDVI values over a defined period, has previously been shown to cor-

**Table 1:** Summary of the data used in this study

Species	Body mass (kg)		Sites where densities estimated	Density (individuals/km <sup>2</sup> )		Grass in diet (%)	Range in INDVI
	Range	Average		Range	Average		
<i>Aepyceros melampus</i> , impala <sup>a,b</sup>	40–80	60	27	.008–26.3	2.82	57 (M)	6.36–14.9
<i>Connochaetes taurinus</i> , blue wildebeest <sup>a,b</sup>	140–290	215	10	.08–14.5	1.87	93 (G)	4.58–13.17
<i>Giraffa camelopardalis</i> , giraffe <sup>c,d</sup>	1,180–1,930	1,555	28	.0006–.8	.14	~0 (B)	3.13–14.9
<i>Hippotragus equinus</i> , roan antelope <sup>a,b</sup>	225–300	262.5	27	.002–.69	.17	89 (G)	7.82–14.95
<i>Hippotragus niger</i> , sable antelope <sup>a,b</sup>	190–270	230	20	.003–1.3	.18	90 (G)	8.25–14.02
<i>Ourebia ourebi</i> , oribi <sup>b</sup>	12–22	17	13	.02–9.5	1.41	87 (G)	7.82–14.9
<i>Redunca arundinum</i> , southern reedbuck <sup>a,b</sup>	39–95	67	11	.01–1.95	.26	95 (G)	9.35–13.17
<i>Redunca redunca</i> , Bohor reedbuck <sup>b,c</sup>	36–55	45.5	19	.01–5.6	.44	87 (G)	6.82–14.9
<i>Sylvicapra grimmia</i> , Gray duiker <sup>a,b</sup>	10–20	15	15	.02–1.7	.24	5 (B)	3.62–13.17
<i>Syncerus caffer</i> , African buffalo <sup>a,b</sup>	250–850	550	51	.008–21.6	1.81	91 (G)	6.36–14.9
<i>Taurotragus oryx</i> , common eland <sup>a,b</sup>	300–1,000	650	35	.01–3.8	.39	36 (M)	3.44–13.78
<i>Tragelaphus scriptus</i> , bushbuck <sup>b,e</sup>	30–80	55	12	.008–13.3	1.24	11 (B)	7.72–13.78
<i>Tragelaphus strepsiceros</i> , greater kudu <sup>a,f</sup>	120–315	217.5	22	.002–2.1	.22	~0 (B)	2.56–13.17

Note: INDVI, integrated normalized difference vegetation index; G, grazers; B, browsers; M, mixed feeders.

<sup>a</sup> Brent Huffman, <http://www.ultimateungulate.com>.

<sup>b</sup> Perez-Barberia and Gordon 2005.

<sup>c</sup> Estes 1991.

<sup>d</sup> University of Michigan Museum of Zoology Animal Diversity Web, <http://animaldiversity.ummz.umich.edu>.

<sup>e</sup> African Wildlife Foundation, <http://www.awf.org>.

<sup>f</sup> Funioli and Simonetta 1962.

relate with primary productivity during the same period (Pettorelli et al. 2005).

NDVI is a crude estimate of vegetation health (Goward and Prince 1995), and its ability to monitor variation in primary productivity can sometimes be reduced (Markon et al. 1995; Markon and Peterson 2002). The quality of the information regarding primary productivity variation encompassed in NDVI values is a function of the type of processing applied on raw data (Markon and Peterson 2002; Tucker et al. 2005) as well as the spatial location. Although limitations exist in the ability of NDVI to capture primary productivity variations, remote-sensing-based indexes remain the only possible way to obtain quantified measures of this parameter at such spatial and temporal scales (Kerr and Ostrovsky 2003; Pettorelli et al. 2005). In Africa, several ungulate populations have been demonstrated to react to NDVI variation (e.g., van Bommel et al. 2006; Ryan et al. 2007), sometimes more so than to rainfall (Rasmussen et al. 2006). Our aim was to contrast annual primary productivity across vast differences in habitats, that is, from semidesert areas to grasslands and dense forests. Consequently, we expected that INDVI would provide a useful estimate of this broadscale variation in primary productivity.

#### *Statistical Analysis*

Individual locations were expected to generate nonindependent estimates of ungulate abundance. Due to variation in national policy regarding wildlife management, each country was also expected to generate nonindependent estimates. Therefore, we used a linear mixed model approach, to account for nested random effects of location and country. Methodological factors have been previously reported to affect density estimates (Blackburn and Gaston 1996; Gaston et al. 1999; Jachmann 2002). We therefore considered the size of the sampled area and the survey type as explanatory variables in our analysis. Since these variables are collinear (with ground surveys associated with small sampled areas;  $t = -5.30$ ,  $P < .001$ ), these variables were never considered together in the same model. This limited our ability to disentangle the independent effects of these two variables.

We modeled density variations as follows: first, the effects of (1) the species identity, (2) the survey type or the size of the sampled area, and (3) the INDVI on density estimates were modeled. Survey type was considered as a bimodal factor, while species identity was treated as a factor with 13 levels. Then, we replaced species identity with characteristics of the species (i.e., average body mass and diet category) and explored the effects of these biological traits on density estimates. Diet category was a variable with three levels (grazer, browser, mixed feeder).

Density estimates, the size of the sampled area, and the average body mass of the species were log transformed (Sokal and Rohlf 1995). For each of the two modeling approaches (incorporating species identity or species traits), several candidate models were considered, and model selection was performed using Akaike Information Criterion (AIC; Burnham and Anderson 1998). The best model of any candidate set applied to a given data set is that with the lowest AIC value. Reasonable alternatives to the best model have AIC  $< 2$  higher, while a difference in AIC  $> 10$  indicates that the model with the higher AIC is a poor alternative. All statistical analyses were performed in the statistical package R (<http://www.r-project.org>).

## Results and Discussion

### *Primary Productivity and Ungulate Density*

Although there have been several studies relating NDVI to herbivore distribution and performance at local scales (e.g., Herfindal et al. 2006; Rasmussen et al. 2006; van Bommel et al. 2006), there have been few previous attempts to link herbivore abundance to this index of primary productivity (but see Verlinden and Masogo 1997; Oosterheld et al. 1998), and none of them have been performed at the continental scale. Our results thus demonstrate for the first time that the previously identified positive relationships between herbivore densities and annual primary productivity (Coe et al. 1976; East 1984; Georgiadis et al. 2003) can be extended to the continental scale, using NDVI as the measure of primary productivity.

The positive and linear continental-scale relationship between INDVI and ungulate abundance needs to be interpreted with caution, for four reasons. First, the range of INDVI values covered in this analysis excludes extremes in which we would not expect to observe linear trends. Had this study included such extremes, we could have expected to find the overall shape of INDVI-density relationship to be nonlinear. Second, satellite indexes generally perform badly over sparsely vegetated areas, densely vegetated areas, cloudy areas, and areas including a high proportion of water (Justice et al. 1985; Huete 1988; Pettorelli et al. 2005). Although we used the best available corrected NDVI time series, the correlation between primary productivity and INDVI might be weaker in some of the national parks than in others. Third, other factors have been suggested to affect spatial and temporal variations in ungulate densities, among them seasonal migrations (Boone et al. 2006), large predator densities (Grange and Duncan 2006), megaherbivore densities (Fritz 1997), soil nutrient status (Bell 1982, 1986), and poaching and hunting rates. We did not have information on these variables for all the locations we considered and thus could

not include them in this study. Finally, given that we had no information as to where exactly the surveys were performed, we systematically associated density estimates of ungulates to INDVI values from the whole national parks. This led to a relatively high spatial mismatch in the remote sensing data and the population density data and probably also reduced the strength of the relationship. All these caveats suggest that the underlying relationship between INDVI and abundance is likely to be stronger than is apparent from our analysis.

### *The Importance of Integrating Information on Surveys in Broadscale Studies*

Ground surveys showed a weak tendency to be associated with higher density estimates than aerial surveys and total counts (estimate =  $0.20 \pm 0.13$ ,  $t = 1.51$ ,  $P = .13$ ). This trend was consistent with previous results from a local scale study performed by Jachmann (2002), suggesting that, at a broader scale too, survey types might represent an important factor determining ungulate abundance estimates. In contrast to Jachmann (2002), however, we did not have locations where the same species was monitored using both aerial and ground surveys, at the same spatial scale: the “true” density being unknown, the differences in density estimates associated with different survey types are therefore not absolutely comparable.

As survey type is correlated with the size of the sampled area, it was no surprise that we also found a strong relationship between the size of the area sampled and ungulate density, with lower densities found in larger sampled areas (tables 2, 3; appendix in the online edition of the

**Table 2:** Candidate models for ungulate density in African national parks

Model	AIC	$\Delta$ AIC
INDVI + species + sampled area	607.28	.00
INDVI + species + survey type	636.40	29.12
Factor (diet) + INDVI + sampled area	647.12	39.84
INDVI $\times$ species + sampled area	649.41	42.13
Factor (diet) + log ( $m$ ) + INDVI + sampled area	652.49	45.21
Factor (diet) $\times$ INDVI + sampled area	657.46	50.28
INDVI $\times$ species + survey type	678.87	71.59

Note: AIC, Akaike Information Criterion;  $\Delta$ AIC, difference between the model AIC and that of the best model in the candidate set; INDVI, integrated normalized difference vegetation index. Log of species density modeled as a function of the species identity or characteristics, the annual INDVI (an index of primary productivity) in the national park sampled, and the survey type or the size of the sampled area. Species’ characteristics include diet (distinguishing three categories: mixed feeders, grazers, and browsers) and log-transformed average body mass: log ( $m$ ). Here a multiplication sign ( $\times$ ) means that both the individual predictors and the interaction between them have been considered.

**Table 3:** Estimates from the best model, considering the additive effects of species identity, INDVI, and the size of the sampled area on the log of the density estimates

Parameter	Estimate	SD	$t$ value	$P$ value
Intercept	.62	.39	1.56	.120
Bohor reedbuck	-.58	.24	-2.41	.020
African buffalo	.22	.21	1.07	.290
Bushbuck	-.42	.26	-1.62	.110
Common eland	-.45	.22	-2.10	.040
Sable antelope	-.61	.23	-2.64	.009
Giraffe	-.64	.22	-2.89	.004
Greater kudu	-.57	.23	-2.53	.010
Gray duiker	-.52	.24	-2.12	.030
Impala	.28	.22	1.27	.210
Oribi	-.20	.26	-.78	.440
Roan antelope	-.55	.22	-2.47	.010
Southern reedbuck	-.47	.26	-1.79	.070
Sampled area	-.46	.08	-6.08	<.001
INDVI	.04	.02	1.99	.050

Note: Wildebeest set as the species of reference, so that all species estimates are given relative to the estimates for wildebeest. INDVI, integrated normalized difference vegetation index.

*American Naturalist*): models with the size of the surveyed area always provided substantially better fits to the density data than equivalent models with survey type ( $\Delta$ AIC > 20). This result is in accordance with previous studies exploring the relationship between sampling area and abundance estimates (Blackburn and Gaston 1996; Gaston et al. 1999). Of the explanations previously suggested to account for similar results, the suggestion that it arises from a negative correlation between sampling efficiency and the size of the area sampled (Gaston et al. 1999) seems to be most likely for our data. If larger areas are sampled with lower efficiency, individuals in these larger areas may be missed, leading to an apparent negative relationship between density and sample area, even in cases in which density does not vary systematically with area. The strong association between the area sampled and the type of survey and the fact that ground surveys have been previously reported to generate higher density estimates (Jachmann 2002) are consistent with this hypothesis.

### *Interspecific Differences in the Relationship between Energy and Abundance*

Although the interaction between species identity and INDVI was not significant (table 2), not all of the species considered displayed a strong positive relationship between INDVI and density, and the correlation was notably weak (or even negative) for giraffes, bushbuck, eland, sable and roan antelopes, and duikers (appendix). These differences between species might be explained by the fact that (1) some species might be habitat specific at the local scale

of the national park considered, so that the INDVI at the scale of the national park does not reflect the primary productivity in the habitat used by these species; (2) INDVI might be a better index of primary productivity in homogeneous grasslands than in more heterogeneous, forested areas, and therefore a better relationship between INDVI and abundance is expected for species predominantly grazing on more open grasslands (e.g., wildebeest *Connochaetes taurinus*, buffalo *Syncerus caffer*, oribi *Ourebia ourebi*, impala *Aepyceros melampus*, and reedbuck *Redunca* spp.); or (3) INDVI might better index resource availability for nonselective species than selective species (Pettorelli et al. 2006).

Replacing species identity with species characteristics, we then showed that diet was an important biological determinant of density estimates (tables 2, 3). Mixed feeders were indeed the most abundant species ( $P < .001$ ), a result accounted for by the impala. Interestingly, if we look closely at the spatial distribution of ungulates according to INDVI values, we note that browsers were found to be associated with higher INDVI ranges than were grazers (table 1). Since the species that were underrepresented in this data set were mainly forest species, and since these are predominantly browsers associated with high rainfall (Jarman 1974), the reported higher INDVI ranges of browsers appear to be a robust result (the inclusion of forest species would indeed increase the INDVI range of browsers more than of grazers). It is worth noting, however, that the fact that browsers can be described as more “generalist” in relation to the INDVI of their habitat when taking a continental perspective does not imply that browsing species are not selective at a smaller scale, and it may indeed be that browsers use a narrow range of the primary productivity within their habitat. Browsers might thus be selective at a finer scale than grazers, which are selective for patches within a smaller INDVI range at the larger scale but may be generally more unselective than browsers within patches. Further analyses are needed to explore such patterns in the spatial distribution of African ungulates in relation to their diet.

Population density estimates were not significantly affected by body mass variation (all  $P > .10$ ), which is perhaps surprising in light of the many studies reporting a reduction in density with increasing body mass (e.g., Damuth 1981). However, it has recently been stressed that care should be taken to distinguish between co-occurring processes when interpreting density–body size relationships (White et al. 2007), and the explanation for our result is possibly related to the fact that our study was restricted to only 13 ruminant species with a body mass range just over two orders of magnitude. This is smaller than the range generally used in major studies (around six orders of magnitude; e.g., Damuth 1981). It has also been suggested that the relationship between body mass and density

flattens out at the upper end of the mammalian body size range, with no negative relationship for artiodactyls (Silva and Downing 1995), although this may alternatively be another consequence of the effect of sample area on density estimates (Blackburn and Gaston 1996).

## Conclusions

Our results identify a link between primary productivity and abundance of certain African ungulate species at the continental scale. The correlation reported between INDVI and density demonstrates the potential usefulness of remote sensing data in assessing consequences of climate change on several species' abundance in Africa: many climatic models can indeed be used to predict spatiotemporal changes in NDVI, potentially enabling us to forecast how climatic changes might affect primary productivity and, ultimately, wildlife. Moreover, our results demonstrate the importance of taking information on the size of the surveyed area into account when modeling variations in density estimates: such considerations are particularly important when comparing densities between areas since such comparisons not only constitute an integral part of many macroecological studies but also form the basis of priority settings in conservation.

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Impalas in the Masai Mara in Kenya. Photograph by Jakob Bro-Jørgensen.