Bottom-up and top-down processes in African ungulate communities: resources and predation acting on the relative abundance of zebra and grazing bovids

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African ungulate populations appear to be limited principally by their food resources. Within ungulate communities, plains zebras coexist with grazing bovids of similar body size, but rarely are the dominant species. Given the highly effective nutritional strategy of the equids and the resistance of zebras to drought, this is unexpected and suggests that zebra populations may commonly be limited by other mechanisms. Long-term research in the Serengeti ecosystem and in the Kruger National Park suggests that zebra could be less sensitive to food shortage, and more sensitive to predation, than grazing bovids: if this is a general principle, then, at a larger scale, resource availability should have a weaker effect on the abundance of zebra than on grazing ruminants of similar body size (wildebeest and buffalo), and zebras should be relatively more abundant in ecosystems where predators are rare or absent. We test these expectations using data on 23 near-natural ecosystems in east and southern Africa. The abundance of wildebeest is more closely related to resources than is that of zebra; buffalo are intermediate. We show that hyena densities are closely correlated with those of lions, and use the abundance of lions as an index of predation by large predators. The numerical response of lions to increases in the abundance of their prey was linear for mesoherbivores, and apparently so for the three species alone. Finally, the abundance of zebra relative to grazing bovids is lower in ecosystems with high biomasses of lions. These results indicate that zebras may commonly be more sensitive to top-down processes than grazing bovids: the mechanism(s) have not been demonstrated, but predation could play a role. If it is true, then when numbers of the large mammalian predators decline, zebra populations should increase faster than buffalo and wildebeest.

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In some near-natural African savanna ecosystems which have not been greatly altered by human activities in the last centuries, large mammals are both diverse and abundant. Medium-sized ungulates constitute a major part of the vertebrate biomass (Cumming 1982) and therefore play an important role in the structure and the functioning of these ecosystems. The ecological impact of these herbivore communities depends on their abundance and also their species composition: it is now widely accepted that their abundance is determined principally by the abundance of their food resources (Coe et al. 1976, East 1984, Fritz and Duncan 1994).The species composition of ungulate communities results from the interaction of several processes which influence

the dynamics of coexisting populations. "Bottom-up" processes depend on the food resources (both quantity and quality) whereas "top-down" processes involve natural enemies (predators, and also diseases). Both types of processes shape ungulate communities, and their respective impacts can vary between different ecosystems.

Among medium-sized grazing herbivores, equid and bovid species are important components of these communities. Convergent evolution has led these 2 families to acquire similar adaptations to life in open savannas, and equids have highly effective foraging strategies which can allow them to out-compete ruminants (Duncan et al. 1990, Ménard et al. 2002). Indeed, in the reserve of Oostvaardersplassen in the Netherlands, cattle and horses have been left unmanaged since the 1980s and have reached relatively high densities. In this ecosystem without large predators, Konik horses showed a higher intrinsic rate of population increase compared to Heck cattle (Vulink 2001, T. Vulink pers. comm.), and currently outnumber the cattle which apparently are regulated by food shortage in winter. In Africa, plains zebra *Equus quagga* and grazing ruminants coexist widely, but bovids such as blue wildebeest *Connochaetes taurinus* and buffalo *Syncerus caffer* are clearly more successful, since one of these species dominates the guild of grazing ungulates in most near-natural African savanna ecosystems (87% of those studied here). Consequently, the processes limiting the abundance of zebra and grazing bovids of similar body size are of particular interest: we focus this study on buffalo and wildebeest, which use similar resources to the zebra. In the Serengeti the wildebeest and buffalo populations are limited by their food supply (Sinclair 1977, Mduma et al. 1999), whereas zebra are limited by their low juvenile survival. The cause of the high foal mortality in this ecosystem is not known, but it has been suggested that it could be predation (Grange et al. 2004). In Kruger National Park, where annual rainfall did not have a direct effect on zebra survival rates, it has been suggested that lion predation could have an effect on survival rates of immature zebra (Owen-Smith et al. 2005). On the other hand, in Laikipia, where large mammalian predators are not abundant, zebras are limited by their food resources (Georgiadis et al. 2003).

These results indicate that there are important differences among ecosystems in the factors which regulate zebra populations, and that predation may play a major role. Since the abundance of predators and of resources varies among ecosystems we test the hypothesis that the abundance of equids shows a different response to these variables, compared to wildebeest and buffalo. We use census data from 23 near-natural ecosystems in east and southern Africa, in the 1990s. We first analyse the influence of the quantity and quality of food resources on the abundance of these species using rainfall and soil nutrient availability as proxies: from previous studies we expect positive effects on herbivore biomasses, and expect the abundance of the grazing bovids to be more tightly determined by food resources than zebra. We then examine the relationships between the abundance of medium-sized ungulates and of large predators, and test the hypothesis that the ratio "zebra/grazing bovids" declines as predator biomass increases.

Material and methods

Protected areas

We established a database which includes protected areas in east and southern Africa where data are available on the abundance of the herbivores and their predators (Appendix 1). To avoid biases due to predation by people we included only near-natural areas which are effectively managed: this selection was based on information in the UNEP-WCMC website (<http:// quin.unep-wcmc.org >; Table 1), completed for a few areas with information published elsewhere (Lake Manyara, Serengeti, Kruger, Etosha and Ngorongoro Crater). Among the 81 areas we examined, 4 where poaching focused on megaherbivores (elephant and rhino; Ruaha, North and South Luangwa, and Tarangire) were included as this study concerns mesoherbivores. Ninety-one percent of the 23 protected areas we retained are classified in IUCN category "II" (National Park). Ngorongoro Crater is in category "VI" (Management Area), and Selous in "IV" (Nature Reserve), but they are as well protected as the National Parks. Sixteen of these areas are >1000 km^2, the other 7 are 100–1000 km^2 (Appendix 1).

The mean annual rainfall for each area was derived from a global model based on monthly measurements of rainfall between 1980 and 1999 (Willmott and Matsuura 1998). The geographical coordinates of each site were obtained from the UNEP-WCMC website (<http:// quin.unep-wcmc.org >) and the estimates were compared with published measurements where available; the data from the two sources differed by >50% for Amboseli (Coe et al. 1976), Hluhluwe-iMfolozi (Coe et al. 1976), Mikumi (UNEP-WCMW website), Selous (Bell 1982) and Tsavo (Coe et al. 1976), so we used the published rainfall data in these cases.

The soil nutrient availability (SNA) in each area was determined from a geological map (Clark 1967, in Bell 1982): "high" SNA for volcanic and marine sediments, "medium" for rift valley and cratonic sediments, and "low" for basement, granite and Kalahari sands (for more information see Bell 1982).

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Table 1. Information on the 23 African protected areas selected for this study. The period indicated for ungulate censuses is the whole period and can vary between species. Notes for population trends: ZB =zebra, WB =wildebeest, BU =buffalo; S =stable, D =decreasing, I =increasing.

| Protected area | Perturbations | Period for data used | | | Population trends | | |
	(source: UNEP-WCMC web site, other publications see Methods section)	Ungulates	Lion	Hyena	ZB	WB	BU
Amboseli		1991–1996	2001	no data	S	S	S
Etosha	Fences stop migrations, anthrax+lion contraception (1986)	1995	1991	1979–1986	S	S	
Hluhluwe-iMfolozi	Fenced	1991–1998	2002	1975–1981	S/I	S	S
Hwange	Artificial waterholes	1990–1999	2001–2002	2004	S/D	S/I	S/I
Katavi	Some poaching	1991–1995	2002	1996	I		S/D
Kruger		1980–1993	2002	1984	S/I	S	S
Lake Manyara	Rinderpest (1959), anthrax (1984), fences	1959–1990	no data	no data	S/I	S/I	S
Lake Mburo		1995	no data	present; no data	D		S
Lake Nakuru	Water pollution	1990–1995	1997–2002	no data	?		I
Luambe		1994	no data	no data	S	S	S
Makgadikgadi-Nxai Pan		1994	2001	no data	D	S/I	
Mana Pools		1995	2002	no data	S		S
Mikumi	Some poaching and grazing, a highway in Park	1994	no data	no data	D	S/D	S
Nairobi	Fences stop migration+buffalo introduced	1990–1995	2001	1976	S	S	S/D
Ngorongoro Crater	Some poaching, disease in lions and malignant catarrh in wildebeest	1963–1992	1962–1998	1966–1968	S	S	S/I
North Luangwa	Some poaching on elephant and rhino	1995	2002	no data	S	S	I
Okavango		1989–2002	1990–2002	1991–1999	S/D	S/I	S
Ruaha	Heavy poaching on rhino	1993–1996	2002	no data	S		D
Selous	Some poaching	1994	2002	1994	I		I
Serengeti	Rinderpest (1960s), some poaching (1980s)	1971–1996	1991–2002	1967–1991	S	S	S/D
South Luangwa	Some poaching on elephant and rhino	1994	2002	no data	S	S	S
Tarangire	Fences stop migration, poaching on black rhino	1994	no data	no data	S	S	S
Tsavo	Some poaching, highway+railway in Park	1991–1997	1991–2002	no data	S/D		D

Animal data

Lions *Panthera leo* and spotted hyenas *Crocuta crocuta* are the main predators of medium-sized ungulates in these ecosystems. Lion and hyena densities were obtained from reports (East 1997a, b, Mills and Hofer 1998, Chardonnet 2002 and Bauer and Van der Merwe 2002), papers (Sinclair and Arcese 1995, Caro 1999, Du Toit et al. 2003 and Kissui and Packer 2004), theses (Bonyongo 2004), and a personal communication (N. Drouet-Hoguet for Hwange). These were based on field studies (60 and 100% of lion and hyena data respectively) or on expert opinion, based on comparisons with densities measured in neighbouring or similar situations (40% of the lion data); data on lion were available for 18 areas, and on hyena for only 10. There is a significant relationship between lion and hyena biomasses: $\log_{10}(\text{HyenaBIOMASS}) = 1.0794 \times \log_{10}(\text{LionBIOMASS}) - 0.0247$ ($n = 10$; $R^2 = 0.7092$; $p = 0.0022$; Shapiro test: $W = 0.8914$, $p = 0.1758$). We therefore consider that lion biomasses are a good indicator of the abundance of large predators (both lions and spotted hyenas), and use data on lions only in the analyses.

Data on ungulate population sizes were compiled from IUCN reports (East 1996a, b, 1997a, b, c, 1999, Moehlman 2002), theses (Bonyongo 2004), published papers (Sinclair 1977, Sinclair and Norton-Griffiths 1979, Prins and Douglas-Hamilton 1990, Dublin et al. 1990, Sinclair and Arcese 1995, Mduma et al. 1999, Du Toit et al. 2003), reports (Zimbabwean Parks and Wildlife Management Authority and WWF for Hwange NP), and a personal communication (S. Van Rensburg for Hluhluwe-iMfolozi). Data from five protected areas where no lion data were available were included to increase the sample size for the analyses of the effect of variations in resource availability. Most of the censuses were aerial counts (83%), but ground counts were used for Hluhluwe-iMfolozi, Lake Manyara, Lake Nakuru, and Nairobi. Censuses are of course subject to errors (bias and precision), but these are likely to induce noise rather than pattern. We used ungulate censuses conducted in the same decade as the estimates of lion numbers, generally the 1990s (Table 1). Populations of large herbivores in some of these areas have varied: in order to obtain representative population sizes comparable with the predator data, we chose periods of relative stability as close as possible to the dates of the predator estimates. In 8 of the 23 near-natural areas several annual population censuses were available (Hluhluwe-iMfolozi, Hwange, Kruger, Lake Manyara, Nairobi, Ngorongoro Crater, Okavango, and Serengeti). We therefore estimated population growth rates (r) and considered that populations were sufficiently stable when $r < 10\%$ (noted as S, S/I or S/D in Table 1). For the other areas we used the IUCN reports, and as far as possible retained periods when the populations were classed as stable: 83% of the populations of the 3 species in the 23 areas were stable during our study periods (Table 1). The periods used for ungulate and predator censuses do not always overlap, but never differ by >9 yr (mean $= 4.8$ yr; range $= 0–9$). This temporal difference could not affect the results strongly, given the stability of the ungulate populations.

Most of the prey of lions are "mesoherbivores" (ungulates weighing 10–1000 kg), so we restricted the analysis to this set of ungulates (giraffes were not included). To determine ungulate and lion biomasses (kg km^{-2}), data on body weights were obtained from a compilation of published data (Appendix 2). We used the mean population body weight – i.e. $\frac{3}{4}$ of female body weight (Owen-Smith 1988).

Statistical analyses

As lion biomass and rainfall are collinear ($\log_{10}$ transformation, $r = 0.6531$, $p = 0.0033$), we have analysed the effects of resource availability ("rainfall" and "SNA") and of lion biomass on the relative abundances of medium-sized herbivores separately. The linear models were tested with the Shapiro test for the normality of residuals.

The effect of rainfall and soil quality on ungulate biomasses

To test for effects of resource availability on ungulate biomasses, we performed analyses of covariance with R-software (< www.r-project.org >). The ungulate biomasses were normalized with a $\log_{10}(x)$ transformation, and the homogeneity of their variances among the classes of soil richness was assessed using Bartlett's test (K-squared $= 2.1869$, DF $= 2$, $p = 0.3351$ for mesoherbivores; K-squared $= 1.771$, DF $= 2$, $p = 0.4125$ for zebra; K-squared $= 0.8903$, DF $= 2$, $p = 0.6407$ for buffalo; and K-squared $= 0.1922$, DF $= 2$, $p = 0.9084$ for wildebeest). The analyses were performed for each species using only the protected areas where they occurred (23 areas for mesoherbivores and zebra, 21 for buffalo, and 17 for wildebeest; Appendix 1).

Predation

We examined the numerical responses (Messier 1994) of lions to the abundance of mesoherbivores, and also to zebra, wildebeest, and buffalo. We first used a non-parametric smoothing program based on locally weighed regressions (LOWESS program; in Crawley 2002) to describe the general tendency of our different numerical responses. The results suggested linear relationships, but with a break in the line. We therefore compared linear

and non-linear responses and selected the best model. We used non-linear regressions which can allow a threshold in the numbers of the lions at higher prey biomasses: the model was $y = \dfrac{b \times x}{a + x}$ where y represents lion biomass, x is prey biomass, b is the asymptote, and a is the value of prey biomass for the lion biomass reaches 50% of the asymptotic value. To estimate the goodness of fit of these regressions, we calculated the % of variance explained by the linear regression of predicted on observed values.

Food selection by lion is described for 5 sites (Etosha, Kruger, Lake Manyara, Ngorongoro Crater, and Serengeti) where data on lion diets were available, by comparing the proportions of zebra, wildebeest, and buffalo in the lion diet with their proportions in the prey populations.

The ratio of "zebra/buffalo and wildebeest" (Z/BW, biomasses) was used to examine the relative abundances of these 3 ungulate species in relation to lion biomass. We used a $\log_{10}$ transformation for our variables (Z/BW ratio and lion biomass) and checked the normality of the residuals.

Results

Rainfall and soil quality

The mesoherbivore model accounted for 72% of the variance (additive model: $F_{3;19} = 16.65$; $p = 1.5 \times 10^{-5}$) and as expected, mesoherbivore biomass increased with rainfall ($F_{1;19} = 20.266$; $p = 0.0002$) and SNA ($F_{2;19} = 14.842$; $p = 0.0001$). The buffalo model accounted for almost half of the variance in the abundance of this species (44%, $p = 0.0276$), with biomass lower on low nutrient soils (349 kg km^{-2}) than on medium and high (1967 and 2326 kg km^{-2}), and also increasing with rainfall ($p = 0.0453$; Table 2). The abundance of wildebeest increased with SNA ($p = 0.0011$) and tended to increase with annual rainfall, but not significantly ($p = 0.0848$; Table 2). The model accounts for 68% of the variance and wildebeest biomasses were much higher in ecosystems with high SNA (2784 kg km^{-2}) compared to medium and poor soils (115 and 48 kg km^{-2}).

For zebra, the model was significant (additive model: $p = 0.0364$), but explained only 35% of the variance:

annual rainfall had no significant effect ($p = 0.2210$), but there was an effect of SNA ($p = 0.0267$; Table 2). As in wildebeest, the abundance of zebra was much higher in areas with high SNA than elsewhere (the mean biomasses were 172, 242 and 1040 kg km^{-2} on low, medium, and high SNA respectively).

Predation

The biomasses of both lions and ungulates in the Ngorongoro Crater were considerably higher than in the other areas; this point is an outlier and has therefore been removed from all our numerical responses. The abundance of lions increased with the biomass of mesoherbivores: the best model was a linear regression which explained 60% of the variance ($b = 0.0019$, $p = 0.0003$; Shapiro test: $W = 0.9402$, $p = 0.3211$; Fig. 1). The abundance of lions therefore increased with that of their prey, within the range 0–9000 kg km^{-2}, and the data from Ngorongoro fitted the pattern of the other points. The patterns for the different species were rather similar: lion numbers increased with wildebeest and tended to do so with zebra and buffalo biomasses (Fig. 2). For wildebeest, the best model was linear ($p = 0.0397$, $R^2 = 0.3585$; Shapiro test: $W = 0.9099$, $p = 0.2130$); the zebra and buffalo models were not significant (respectively $p = 0.1256$, $R^2 = 0.1492$; and $p = 0.0607$, $R^2 = 0.2450$).

Preferences for the 3 species of prey were compared using linear regressions through the origin of the proportion of different prey in lion diets and in the mesoherbivore community (measured in numbers, not biomass; Fig. 3) in the few areas where data were available (Etosha, Kruger, Lake Manyara, Ngorongoro Crater, and Serengeti). The slopes of the regressions for the bovids tended to be weaker than the slope for the zebras, but did not differ significantly from the diagonal (Kolmogorov-Smirnov test: $D = 0.2$ and $p = 1$ for zebra; $D = 0.4$ and $p = 0.873$ for wildebeest; $D = 0.25$ and $p = 1$ for buffalo).

Zebras were the dominant grazing herbivore in 2 systems, Makgadikgadi and Etosha, which had low densities of lions (biomass <1 kg km^{-2}); and across the 18 areas, the ratio of zebras to wildebeest and buffalo decreased significantly as lion biomass increased (linear regression: $b = -0.5204$, $p = 0.0370$ and $R^2 = 0.2444$; Shapiro test: $W = 0.9625$, $p = 0.6503$; Fig. 4).

Table 2. Analyses of covariance of ungulate biomasses with one covariate (mean annual rainfall) and one factor (SNA). Significance codes: * <0.05, ** <0.01, *** <0.001.

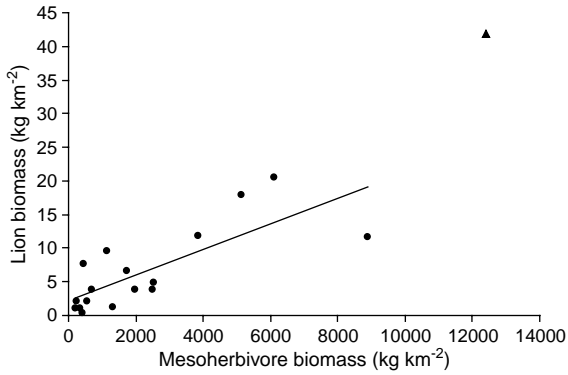| Species	Rain		SNA		Model		
	$F_{(df)}$	p	$F_{(df)}$	p	$F_{(df)}$	p	R^2
Buffalo	$4.6657_{(1;17)}$	0.0453*	$4.4665_{(2;17)}$	0.0276*	$4.5330_{(3;17)}$	0.0165*	0.4444
Wildebeest	$3.4811_{(1;13)}$	0.0848	$12.1311_{(2;13)}$	0.0011**	$9.2480_{(3;13)}$	0.0015**	0.6809
Zebra	$1.6013_{(1;19)}$	0.2210	$4.4127_{(2;19)}$	0.0267*	$3.4760_{(3;19)}$	0.0364*	0.3543

Fig. 1. The linear numerical response of lions to mesoherbivore biomass across 17 protected areas, excluding the outlier, Ngorongoro Crater, represented by a black triangle: $LIONbiomass = 0.0019 \times MESbiomass + 2.1942$ (p = 0.0003; $R^2 = 0.60$).

There was no effect of rainfall on the Z/BW ratio (linear regression: b = −0.0004, p = 0.4840 and $R^2 = 0.0261$; Shapiro test: W = 0.9563, p = 0.4449).

Discussion

The buffalo model, which explained 44% of the variance in the abundance of this species, indicated a limiting effect of food resources – both in terms of quantity and quality. Sinclair (1977) has already shown for 12 east African parks that buffalo density in the 1960s and 1970s increased with mean annual rainfall, and we show here that buffalo are much less abundant on low nutrient soils than on the other types.

Wildebeest were abundant only on rich soils: this difference with buffalo is not surprising as wildebeest are much smaller (wildebeest females weigh 163–180 kg; buffalo females weigh >500 kg, Appendix 2), and
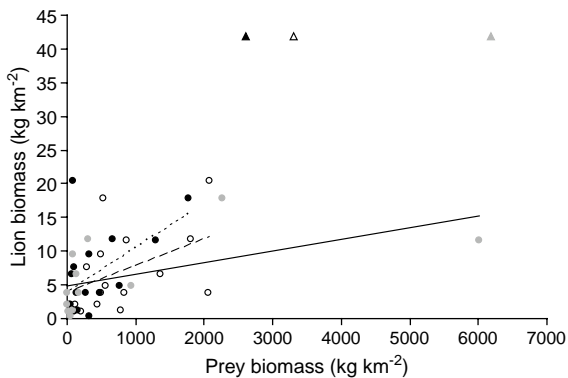

Fig. 2. The numerical responses of lions to the biomasses of three prey species: zebra (black circles; dotted line), wildebeest (grey circles; solid line), and buffalo (open circles; dashed line). The linear models for zebra and buffalo are indicated, but are not significant. The points representing the outlier, Ngorongoro Crater, figure as triangles.
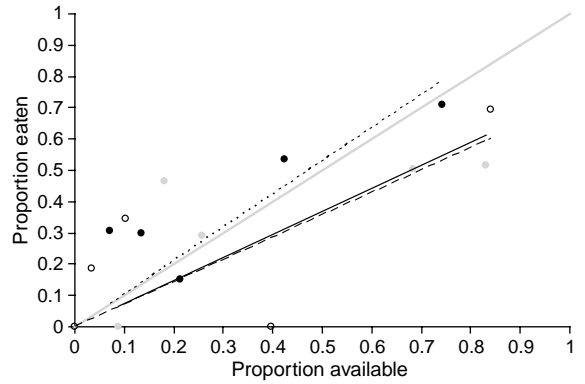

Fig. 3. The proportions of zebra (black circles and dotted line), wildebeest (grey circles and solid line), and buffalo (open circles and dashed line) in the ecosystems and in the lion kills. The proportions are based on numbers of kills, not biomass; the regression lines were forced through the origin; the grey line is the diagonal.

therefore require higher quality forage. Wildebeest survival in the Serengeti is limited by dry season rainfall (Mduma et al. 1999), so it is surprising that the abundance of this ruminant was not affected by rainfall. This is perhaps because the range of rainfall in our sites was small (there are no sites with rainfall <300 mm in the database), and we did not separate dry and wet-season rainfall.

The pattern observed here, which suggests that grazing bovids generally are food-limited, is consistent with the few fine-grained studies of the dynamics of ungulate populations (in particular the buffalo and wildebeest populations in the Serengeti ecosystem [Sinclair 1977, Mduma et al. 1999], although there are exceptions, as wildebeest are limited by disease and predation in Etosha [Gasaway et al. 1996]). This study therefore confirms a previous analysis of data collected before 1980, that the main factor limiting the abundance of
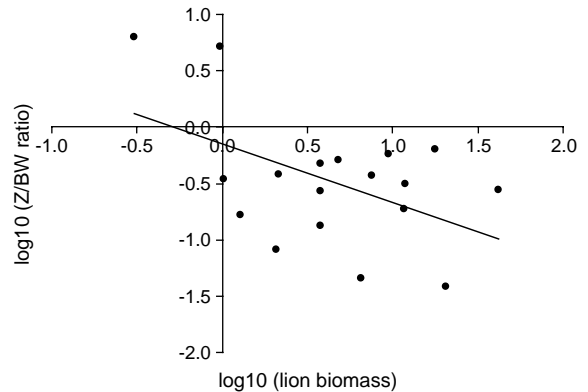

Fig. 4. Linear regression of the ratio of zebra to the sum of the biomasses of buffalo and wildebeest in relation to lion biomass in 18 protected areas: log10(Z/BWratio) = −0.5204 × log10(LIONbiomass) −0.1477; p = 0.0370; $R^2 = 0.2444$.

African ungulates is their food resources, both in amount (via rainfall) and quality (via soil richness; Fritz and Duncan 1994).

Though the range of rainfall studied here had no significant effect, resource quality has some effect on the abundance of zebras, which were more abundant on rich soils. However, the model accounted for only 35% of the variance in zebra biomasses, which indicates that other factors than resources were more important in determining variations in zebra biomass across ecosystems. This result is consistent with observations during the 1973 drought in Nairobi National Park, that hartebeest *Alcelaphus buselaphus* and wildebeest were affected by food shortage more than the zebra (Hillman and Hillman 1977). In Kruger Park too, zebras appear to be less affected by water availability than were grazing ruminants (Redfern et al. 2003).

Lion populations responded positively to the biomass of mesoherbivores with a linear response in at least the range $0-9000 \, \mathrm{kg \, km^{-2}}$, suggesting that lions generally were limited by prey biomass. Lions can be limited by severe disease outbreaks, as occurred in the Ngorongoro Crater (Kissui and Packer 2004); this effect appeared to be density-dependent, and occurred when the density was >400 lions/1000 $\mathrm{km^2}$. The numerical response we have found across ecosystems is consistent with their response in the Serengeti ecosystem to the strong increase in the numbers of ruminants in the 1970s; lion and hyena numbers increased by 100 and 135%, respectively, between the early 1970s and 1990s (Hofer and East 1995, C. Packer pers. comm.). More generally, the community of large mammalian predators in African savannas shows an apparently linear numerical response to increases in the abundance of large herbivores (East 1984).

The lion numerical response may be linear for wildebeest; one data point (the Serengeti, bottom right corner of the graph, Fig. 2) is very low, which is not surprising as the migration in the Serengeti ecosystem reduces the availability of wildebeest to lions (Mduma et al. 1999). Lions tend to increase with zebra and buffalo numbers too, but not significantly. These apparently linear numerical responses for different prey species and for the ungulate community mean that lion populations do not show saturation.

Interestingly the abundance of lions is unrelated to the diversity of the prey community (multiple regression with mesoherbivore biomass and H; $R^2 = 0.6538$, p = 0.0001 for mesoherbivore biomass, and p = 0.4388 for H, where H is the Shannon index of diversity). This result implies that the abundance of prey is more important than the species composition of the community for this generalist predator.

The linear numerical response of lions to increases in the abundance of their prey allows them to reach high densities, over 100 lions per 1000 $\mathrm{km^2}$ in Lake Nakuru,

Nairobi, Kruger, Hluhluwe-iMfolozi, and the Serengeti ecosystems and over 400 lions per 1000 $\mathrm{km^2}$ in Ngorongoro Crater. This is in striking contrast to the non-linear response of another mammalian predator, the wolf *Canis lupus*, to their main prey, moose *Alces alces*. Wolf numbers increase sharply at low moose densities and then reach a plateau at ca 60 wolves per 1000 $\mathrm{km^2}$ (Messier 1994), presumably limited by social behaviour. In wolf societies, the alpha female breeds and subordinate females are non-breeding helpers (Mech 1970); in lion societies, all females in the pride can breed. Though there is no evidence for a limiting effect of social behaviour in lion populations, disease may come into play when densities are very high (Kissui and Packer 2004).

The limited data available on lion diets in relation to the availability of the different prey species show no evidence for consistent selection or avoidance of any of these three ungulates. There is a suggestion that the 2 bovids may have been under-used, which apparently was not the case for zebras.

The Z/BW ratio declined with increasing lion biomasses. Zebras were more abundant than grazing bovids in only 2 of these ecosystems, Etosha and Makgadikgadi, which had very low densities of lions, and thus a low predation pressure on medium-sized ungulates. This effect is unlikely to be an artefact due to a negative correlation between zebra and grazing bovid biomasses since these are positively correlated: $\log_{10}(\mathrm{Zbiomass}) = 0.3964 \times \log_{10}(\mathrm{BWbiomass}) + 1.1943$ (p = 0.0074; $R^2 = 0.2951$; Shapiro test: W = 0.9408, p = 0.1868). Further rainfall had no effect on the ratio (see Results).

Though this model explains only 24% of the variance in the relationship between lions and the Z/BW ratio, it suggests, as expected, that predation had a stronger effect on zebras than on grazing bovids. The mechanism could be a greater availability of zebras compared to wildebeest, spatially and temporally. The spatial distribution of wildebeest is more clumped: this is very clear in Serengeti (Maddock 1979), but it is also true in dystrophic ecosystems (Redfern et al. 2006). Since the minimum inter-foal interval in zebras is 13 months (Klingel 1969), zebra mares cannot produce successive foals in the same season, and zebra foals are available to predators throughout the year. Conversely, wildebeest and, to a lesser extent buffalo, show strong birth synchrony (Sinclair et al. 2000) with the majority of births occurring at the beginning of the wet season.

Although predator-prey relationships at the local scale are clearly variable, this analysis at a regional scale suggests that there is a general principle: zebra are more strongly influenced by lion predation than are these grazing bovids. An experimental approach would of course be ideal to demonstrate this: since this obviously is not feasible, analysis of long-term data sets on

ungulate population trends before and after important variations in predator densities (due to removals or disease outbreaks) would be a useful test of this principle.

In this paper we have considered the effects of variations in resources and predation on the abundance of these species, but other factors we have not been able to consider here, such as parasites, diseases, and social factors, may play important roles too. Little information is available on the impact of diseases on zebra population dynamics: anthrax was reported during the 1990s in Etosha, Kruger, South Luangwa, and Tarangire (Moehlman 2002). However, anthrax affects bovids too, and there is no suggestion that zebras are more sensitive to this disease. Equine diseases have been reported in Kruger and Nairobi (African Horse Sickness), and Etosha (Equine Encephalosis Virus), but zebra are not known to show clinical effects, and zebra biomasses are not particularly low within these parks. Social factors are another possibility: infanticide has been noted in captive plains zebra (Pluhacek and Bartos 2000), as well as in wild horses (Berger 1986), but not yet in zebras in the wild.

In conclusion, this study has clarified the interactions between large mammal herbivores, their resources, and their predators in savanna ecosystems. The relative abundances of zebra and grazing bovids vary widely among ecosystems, and result from the action of "top-down" and "bottom-up" ecological processes whose strength varies. First, wildebeest, as expected, appeared to be more closely tied to the resources than were zebra; buffalo were intermediate. The abundance of hyenas was closely and positively correlated with that of lions. The numerical response of lions, our proxy for predation pressure, to mesoherbivores was close to a type I (linear), so it is possible that their densities are limited by prey availability, at least until they reach very high densities. Zebras were more abundant than wildebeest and buffalo in ecosystems with low lion densities. The mechanism involved may not simply be a selection for zebras, but could be linked to their greater spatial and temporal availability. The results of this study suggest that the role of predation is particularly important for zebras; if this is true, in ecosystems where predator numbers (particularly lions) decline strongly (e.g. as a result of predator control), zebras should increase faster than grazing bovids.

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