

On the carrying capacity for large ungulates of African savanna ecosystems

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SUMMARY

The effect of pastoral management on the standing crop biomass of large ungulates, an index of carrying capacity, is analysed at a regional level by using data compiled from published sources covering east and south Africa. The effect of primary production is controlled for by using two environmental factors, rainfall and soil nutrient availability, and the effect of species richness of the ungulate community is evaluated. The results confirm the dominant effect of rainfall, and demonstrate that soil nutrient levels also strongly affect the biomass of large ungulate communities. For a given level of rainfall, on rich soils (high nutrient availability) the biomass of large ungulates is about 20 times as great as on poor soils with low nutrient availability. The model based on rainfall and soil nutrient classes accounts for 87 % of the variance in large ungulate biomass. Pastoral and natural ecosystems do not differ significantly in large ungulate biomass; there is therefore currently no evidence that extensive pastoral management increases carrying capacity for large ungulates above the levels observed in natural communities. Species richness, a measure of biodiversity, had a 'significant but very small effect on the biomass-rainfall relation in the complete data set. When analysed by pastoral management, the effect of this factor was significant for the set of natural ecosystems only. Pastoral management and species richness may therefore have compensatory effects. These results suggest that the carrying capacity is limited at the community, rather than the species, level.

1. INTRODUCTION

Savanna and grassland ecosystems occupy a quarter of the Earth's land surface, and are at the centre of the debate on the means of achieving sustainable use of global natural resources (cf. IUCN/UNEP/WWF 1991). The integration of pastoralism, rangeland management and wildlife conservation has received special attention (Walker 1979; Lamprey 1983; Home-wood & Rodgers 1987; Western 1989; Enghoff 1990; Prins 1992). The African continent is of particular interest, for here the large herbivore communities are relatively intact compared with those of the other continents, where the communities were truncated by the Pleistocene extinctions (Martin 1984). African savanna ecosystems have been studied in some detail, by livestock scientists and ecologists; none the less, many issues relating to their potential productivity, stability and conservation remain unresolved (Ellis & Swift 1988; Coughenour 1991; Prins 1992).

Among these issues, the 'carrying capacity' of ecosystems is central, whether of protected areas with near-natural wildlife communities, or of rangelands with livestock. Its definition poses problems because carrying capacity necessarily involves subjective, goal-related value judgements. Carrying capacity for wild-life is often defined as the maximum number of animals that can be maintained in a given area on a long-term

basis without habitat deterioration. For domestic animals, carrying capacity is the stocking rate which provides the maximum sustainable yield (Eltringham 1979).

An approach which has proved useful in ecological research has been the use of standing crop biomass of animals as an index of carrying capacity (Coe *et al.* 1976; Bourn 1978), and the regional scale has proved appropriate for natural (Coe *et al.* 1976; East 1984), as well as managed, ecosystems (Oesterheld *et al.* 1992).

A key question concerns the effect of pastoral management on the biomass of herbivores. In an early contribution, Petrides & Swank (1965*a, b*) drew attention to the fact that the very high ungulate biomasses in some of the natural African ecosystems like those in northern Kivu 'far exceed those of the best livestock ranges'. Ecological theory on feeding niche separation, specialization and grazing succession suggests that species-rich communities made up of specialist species will use the food resources available more completely (Vesey-Fitzgerald 1960; Bell 1971; Leuthold 1978; Walker 1979). Multispecies herbivore communities have been proposed as a means of increasing large herbivore biomass and production (Hudson & Dezhkin 1989; Lambert & Guérin 1989), particularly in African savannas with communities including both grazing and browsing species (Walker 1979).

Recently, however, Oesterheld *et al.* (1992) have claimed that 'in African systems... agricultural and pastoral systems have greater biomass than their natural counterparts'. There is no doubt that intensive agricultural techniques of sward management, especially irrigation and fertilization, can greatly increase carrying capacity. However, the important question of whether rangelands with extensive management have higher biomasses than natural ecosystems with intact herbivore communities has not yet been answered for the African continent, as the references cited by Oesterheld *et al.* (1992) reported only limited data and contained no statistical tests of such comparisons.

The biomass of herbivores is closely related to net above-ground primary production (ANPP) (McNaughton *et al.* 1991). To compare the carrying capacity of different ecosystems, it is therefore necessary to control for variations in ANPP. The approach used by Oesterheld *et al.* (1992) in their study of South American rangelands was to use a general equation to predict ANPP from rainfall data (Lauenroth 1979); they found that the results fitted closely the available measurements of ANPP for these rangelands.

In African savannas, too, rainfall is known to be correlated with ungulate biomass (Coe *et al.* 1976; Bell 1982; East 1984), but the use of rainfall alone as an index of ANPP is likely to be an oversimplification. Soil nutrient availability (SNA), conditioned by geomorphology, varies strongly across the continent and, through its effect on ANPP, is suspected of influencing ungulate biomasses at a regional scale (Bell 1982; East 1984).

In this paper we report the results of the first detailed statistical analysis of the effect of pastoral management on the carrying capacity of African savannas. Pastoral areas with extensive management practices cover over 20 % of the continent: we focus on those of the eastern and southern parts, because it is here that most of the last near-natural ecosystems, with their communities of wild ungulates, are found.

2. METHODS

Information on ungulate biomasses in savanna ecosystems of Africa east of the Nile and south of Lake Victoria, at a regional scale, were obtained from reviews (Morgan 1972; Coe *et al.* 1976; Bell 1982; Van der Merwe 1983; East 1984; Peden 1987) and field studies (Owaga 1980; Kahurananga 1981; De Leeuw *et al.* 1991). The sites varied in area from Manyara National Park, 100 km², to Marsabit District, 71000 km², and most were between 5000 km² and 20000 km². The following variables were included: (i) biomass (kg km²) of wild ungulates with adult live mass over 15 kg; (ii) biomass of domestic ungulates (cattle, sheep, goats, donkeys, camels and horses; kg km²); (iii) rainfall (mean annual precipitation; mm) was obtained from the original papers; (iv) soil nutrient availability (see below); (v) pastoral-natural (see below); (vi) species richness, the number of ungulate species (domestic and wild), obtained from the original papers or East (1988, 1989).

As usual in comparative analyses of ecosystem structure and processes, most of the data are from instantaneous surveys rather than continuous monitoring. To minimize inaccuracy, some sites were excluded, according to the following rules: (i) natural sites with data that failed to include major components of the large ungulate community

(the same rule was applied by Coe *et al.* 1976), or with known serious disturbance (e.g. shooting using modern arms); and (ii) sites for which the information provided was inadequate to ensure that the censuses were conducted according to the best available methods (*sensu* Norton-Griffiths 1978).

For 13 sites, multiple counts had already been averaged in the source papers. For another site, two counts (wet and dry season) were averaged. When data on densities only were available, biomasses were calculated from the mass table given in Coe *et al.* (1976). Errors remaining in the data base (e.g. due to exceptional years) would tend to mask rather than create significant patterns (cf. Peters *et al.* 1991).

The sites were classified into three groups of soil nutrient availability according to Bell's (1982) broad geomorphological classes: 'high' for volcanic and marine sediments, 'medium' for Rift Valley and Cratonic sediments, and 'low' for basement, granitic shields and Kalahari sands. Within the medium class were included sites with a mixed geology (e.g. of sedimentary and basement geology, with some volcanic intrusions providing that they represented less than 20%). This information was obtained from the papers, or from Saggerson (1972), Scott (1972) and Cole (1986).

Pastoral areas were selected as in Oesterheld *et al.* (1992): they had extensive domestic livestock herding (cattle, goats, sheep, camels, donkeys and horses). Husbandry techniques included protection from predators, selective breeding, some veterinary care and water supplementation (but not food); swards were not irrigated or fertilized. For this analysis we excluded pastoral systems where wildlife comprised an annual average of greater than 30 % of the biomass; 59 sites remained for which information on all the variables was available.

A multifactor covariance analysis of total biomass (*Bt*) was used with rainfall (*P*) as a covariate. Soil nutrient availability (SNA) and pastoral use (*Past*) were included as factors, and species richness (*SpR*) as a second covariate. The numerical variables were log transformed (base 10), and statistical analyses were done with the General Linear Model procedure of the Statistical Analysis System (GLM procedure, SAS 1990). All the factors, covariates and their interactions were initially included in the model; the non-significant terms were then removed step by step starting with the least significant high-order interactions.

3. RESULTS

The resulting model includes terms for rainfall (*P*), soil nutrient availability (SNA), species richness (*SpR*) and the interaction *P.SpR*. It accounts for a large proportion of the variance in the sample, $R^2 = 0.88$ (table 1), and the residues of log total biomass on predicted log total biomass and on actual log total biomass were normally distributed with no significant trend:

$$\log Bt = a \log P + b \log SpR - c \log P \cdot \log SpR - (d + SNA) + E, \quad (1)$$

where *a*, *b*, *c* and *d* are coefficients, SNA is a value given by the soil nutrient availability group, and *E* is the error term.

One covariate, rainfall, and one factor, soil nutrient availability, had highly significant effects. The other covariate, species richness, also had a significant effect, whereas pastoral management or any of its interactions had none (e.g. $F = 1.33$, d.f. = 1, $p = 0.253$, for *Past* only).

Table 1. Analysis of covariance of ungulate biomass (Bt)

(Mean annual rainfall (*P*) and species richness (*SpR*) are covariates; soil nutrient availability (*SNA*) and pastoral management are covariates.)

dependent variable: log <i>Bt</i>					
source	degrees of freedom	sum of squares	mean square	<i>F</i> value	<i>p</i>
model	5	13.511	2.702	79.75	0.0001
error	53	1.796	0.034	—	—
corrected total	58	15.306	—	—	—
	$R^2 = 0.882$	—	—	—	—
source	degrees of freedom	type III SS	mean square	<i>F</i> value	<i>p</i>
log <i>P</i>	1	1.440	1.440	42.50	0.0001
<i>SNA</i>	2	1.376	0.688	20.31	0.0001
log <i>SpR</i>	1	0.171	0.171	5.05	0.0289
log <i>P</i> · log <i>SpR</i>	1	0.136	0.186	5.49	0.0229

Table 2. Analysis of covariance of ungulate biomass (Bt) in which only one covariate, mean annual rainfall (*P*) and one factor, soil nutrient availability (*SNA*) are retained

dependent variable: log <i>Bt</i>					
source	degrees of freedom	sum of squares	mean square	<i>F</i> value	<i>p</i>
model	3	13.250	4.417	118.13	0.0001
error	55	2.056	0.037	—	—
corrected total	58	15.306	—	—	—
	$R^2 = 0.866$	—	—	—	—
source	degrees of freedom	type III SS	mean square	<i>F</i> value	<i>p</i>
log <i>P</i>	1	9.965	9.965	266.52	0.0001
<i>SNA</i>	2	1.279	0.639	17.10	0.0001

(a) Ungulate biomass and soil nutrients

Soil nutrient availability had a strong effect on the *y*-intercept term of the model, an influence which appeared more clearly in a simpler model when the covariate species richness (*SpR*) was removed:

$$\log Bt = a \log P - (d + SNA) + E. \quad (2)$$

This simple model (table 2) showed that 87 % of the variations in the ungulate biomass of this sample are accounted for by variations in rainfall, within three broad classes of soil quality. The relation between ungulate biomass and rainfall for the three groups is shown in figure 1. The *y*-intercepts for the logged data are -0.67, -1.32 and -2.04 for 'high', 'medium' and 'low' classes, respectively. When we tested the model by pairs of *SNA* classes, the *y*-intercept for 'high nutrients' did not differ significantly from 'medium nutrients' ($F = 1.11$, d.f. = 1, $p = 0.29$). 'Low nutrients' differed significantly from each of the 'high' and 'medium' classes ($F = 10.81$, $F = 24.70$; d.f. = 1, d.f. = 1; $p < 0.01$, $p < 0.0001$). The simple model (equation (2)) can therefore be reduced to two nutrient classes ($R^2 = 0.87$): $\log Bt = 1.96 \times \log P - 2.04$ for 'low nutrients' and $\log Bt = 1.52 \times \log P - 0.53$ for Bell's 'high' and 'medium' classes. However, the intermediate values found for the 'medium' group suggest that the reality of the three classes would probably be confirmed by analysis of a larger data set. For a given rainfall, the biomass on high nutrient soil is about 20 times greater than on low nutrient soils.

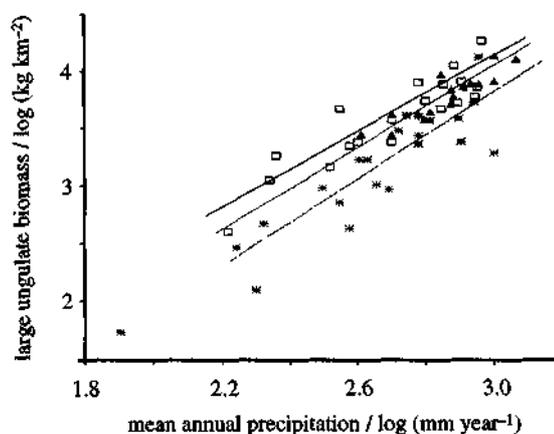


Figure 1. Relations between rainfall (mean annual precipitation, *P*, mm year⁻¹) and large herbivore biomass (*Bt*, kg km²) for the three soil nutrient availability (*SNA*) groups: high (squares), medium (triangles) and low (stars). Logarithms are to the base 10. $\log Bt = 1.58 \log P - 0.67$ ($r^2 = 0.82$, $p < 0.001$, $n = 19$) for high *SNA*; $\log Bt = 1.78 \log P - 1.32$ ($r^2 = 0.85$, $p < 0.001$, $n = 16$) for medium *SNA*; and $\log Bt = 1.96 \log P - 2.04$ ($r^2 = 0.85$, $p < 0.001$, $n = 24$) for low *SNA*. Although the slopes are not significantly different (covariance analysis in this and subsequent comparisons, $F = 0.82$, $p > 0.05$, d.f. = 2), the *y*-intercepts are ($F = 20.01$, $p < 0.001$, d.f. = 2).

(b) Species richness

Species richness accounted for a small but significant part of the variance (table 1). It was nearly three times higher in natural than in pastoral sites (mean = 13.8

Table 3a. Analysis of covariance of ungulate biomass (Bt) for natural sites only

dependent variable: log Bt					
source	degrees of freedom	sum of squares	mean square	F value	p
model	5	8.767	1.753	49.81	0.0001
error	23	0.810	0.035	—	—
corrected total	28	9.577	—	—	—
	$R^2 = 0.915$	—	—	—	—

source	degrees of freedom	type III SS	mean square	F value	p
log P	1	0.517	0.517	14.68	0.0009
SNA	2	0.786	0.393	11.16	0.0004
log SpR	1	0.165	0.165	4.69	0.0409
log P.log SpR	1	0.131	0.131	3.73	0.0659

Table 3b. Analysis of covariance of ungulate biomass (Bt) for pastoral sites only

dependent variable: log Bt					
source	degrees of freedom	sum of squares	mean square	F value	p
model	3	4.850	1.617	51.05	0.0001
error	26	0.823	0.032	—	—
corrected total	29	5.673	—	—	—
	$R^2 = 0.855$	—	—	—	—

source	degrees of freedom	type III SS	mean square	F value	p
log P	1	3.790	3.790	119.65	0.0001
SNA	2	0.442	0.221	6.78	0.003

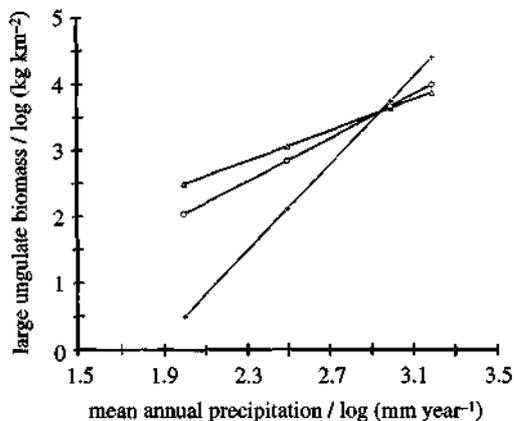


Figure 2. The effect of species richness on the relation between ungulate biomass and rainfall, for sites with low soil nutrient availability: species richness = 20 (triangles), 10 (circles) and 1 (crosses).

and 5.0, respectively; Newman-Keuls, $t = 13.55$, $p < 0.0001$, d.f. = 57). To investigate further the influence of species richness we repeated the analysis for pastoral and natural sites separately. The effect of species richness was still significant for natural sites (table 3a), giving a model similar to the first one (equation (1)) with $R^2 = 0.92$, although the interaction $P.SpR$ only approached significance. No influence of SpR was found for the pastoral sites, leaving a simple model (equation (2)) with rainfall and soil nutrient availability only (table 3b), $R^2 = 0.85$.

Species richness affected the slope of the biomass-rainfall relation. When we calculate the parameters of the model, for each of the three SNA classes, species-rich

natural communities start with a greater biomass at low rainfall, and they have a slower increase in their biomass with increasing rainfall. The result for 'low nutrients' is given in figure 2.

4. DISCUSSION

This analysis confirms and extends previous suggestions that soil quality, in addition to rainfall, has important effects on the carrying capacity of African savannas for ungulates (Bell 1982; East 1984). The inclusion of the soil nutrient availability factor in our model extends its validity to ecosystems with 1000 mm rainfall, compared with the 700 mm to which the previous model was limited (Goe *et al.* 1976). This model could be improved by the use of a more accurate measure of soil quality but, even in its present form, based on these two parameters, the model is reasonably precise and provides a useful tool for the prediction of the carrying capacity of African savanna ecosystems. This result suggests that the biomass of these ungulate communities is closely regulated by food availability.

These data provide no evidence that extensive pastoral management has an effect on the carrying capacity of African savanna ecosystems. This conclusion differs from Oesterheld *et al.* (1992), who showed that pastoral management in South America increased carrying capacity by a factor of 10 compared with a set of natural ecosystems worldwide. Either African pastoral management is less effective than South American, or natural ecosystems in Africa have higher carrying capacities relative to net above ground primary production (ANPP) than the set of natu-

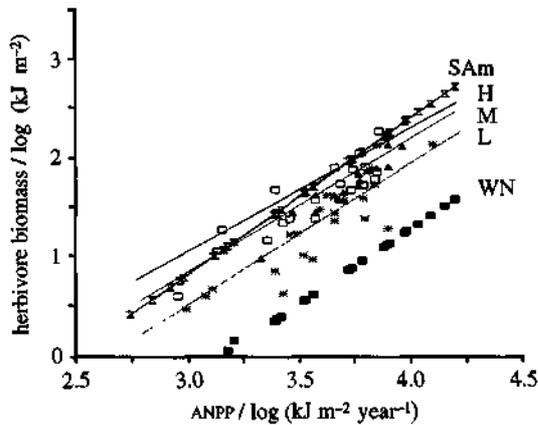


Figure 3. The relations between herbivore biomasses and net annual primary production (ANPP, $\text{kJ m}^{-2} \text{ year}^{-1}$) for: SAm, South American pastoral areas (open double triangles); WN, World natural areas taken from Oesterheld *et al.* 1992 (filled squares), and for ungulate biomasses and ANPP for natural and pastoral sites in African savannas; H, high soil nutrient availability (open squares); M, medium nutrient availability (filled triangles); L, low nutrient availability (stars).

ral ecosystems chosen for comparison. We tested these hypotheses by using our data on rainfall and the regression applied by Oesterheld *et al.* (1992) to calculate ANPP ($\text{ANPP} = 0.5P - 29$, where P = annual precipitation in millimetres) (Lauenroth 1979).

Relative to this index of ANPP, ungulate biomasses in natural as well as pastoral African ecosystems are similar to those in South American rangelands (figure 3), which excludes the first hypothesis. The natural ecosystems used by Oesterheld *et al.* (1992) in the comparison included many with incomplete communities of large ungulates, especially the mega-herbivores. The important dichotomy in terms of herbivore carrying capacity may not be between pastoral and natural ecosystems, but between ecosystems which have large ungulates (wild or domestic) and high herbivore biomasses, and ecosystems in which the large herbivores are absent or rare, where herbivore biomasses are on average some ten times lower.

The results reported here suggest that species richness for large ungulates may have a slight effect on the carrying capacity of natural savanna ecosystems. At low rainfall, species-rich ecosystems had higher biomasses than their species-poor counterparts. In less-productive ecosystems, high species richness may increase carrying capacity by allowing complementary use of the various vegetation components (grazing and browsing etc.). As the biomasses of the species-poor pastoral ecosystems were not lower than the species-rich natural ones, it is possible that high species richness and pastoral management have compensatory effects, with management practices such as protection from predators allowing species-poor pastoral systems to reach the high carrying capacity of diverse natural systems.

However, this data set is small and was selected to examine the effect of pastoral management. This result needs to be tested further, on a larger data set containing more systems with mixed communities of wildlife and livestock. Recent findings in Kenyan

rangelands suggest that mixed ecosystems with cattle and wild ungulates may have a higher carrying capacity than either pastoral or natural ones (Western 1989).

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