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What limits the Serengeti zebra population?

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Abstract The populations of the ecologically dominant ungulates in the Serengeti ecosystem (zebra, wildebeest and buffalo) have shown markedly different trends since the 1960s: the two ruminants both irrupted after the elimination of rinderpest in 1960, while the zebras have remained stable. The ruminants are resource limited (though parts of the buffalo population have been limited by poaching since the 1980s). The zebras' resource acquisition tactics should allow them to outcompete the ruminants, but their greater spatial dispersion makes them more available to predators, and it has been suggested that this population is limited by predation. To investigate the mechanisms involved in the population dynamics of Serengeti zebra, we compared population dynamics

among the three species using demographic models based on age-class-specific survival and fecundity. The only major difference between zebra and the two ruminants occurred in the first-year survival. We show that wildebeest have a higher reproductive potential than zebra (younger age at first breeding and shorter generation time). Nevertheless, these differences in reproduction cannot account for the observed differences in the population trends between the zebra and the ruminants. On the other hand, among-species differences in first-year survival are great enough to account for the constancy of zebra population size. We conclude that the very low first-year survival of zebra limits this population. We provide new data on predation in the Serengeti and show that, as in other ecosystems, predation rates on zebras are high, so predation could hold the population in a "predator pit". However, lion and hyena feed principally on adult zebras, and further work is required to discover the process involved in the high mortality of foals.

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Introduction

An important aspect of community ecology is to understand the mechanisms which structure multi-species assemblages in natural ecosystems. Large mammal herbivores are of particular interest because they are commonly "keystone" species, so variations in the species composition of ungulate communities can have powerful impacts on the structure and functioning of whole ecosystems. Ungulate communities in Africa are the richest of any continent, with about 100 species, which are mostly bovids (75%), though equids coexist with them in virtually all ecosystems (Cumming 1982). A well-known example is the Serengeti ecosystem (Tanzania) which has high biodiversity and where long-term data are available on ungulate populations. The two dominant bovids are the wildebeest, *Connochaetes taurinus*, and

buffalo, *Syncerus caffer*, which coexist with one equid (plains zebra, *Equus burchelli*).

In the early 1960s, the numbers of zebra and wildebeest in the Serengeti were about the same (ca. 200,000). These two species that have evolved in parallel have similar body size, and very similar patterns of resource use (Gwynne and Bell 1968; Maddock 1979; Hansen et al. 1985). These ecological similarities mean that there is a potential for interspecific competition for food resources between plains zebra and wildebeest (Bell 1970; Sinclair 1977; De Boer and Prins 1990). Before 1960 the Serengeti populations of wildebeest and buffalo were limited by rinderpest, a viral disease. After its eradication in the early 1960s these two ruminant populations grew exponentially (Sinclair 1977; Mduma et al. 1999) until limited by resources (or poaching) after 1980 (Dublin et al. 1990). The zebra population, which was unaffected by rinderpest, remained remarkably constant in size during this period (Fig. 1). The exponential increase in wildebeest and buffalo proves that in 1960 the community of grazers in the Serengeti was not at carrying capacity, and that they were not resource limited at that time. As the foraging tactics of equids can allow them to acquire nutrients at much higher rates than bovids, zebra should have a competitive advantage over ruminants in grassland ecosystems, so we would expect that when food became limiting in the 1980s zebra should have outnumbered the ruminants (Duncan et al. 1990; Ménard et al. 2002). In spite of this physiological advantage, the Serengeti zebras have remained at the same population level since 1960. In particular the zebra population did not decrease when the populations of these two ruminants increased sharply, reaching in 1972 a biomass 4 times higher than in 1962: interspecific competition for resources clearly did not have a major impact on the Serengeti zebra population. The differences in population trends observed after 1960 suggest that the zebra population was not influenced by the same limiting factors as wildebeest and buffalo (Sinclair and Norton-Griffiths 1982).

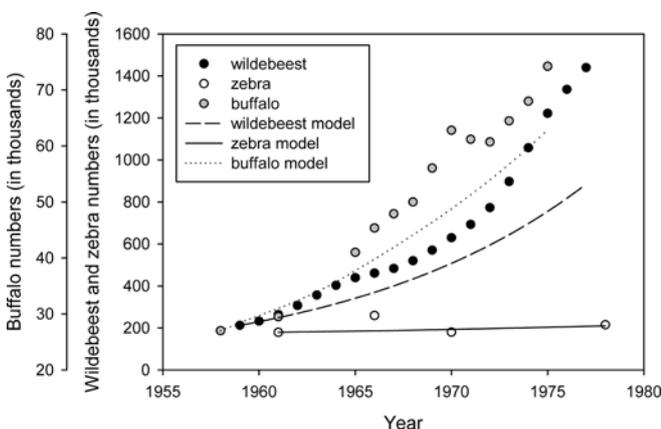


Fig. 1 Population sizes (*symbols*) and model simulations (*lines*) of wildebeest, zebra and buffalo populations between 1958 and 1978. The population sizes are given by Mduma et al. (1999), Sinclair and Arcese (1995) and Sinclair (1977)

Two major processes determine the abundance of animal populations: resource competition (a “bottom-up” process) and/or predation (a “top-down” process; Hairston et al. 1960). In the Serengeti ecosystem long-term studies on buffalo (Sinclair 1974, 1977) and wildebeest (Sinclair et al. 1985) demonstrated that predation did not have a major impact on these populations which were mainly regulated by food supply, especially during dry years.

Little information is available on plains zebra demography in the Serengeti ecosystem. A comparative analysis based on the dynamics of 12 ungulate populations in the Kruger National Park (South Africa) demonstrated that zebras are less sensitive to droughts than most bovids (Ogutu and Owen-Smith 2003). Another study in the Kruger National Park demonstrated that in comparison to buffalo and wildebeest, zebra showed a weaker trade-off between nutritional requirements and surface-water constraints (Redfern et al. 2003). These studies suggest that zebra should be less sensitive to resource limitation compared to ruminants. In Laikipia District (Kenya), where the density of large predators is about 5 times lower than in the Serengeti ecosystem (Bauer 2003), rainfall, and consequently resource availability, strongly influences the abundance of plains zebras (Georgiadis et al. 2003). Conversely in Etosha National Park, periods of low rainfall have no influence on the zebra population which seems to be mostly limited by predation (Gasaway et al. 1996), and where predators are abundant, zebras do suffer heavy predation, notably the young age-classes (Cooper 1990; Mills and Shenk 1992). For the Serengeti, the abundance of large predators and the behaviour of the zebras and their population trends suggest that this population may be mainly limited by predation (Sinclair 1985)

The life history tactic of a species can constrain the response of the population to environmental pressures, and thereby population trends. Perissodactyls breed later, have longer gestation periods and lower fecundity compared to Artiodactyls of similar size (Van Wieren 1996). Both the rate of recruitment and the maximum rate of increase should therefore be lower in zebra populations than in similar-sized Artiodactyls. Such a constraint may strengthen the effect of other factors, like predation, to limit zebra population sizes. We therefore expect zebra to show dampened responses to environmental variations compared with the more productive wildebeest and buffalo, because variation in population size over time is positively related to population growth rate (Sinclair 1997).

In this paper we used the long-term data from the Serengeti ecosystem to clarify the issue of the limitation of the zebra population by testing the following predictions:

1. According to the predation hypothesis, zebra should have lower survival rates than the ruminants, especially during their first year when they are most sensitive to predators.
2. Zebra should have lower fecundity and a longer generation time than these ruminants.

Table 1 Vital rates used in the buffalo, wildebeest, and zebra models. The data for zebra juveniles are given with 95% confidence intervals

Parameter	Age-classes	Species		
		Buffalo ^a	Zebra ^{b, c}	Wildebeest ^d
Survival	First year	0.670	0.389 (0.297–0.480)	0.746
	Yearling	0.860	0.847 (0.724–0.970)	0.885
	2 Year olds	0.981	0.979	0.865
	3–5 Year olds	0.971	0.954	0.888
	Mature female	0.927	0.875	0.792
	Senescent female	0.599	0.768	0.780
Fecundity	2 Year olds	0	0	0.371
	3–5 Year olds	0.200	0.686	0.889
	Mature female	0.820	0.883	0.945
	Senescent female	0.660	0.883	0.945

^aSinclair (1977)

^bA. R. E. Sinclair (unpublished data)

^cR. O. Skoog and P. J. P. Gogan (unpublished data)

^dWatson (1967)

We built demographic models for buffalo, wildebeest and zebra, and then compared the population trends obtained from modelling with those observed from censuses. We used demographic simulations to determine which vital rates could account for the striking differences observed in population kinetics between zebra and the two ruminant species. Finally, in order to test whether the ecological mechanism involved could be predation, we estimate the offtake of zebras by predators.

Materials and Methods

Study area

The Serengeti ecosystem is in southern Kenya and northern Tanzania, and covers 25,000 km² (34–36°E, 1°15′–3°30′S). Rainfall shows a north-west to south-east gradient, decreasing from 1,100 to 500 mm and is seasonal with the wet season between November and June. This ecosystem is characterised by large herds of migrating ungulates, and also by high concentrations of large predators, with approximately 0.3 hyaenas/km² and 0.1 lions/km² (Sinclair and Norton-Griffiths 1979; Sinclair and Arcese 1995).

Aerial and ground censuses of ungulate populations

Aerial and ground censuses of wildlife populations have been conducted from 1958 to 1999. Aerial censuses were performed by a pilot and one or two observers in each aircraft. Total counts were used for buffalo: each herd size was estimated from the air, and most herds were also counted on aerial photographs. The latter counts were used, except where photographs were not available. The wildebeest population censuses were based on aerial transects on each of which about 20 vertical photographs were taken at known altitude. The density of animals was calculated for each photo, and the population size calculated using Jolly's method (1969; see Mduma et al. 1999 for details). Population structure (sex and age-class) was determined for buffalo from aerial and ground censuses, using a method based on horn shape and size (Sinclair 1977). The wildebeest and zebra population structures were obtained from ground counts (Watson 1967; Mduma et al. 1999; A. R. E. Sinclair, personal observation).

We restricted our analyses to the phase of exponential growth for wildebeest and buffalo populations: 1958–1978 (Fig. 1). To test the validity of our models, we estimated the finite rate of increase (λ) from census data using the regression method for buffalo and wildebeest:

$\ln N = a + \ln \lambda \times t$ (Lebreton and Millier 1982; where a is a constant, and N represents the total population size in year t).

As there were only four zebra censuses between 1961 and 1978, we used another estimator for this population: $\lambda = (N_t/N_0)^{1/t}$ (Lebreton and Millier 1982; where N_0 represents the initial population size, N_t the population size in year t , and t is the number of years).

Vital rates

Estimates of survival and fecundity rates for zebra and the two ruminants from the long-term studies in the Serengeti are given in Table 1.

Buffalo

Pregnancy rates were estimated from examination of female reproductive tracts ($n=69$, from shot samples between 1967 and 1969); care was taken to avoid bias with respect to sex and age-classes (Sinclair 1977). Survival rates of female buffalo were obtained from a life table (Sinclair 1977) constructed during the exponential stage of population increase (246 female skulls collected between 1965 and 1969). Age determination was based on the tooth-eruption pattern (Grimsdell 1973) and horn shape. Mortality rates were estimated from the life table, taking into account the exponential growth rate of the population ($r=0.077$).

Wildebeest

Pregnancy rates were estimated from shot samples between 1964 and 1966: 153 cows from the Serengeti population were shot by National Park Wardens. Female survival and fecundity rates were obtained from a life table derived from the age distribution of female deaths over the period 1962–1965 in the Serengeti ecosystem (Watson 1967, 1969).

Zebra

Zebra pregnancy rates were calculated from 178 females shot by the Tanzania Game Department in 1969–1971 (Table 2) and age structure of adult females during the same period derived from ground counts and the shot sample (R. O. Skoog and P. J. P. Gogan, unpublished data). Survival estimates were also calculated from data collated for the Loliondo zebras (one of the four subpopulations in the Serengeti ecosystem; R. O. Skoog and P. J. P. Gogan, unpublished data; Table 3). We built a life table based on the shot sample age structure, assuming that this sample was not biased and was representative of the age distribution in the living population. The number of foals was corrected and estimated from the number

Table 2 Age structure and pregnancy rates for female zebra in the Serengeti ecosystem

Age-class	Age (years)	Percentage of adult females ($n=134$)	Number of females	Percentage pregnant	Pregnancy rate
Subadults	3–5		33	68.6	0.686
Adults	5–8	0.51	65	81.5	
	9–12	0.36	45	93.3	
	13–16	0.08	10	90	0.883
	17–20+	0.05	7	85.7	
	Not aged		18	100	

of reproductive females in the sample and their fecundities, and the proportions of individuals surviving at the start of each age class (l_x) were smoothed by a polynomial regression. The life table provided adult survival estimates (>2 year olds) for zebra females, consistent with the estimates calculated by Spinage (1972) for the Akagera zebra population. We therefore assumed that these estimates are sufficiently accurate because adult survival rates are rather resilient to environmental variation in ungulates (Gaillard et al. 1998, 2000 for reviews). The trends in the two populations were similar since the Akagera zebra population was near stationary in the 1960s (Spinage 1972), while the Serengeti population may have declined slightly between 1961 ($n=179,000$, Sinclair and Norton-Griffiths 1979) and 1996 ($n=150,834$, Moehlman 2002).

For Serengeti plains zebra, no individually based estimates of foal and yearling survival are available. As these vary widely both between and within ungulate populations (Gaillard et al. 1998, 2000 for reviews), we used data on the Serengeti zebra population structure: over 20 years a sample of the population was classified by one observer (A. R. E. Sinclair) into adults, yearlings and foals on the basis of their shoulder height, using criteria from H. Klingel (personal communication; Table 4). We estimated the survival rates from variations in the proportions of foals and yearlings in successive years (see Appendix) since more accurate estimates are not available, recognizing that these estimates are subject to error.

We tested for effects of rainfall on zebra age structure between 1980 and 1999 using logistic models to analyse variations in foal or yearling proportions in relation to season (dry vs. wet) and rainfall (annual rainfall and dry season rainfall). The rainfall data are from the Banagi station, approximately in the centre of the Serengeti National Park; the year was taken as November–October and the dry season as May–October, and data are available for all the years except 1991.

Modelling

Population models

We used pre-breeding models based on Leslie matrices (Caswell 2001). Each population was divided into six age-classes: calf or foal (the first year of life), yearlings (1–2 year olds), 2 year olds (2–

Table 3 Shot sample of females from the Loliondo zebra population (1969–1970)

Age-class	Number of shot females ($n=205$)
Foals	4
Yearlings	15
2 Years	14
3 Years	20
4 Years	18
5–8 Years	68
9–12 Years	48
13–16 Years	11
17–20+ Years	7

3 year olds), 3–5 year olds, mature females (5–11 year olds for buffalo, and 5–13 year olds for zebra and wildebeest), and senescent females (>11 year olds for buffalo, and >13 year olds for zebra and wildebeest; Table 1).

The models are based on females, assuming that male numbers are not limiting. We also considered an equal sex ratio at birth (see Sinclair 1977 for buffalo; Watson 1967 for wildebeest). For the three species, fecundity was assumed to be equal to the pregnancy rate. This assumes that very little resorption or abortion occurred: the incidence of Brucellosis is low in Serengeti ruminants and absent in zebras (Sinclair 1977).

Simulations were performed using the ULM software (Legendre and Clobert 1995). For each population, an elasticity analysis was performed on the survival rates of first-year animals, yearlings and adults, and on female fecundity (>3 year olds for buffalo and zebra, >2 year olds for wildebeest). For each simulation, outputs are the estimated population size (in successive years) and the λ . We also used ULM to estimate demographic outputs such as the natural rate of increase (r) and the generation time (sensu Leslie 1966), denoted as \bar{T} .

Simulations

We used the models to simulate the effects of variations in the first-year survival. According to the predation hypothesis, we predicted that:

1. Replacing foal survival in the zebra model with estimates of calf survival for wildebeest or buffalo should lead the zebra population to increase strongly.
2. Replacing calf survival in the wildebeest or buffalo models with estimates of zebra foal survival should lead the wildebeest and buffalo populations to stop growing.

We then tested the demographic impact of switching reproductive parameters among species. Since zebra fecundity should be lower and generation time longer, we predicted that:

1. Replacing the reproductive rates of buffalo and wildebeest with the zebra values should lead the wildebeest and buffalo populations to stop growing.
2. Replacing reproductive rates of zebra with the buffalo and wildebeest values should lead the zebra population to increase.

The impact of lion and hyena predation on wildebeest, zebra and buffalo in the Serengeti ecosystem

Lions and hyenas account for about 85% of the predation on large herbivores in the Serengeti (Schaller 1972), so we focus our analysis on these two species. The functional and numerical responses of the predators to the increase in the ruminant populations cannot be described in detail, but data are available on changes in the diet and numbers of lions and hyenas between the late 1960s (referred as pre-1970) and the period of peak numbers of the ruminants (post-1975). The impact of predation is measured as the annual offtake of each prey species (numbers of herbivores killed by lions and hyenas) and can be expressed as a percentage of the prey population size.

Table 4 Data on sex/age structure of zebra herds in the Serengeti ecosystem between 1980 and 1999; with mean annual rainfall (*Annual*) and dry season rainfall (*Dry*)

Year	Month	Season	Foals	Yearlings	Adults	Total sample	Percentage of foals	Percentage of yearlings	Annual (mm)	Dry (mm)
1980	5	Wet	517	327	2,846	3,690	0.140	0.089	581.4	48.3
1982	5	Wet	685	616	2,978	4,279	0.160	0.144	716.5	55.9
1983	7	Wet	439	464	1,933	2,836	0.155	0.164	610	165
1984	8	Dry	453	352	1,946	2,751	0.165	0.128	410	146
1986	5	Wet	705	667	3,025	4,397	0.160	0.152	675	88
1987	9	Dry	549	606	2,566	3,721	0.148	0.163	763	61
1987	11	Dry	115	137	292	544	0.211	0.252	763	61
1988	6	Wet	97	118	627	842	0.115	0.140	656	186
1989	2	Wet	311	256	1,835	2,402	0.129	0.107	856	135
1989	7	Wet	531	525	2,710	3,766	0.141	0.139	856	135
1990	2	Wet	406	360	2,662	3,428	0.118	0.105	785	41
1990	6	Wet	286	115	883	1,284	0.223	0.090	795	41
1991	1	Dry	194	114	935	1,243	0.156	0.092		
1992	7	Wet	83	97	495	675	0.123	0.144	815	118
1993	1	Dry	187	102	918	1,207	0.155	0.085	705	77
1993	6	Wet	146	91	637	874	0.167	0.104	705	77
1994	1	Dry	76	93	666	835	0.091	0.111	943	98
1994	4	Wet	82	173	1,027	1,282	0.064	0.135	943	98
1994	11	Dry	53	50	652	755	0.070	0.066	943	98
1997	7	Wet	333	261	1,469	2,063	0.161	0.127	856.9	117
1998	12	Dry	16	6	68	90	0.178	0.067	822	116
1999	7	Wet	52	29	153	234	0.222	0.124	614	110

Table 5 Changes in the numbers of different prey species in the diets of lions between the pre-1970 and the post-1975 periods (Schaller 1972; C. Packer, unpublished data)

Prey species	Lion diet (%)	
	Pre-1970	Post-1975
Wildebeest	20–25	41
Zebra	30	24
Buffalo	15	15

An estimate of the offtake of wildebeest, zebra and buffalo by lions in the pre-1970 period is provided by Schaller (1972), based on an estimate of the amount of prey consumed per lion per day (kg), the number of lions, their diet (percentage of kills) and the average body mass of the different prey. We estimated the offtake for the period post-1975 using the same method, taking into account the increase of about 40% in the lion population since the pre-1970 period (C. Packer, unpublished data) and the diet of the lions in the period of peak numbers of ruminants (post-1975; see Table 5).

For hyena predation, we used the estimates for the pre-1970 and the post-1975 periods (H. Hofer and M. East, unpublished data) and applied the same method as Kruuk (1972) to calculate the offtake of different prey species (Table 6). We took into account changes in hyena diet between our two study periods (Table 7) and the strong increase in hyena numbers (133% of increase between our two study periods; H. Hofer and M. East, unpublished data), which lead respectively to 3,285,000 and 7,654,050 kg of prey consumed by hyena in the pre-1970 and in the post-1975 periods.

We used 200,000 for the zebra population size during the whole study period, 490,000 and 1,200,000 wildebeest and 48,000 and 74,000 buffalo, respectively in the pre-1970 and in the post-1975 periods (see Sinclair 1977; Sinclair and Arcese 1995; Mduma et al. 1999).

Table 6 Comparison of the combined off-take of zebra, wildebeest and buffalo by lion and hyena between the pre-1970 and the post-1975 periods (data from Schaller 1972; Kruuk 1972; Hofer and East 1995; C. Packer, unpublished data; H. Hofer and M. East, unpublished data)

	Pre-1970			Post-1975		
	Wildebeest	Zebra	Buffalo	Wildebeest	Zebra	Buffalo
Lion	14,028	10,834	2,115	35,786	12,135	2,961
Hyena	8,475	5,310	161	24,135	4,285	4,728
Total	22,503	16,144	2,276	59,921	16,420	7,689

Table 7 Changes in the numbers of different prey species in the diets of hyenas between the pre-1970 and the post-1975 periods (Kruuk 1972; H. Hofer and M. East, unpublished data)

Prey species	Hyena diet (%)	
	Pre-1970	Post-1975
Wildebeest	19.4–43.8	49
Zebra	19.4–20.0	8.7
Buffalo	0.6	9.6
Gazelle	48.6–21.9	14.5
Others	12.1–13.7	18.3

Results

Temporal variation in zebra age structure

There was no significant effect of “season” on the proportion of foals (Table 8). Between 1980 and 1999, the proportion of foals was strongly and negatively

Table 8 Logistic models with young zebra proportions (foals and yearlings). For abbreviations, see Table 4

Logistic model	Factor	Estimate	SE	Z-value	P-value
Foal proportion	Season	0.04190	0.03328	1.259	0.2080
	Annual	-0.00081	0.00011	-7.445	<0.0001
	Dry	-0.00075	0.00033	-2.276	0.0229*
Yearling proportion	Season	-7.076e ⁻²	3.442e ⁻²	-2.055	0.0398*
	Annual	-1.036e ⁻⁵	1.120e ⁻⁴	-0.093	0.9263
	Dry	1.511e ⁻³	3.481e ⁻⁴	4.340	<0.0001

*P<0.05

influenced by the mean annual rainfall, so in wet periods the proportion of foals declined. The same pattern, but much weaker, was observed with dry season rainfall.

For yearlings there was a weak and barely significant effect of season, with higher proportions of yearlings in the wet season. In contrast to the foals, there was a strong positive relationship with the dry season rainfall (Table 8).

Vital rates and population models

Wildebeest females may calve at 2 years of age, 1 year before zebra and buffalo females. Adult fecundity differed little among the species, except for 3–5 years old buffalo, which had lower fecundity than the other two species. Adult zebras showed intermediate fecundity compared to the ruminants. The age-dependent survival rates were similar among species except for first-year animals (Table 1): the ruminants were about twice as likely to survive over their first year of life as zebra.

The estimates of λ obtained from modelling matched closely those calculated from censuses but for wildebeest the matrix model led to a slight underestimate of the observed rate of population increase (Table 9).

These simple demographic models led to patterns broadly consistent with the observed trends. The first prediction, that survival is lower in young zebras than in wildebeest and buffalo, is supported. On the other hand, we did not find support for the second prediction as the fecundity of the zebra was intermediate between the values for the two ruminants.

Elasticity analysis and generation time

Elasticities of first-year and adult survival rates, and of adult fecundity (all reproductive age-classes combined) were similar for the three species: adult survival consistently showed the highest elasticity, indicating that this demographic parameter has the greatest potential influence on the population growth rate for these ungulates. For buffalo, the elasticity of adult survival was approximately 0.60, and 0.13 for calf survival and adult fecundity. Zebra and wildebeest showed similar values: the elasticities of adult survival were both 0.64, and the values for first-year survival and adult fecundity were 0.12 (for zebra) and 0.18 (for wildebeest).

The generation time (\bar{T}) for the wildebeest population was the shortest ($\bar{T} = 5.55$ years) and the zebras' the longest ($\bar{T} = 8.24$ years) (Table 9), which is in agreement with our expectation that, for similar body sizes, population renewal rates in Perissodactyls are slower than in Artiodactyls.

Simulating the effect of changing vital rates among species

When we replaced the zebra foal survival with estimates from the ruminants, the zebra population increased strongly (Fig. 2), with a λ varying from 1.010 to 1.085 and 1.102, respectively, with buffalo and wildebeest calf survival. When we replaced the calf survival of buffalo and wildebeest with the value for zebra foals, both the ruminant populations decreased, and the λ s declined from 1.052 to 0.982 for buffalo and from 1.083 to 0.975 for wildebeest.

When we replaced the reproductive rates of buffalo with the zebra values, the buffalo population increased faster, with λ increasing from 1.052 to 1.108. Conversely, when we replaced the reproductive rates of the wildebeest with zebra values, the wildebeest population increased more slowly, with its λ changing from 1.083 to 1.041. When we replaced the reproductive rates of zebra with those of ruminants, the zebra population λ (1.010) declined to 0.972 (with buffalo values) or increased to 1.032 (with wildebeest values; Fig. 3).

These simulations support the first prediction stemming from the predation hypothesis, that the differences in first-

Table 9 Demographic output of population functioning for buffalo, wildebeest and zebra models

Models	λ (census)	λ (model)	Rate of increase (r)	Generation time (\bar{T})
Buffalo	1.063	1.052	0.051	7.56
Wildebeest	1.109	1.083	0.079	5.55
Zebra	1.011	1.010	0.010	8.24

Natural rate of increase (r): $\sum(e^{-rx}l_xm_xdx)=1$ Finite rate of increase: $\lambda=e^r$ Mean generation length: $\bar{T} = \sum(xe^{-rx}l_xm_xdx)$

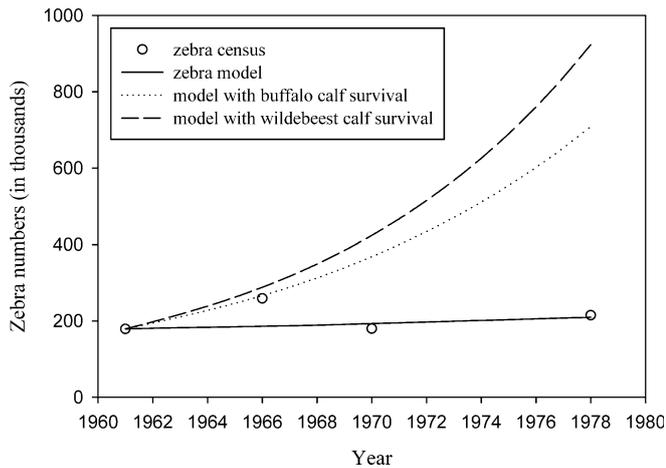


Fig. 2 Simulations of the zebra population using first-year survival values from the two ruminants

year survival between the zebra and the two ruminants are sufficient to account for the observed constancy of zebra population size. The second prediction is rejected, as the reproductive parameters of zebra led them to increase faster than buffalo.

Estimating the annual off-take of wildebeest, zebra and buffalo by lions and hyenas

The lions responded to the increase in the wildebeest population functionally and numerically. In the latter period wildebeest accounted for 41% of the kills, and the estimated numbers killed more than doubled, while the numbers of zebra killed changed very little (Table 6). There was little variation in the numbers of buffalo killed by lions between the two study periods.

The hyenas showed a functional response to the increase in both ruminant populations, showing a particularly strong response for buffalo which accounted for 10% of the hyena diet in the post-1975 period (Table 7). Between the two periods, the numbers of wildebeest killed more than doubled, whereas the numbers of zebra killed decreased slightly (Table 6).

As a consequence the estimated off-take of wildebeest by both predators more than doubled between the two study periods, from close to 22,500 in the pre-1970 period to 60,000 in the second period, accounting for about 5% of the wildebeest population in both periods. For buffalo the impact of lion and hyena predation more than tripled between the late 1960s and the 1980s, accounting for 5 and 10% of buffalo population, respectively.

The estimated numbers of zebra killed showed little change, from 16,100 to 16,400. Predation represented a higher proportion of the zebra population (about 8%) than of the wildebeest. Taking into account the potential number of newborn and the mortality of foals, yearlings and adults, we estimate that about 56,000 of the 200,000 zebra die each year. Natural predators therefore account for about 30% of the annual mortality of zebras.

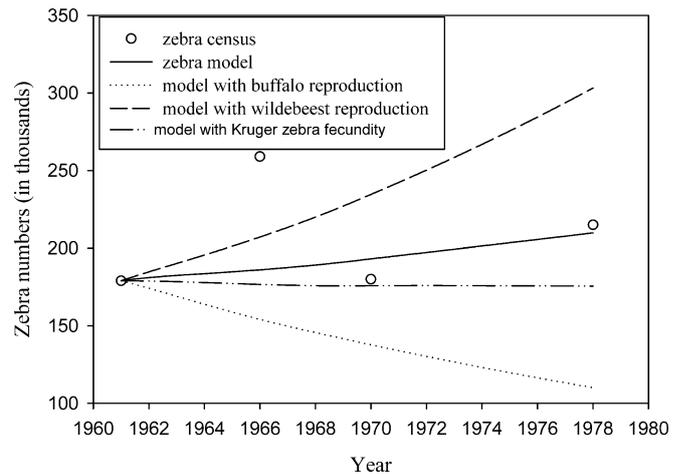


Fig. 3 Simulations of the zebra population using values of reproductive parameters from the two ruminants and from zebra in the Kruger National Park ($f=0.79$, in Smuts 1976)

Discussion

The long-term studies conducted in the Serengeti provide data from which we have estimated rates of fecundity and survival, and built age-structured models for the three species of ungulates. Our population models are based on similar age-classes so comparisons among the species are valid; and we can take into account the decrease in vital rates due to senescence, so the estimates of vital rates during the prime age stage should be unbiased (Loison et al. 1999; Festa-Bianchet et al. 2003). For the wildebeest model we used vital rates estimated at the beginning of their exponential increase (1962–1965), which could have led to an underestimation of the finite rate of increase during the accelerated increase which occurred after 1970. Nonetheless, the simulations derived from these deterministic models lead to patterns broadly consistent with the observed trends, so it is likely that the estimates of the vital rates are reasonably accurate. We discuss first the demographic processes involved, and then the ecological ones.

Demographic processes

The values of the fecundity rates of the ruminants are similar to those in other populations (Gaillard et al. 2000 for a review), but the zebra values are high [e.g., the adult fecundity was 0.79 in the Kruger population (Smuts 1976) compared with 0.88 here]. It is possible that the Serengeti value is overestimated, as the animals were shot by Game Department staff, without any particular procedure to avoid bias as in the other studies. However applying the Kruger value did not change the conclusions of our analysis: the zebra population was constant in size ($\lambda=1.000$; Fig. 3). The reproductive values of zebra were not low enough to stop the increase in the ruminant populations, and the ruminant reproductive rates did not lead to a strong increase in zebra numbers. The differences

in reproductive parameters (age at first reproduction and fecundity) among these species can therefore not account for the differences in population trends between the zebra and the ruminants. The differences found in reproductive traits appear mainly to reflect body size differences, as the reproductive potential of the zebra was intermediate between those of buffalo and wildebeest. The prediction that differences in life history traits between Perissodactyls and Artiodactyls contributed to the constancy of the zebra population size can therefore be rejected.

The only obvious difference in vital rates between the zebra and the ruminants concerns the first-year survival: the zebra value (0.389; Table 1) is about a half of that of the two ruminants and the upper limit of the confidence interval is below both ruminant values. This result is consistent with the value of 0.425 calculated for the Serengeti foals between 1962 and 1965 (from foal/mare ratios, Klingel 1969a).

The results of the simulations show clearly that with the ruminant first-year survival values, the zebra population would have increased fast, and with the zebra value, the ruminant populations would have declined. The difference in first-year survival alone is therefore sufficient to account for the difference in population kinetics observed between zebra and the two ruminant populations.

The results of the demographic analysis are therefore clear:

1. The hypothesis that the lower survival of foals is the key parameter for the zebra population dynamics and prevents an increase in zebra numbers is supported, and
2. The differences in life history traits between the zebra and the ruminants have no major effects on fecundity, and are clearly not sufficient to explain the differences in population dynamics, and the limitation of this zebra population.

Ecological processes

By the 1980s the ruminants were limited by density-dependent intra- and interspecific competition (though buffalo were later limited by illegal hunting; Dublin et al. 1990; Mduma et al. 1999). If resource limitation is the key process in zebras too, survival should have been positively correlated with rainfall. The proportion of foals showed some variability (6–22% between 1980 and 1999), but was negatively correlated with rainfall (mean annual rainfall and dry season rainfall). This suggests that resource availability does not regulate recruitment and that during the wettest periods foals are more vulnerable. In the Kruger National Park, lions killed more zebra during wet periods (Smuts 1978; Mills et al. 1995), and this increase in prey vulnerability is probably due to fragmentation of the herds and an increase in grass cover for the lions. The proportion of yearlings varied between 7 and 25%. It was lower in the dry seasons, and increased with dry season rainfall (Table 9). This result suggests that in their second

year, when most young zebras are weaned and must find their own food resources, survival may be influenced by the abundance of resources. Resource availability therefore appears to have both positive and negative effects on the survival of young zebra, in contrast to the situation in wildebeest, where the effects are clear and positive on the survival of young and adults (Mduma et al. 1999). Consequently there is little empirical evidence for “bottom-up” limitation of the zebra population.

There are no data on the impact of diseases on the Serengeti zebras, but predation has been studied in detail. The lions switched to wildebeest after 1975 (41% of their diet compared with 20–25% in the 1960s, Table 5), but the numbers of lions increased and their offtake of zebras seems to have remained at about the same level throughout the period. The hyenas also switched to wildebeest, and particularly to buffalo after 1975, so the estimated number of zebra killed showed little change (Table 6). The combined impact of lions and hyenas on zebras represented about twice their impact on wildebeest. This could result simply from a difference in availability since zebra families disperse more widely than wildebeest (Maddock 1979; Sinclair 1985), which generally move together as a large herd, so the predation risk per individual is reduced (the “selfish herd”, Treisman 1975). As a consequence, wildebeest are, on average, available to lions 35% of the time, and zebra 63% (Schaller 1972).

Lion and hyena predation accounts for about 30% of the annual mortality of zebras, and could therefore have had a notable effect on the dynamics of the population, especially since this offtake by natural predators is additive to a similar number of zebras estimated to be killed by illegal hunting (19,000; Hofer et al. 1996). The data on the natural predators (their diets and numbers) were measured in the central part of the Serengeti, and extrapolation to the ecosystem as a whole is likely to be subject to error, so the results should be interpreted with caution. Nonetheless it seems safe to conclude that predation could have a more powerful effect on the zebra than the wildebeest in the Serengeti since the calculated impact on zebra is about twice that on wildebeest. The relative stability of the estimated offtake of zebras across the two periods indicates that predation could be the main limiting factor in spite of the considerable fluctuations in the numbers of natural predators. If this analysis is correct, the zebra were in a “predator pit”.

In plains zebra the gestation time is longer than a year (Smuts 1976), so the minimum inter-foal interval is about 13 months (see Klingel 1969b). Consequently, zebra mares cannot foal in the same season each year and some foals are born in every month. 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. Zebra foals are therefore available to predators for more of the year than wildebeest and buffalo calves, and are preferred prey in some ecosystems (see Cooper 1990; Mills and Shenk 1992). However, we calculate that some 60,000 zebra

Table 10 First-year survival. p_a Proportion of adults >5 years old=0.86, SR_f adult sex-ratio (female proportion)=0.64, p_f proportion of adult females within age-class I , f_i female fecundity within age-class I

Year	Live foals (F)	Females of breeding age (B)	Expected live foals (Fe)	First-year survival (s_0)
$t-1$	$foals_{[t-1]}/total_{[t-1]}$	$adults_{[t-1]} \times p_a \times SR/total_{[t-1]}$		
t	$foals_{[t]}/total_{[t]}$	$adults_{[t]} \times p_a \times SR/total_{[t]}$	$B_{[t-1]} \times \sum_i (p_i \cdot f_i)$	$1 - (Fe_{[t]} - F_{[t]})/Fe_{[t]}$

Table 11 Yearling survival

Year	Live foals (F)	Yearlings (Y)	Yearling survival (s_1)
$t-1$	$foals_{[t-1]}/total_{[t-1]}$		
t	$foals_{[t]}/total_{[t]}$	$yearlings_{[t]}/total_{[t]}$	$1 - (F_{[t-1]} - Y_{[t]})/F_{[t-1]}$

foals are born in the Serengeti each year. Lions and hyenas eat more adult zebras than foals (Schaller 1972, Table 47; Kruuk 1972, Table 17; C. Packer, unpublished data; H. Hofer and M. East, unpublished data), so it is unlikely that predation by these species can account for the disappearance of nearly 38,000 foals.

In conclusion, we show here that the Serengeti zebras are limited by the high level of foal mortality. The effect of their particular life history traits on fecundity does not appear to be important, at least in this ecosystem. Predation by wild predators in addition to mortality caused by illegal hunting accounts for a large proportion of the mortality (about two-thirds), and could have a strong limiting effect on the zebra population; however, the processes involved in foal mortality have not been elucidated.

It has been proposed that a function of migration is to escape predation, and this model clearly fits the case of the wildebeest in the Serengeti (Fryxell et al. 1988). If predation is a major cause of zebra mortality, this analysis suggests that migratory zebra do not escape limitation by predators in this system: this could be because their very different pattern of habitat use leads them to be more widely dispersed than the wildebeest, and therefore more available to the predators (see Hofer and East 1995 for other cases where migratory species do not “escape predation”). The relatively high survival of calves in the buffalo, which are resident, can be explained by the highly effective collective defence of their young observed in this species (Prins 1996).

More detailed data on the causes of foal mortality in the Serengeti zebra, based on known individuals, are required to determine with certainty whether the process involved is predation, competition for resources, social limitation or pathogens. In particular it would be necessary to determine the nature and impact of the diseases and causes of malnutrition (e.g., lack of milk, loss of mother due to predation or on migration, etc.). There is also the possibility that social factors contribute to zebra mortality: this does occur in equids (Berger 1986; Pluhacek and Bartos 2000). As is often the case in animal population

dynamics, the answer may well be that it is a combination of these different processes.

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Appendix

Calculations for zebra juvenile survival

Survival rates were estimated from the proportions of successive age-classes in the formulas below. As field observations were not done in the same month each year, we compared only samples obtained in 2 successive years (we included the comparison between January and November in 1994). For example, the yearling survival in 1988 was estimated from the juvenile proportion in the 1987 wet season and the yearling proportion in the 1988 wet season. For foal survival, we calculated the expected number of newborns in one year from the number of reproductive females in the previous year and their fecundity. To estimate first-year survival (Table 10), we compared the expected recruitment to the yearling class with the proportion of yearlings observed in the same year (Table 11).

References

- Bauer H (2003) Lion conservation in West and Central Africa: integrating social and natural science for wildlife conflict resolution around Waza National Park, Cameroon. PhD thesis, Leiden University, Leiden
- Bell RHV (1970) The use of the herd layer by grazing ungulates in the Serengeti. Animal populations in relation to their food resources. Blackwell, Oxford
- Berger J (1986) Wild horses of the Great Basin. Social competition and population size. University of Chicago Press, Chicago, Ill.
- Caswell H (2001) Matrix population models. Construction, analysis and interpretation. Sinauer, Sunderland, Mass.
- Cooper SM (1990) The hunting behaviour of spotted hyaenas (*Crocuta crocuta*) in a region containing both sedentary and migratory populations of herbivores. Afr J Ecol 28:131–141

- Cumming DHM (1982) The influence of large herbivores on savanna structure in Africa. In: Huntley BJ, Walker BH (eds) *Ecology of tropical savannas*. Springer, Berlin Heidelberg New York, pp 217–244
- De Boer W, Prins H (1990) Large herbivores that strive mightily but eat and drink as friends. *Oecologia* 82:264–274
- Dublin HT, Sinclair ARE, Boutin S, Anderson E, Jago M, Arcese P (1990) Does competition regulate ungulate populations? Further evidence from Serengeti, Tanzania. *Oecologia* 82:283–288
- Duncan P, Foose TJ, Gordon I, Gakahu CG, Lloyd M (1990) Comparative nutrient extraction from forages by grazing bovinds and equids: a test of the nutritional model of equid/bovid competition and coexistence. *Oecologia* 84:411–418
- Festa-Bianchet M, Gaillard JM, Coté SD (2003) Variable age structure and apparent density-dependence in survival of adult ungulates. *J Anim Ecol* 72:640–649
- Fryxell J, Greever J, Sinclair A (1988) Why are migratory ungulates so abundant? *Am Nat* 131:781–798
- Gaillard J-M, Festa-Bianchet M, Yoccoz NG (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol Evol* 13:58–63
- Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A, Toïgo C (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annu Rev Ecol Syst* 31:367–393
- Gasaway WC, Gasaway KT, Berry HH (1996) Persistent low densities of plains ungulates in Etosha National Park, Namibia: testing the food-regulating hypothesis. *Can J Zool* 74:1556–1572
- Georgiadis N, Hack M, Turpin K (2003) The influence of rainfall on zebra population dynamics: implications for management. *J Appl Ecol* 40:125–136
- Grimsdell JJR (1973) Age determination of the African buffalo, *Syncerus caffer* Sparman. *East Afr Wildl J* 11:31–54
- Gwynne MD, Bell RHV (1968) Selection of vegetation components by grazing ungulates in the Serengeti National Park. *Nature* 220:390–393
- Hairston NG, Smith FE, Slobotkin LB (1960) Community structure, population control, and competition. *Am Nat* 44:421–425
- Hansen RM, Mugambi MM, Bauni SM (1985) Diets and trophic ranking of ungulates of the northern Serengeti. *J Wildl Manage* 49:823–829
- Hofer H, East M (1995) Population dynamics, population size, and the commuting system of Serengeti spotted hyenas. In: Sinclair ARE, Arcese P (eds) *Serengeti II: dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago, Ill., pp 332–363
- Hofer H, Campbell KLI, East ML, Huish SA (1996) The impact of game meat hunting on target and non-target species in the Serengeti. In: Taylor V, Dunstone N (eds) *The exploitation of mammal populations*. Chapman and Hall, London, pp 117–146
- Jolly GM (1969) The treatment of errors in aerial counts of wildlife populations. *East Afr Agric For J* 34:50–55
- Klingel H (1969a) The social organisation and population ecology of the plains zebra (*Equus quagga*). *Zool Afr* 4:249–263
- Klingel H (1969b) Reproduction in the plains zebra, *Equus burchelli boehmi*: behaviour and ecological factors. *J Reprod Fertil Suppl* 6:339–345
- Kruuk H (1972) The spotted hyena: a study of predation and social behaviour. University of Chicago Press, Chicago, Ill.
- Lebreton JD, Millier C (1982) Modèles dynamiques déterministes en biologie. Masson, Paris, p 208
- Legendre S, Clobert J (1995) ULM, a software for conservation and evolutionary biologists. *J Appl Stat* 22:817–834
- Leslie PH (1966) The intrinsic rate of increase and the overlap of successive generations in a population of guillemots (*Uria Aalge* Pont.). *J Anim Ecol* 35:291–301
- Loison A, Festa-Bianchet M, Gaillard JM, Jorgenson JT, Jullien JM (1999) Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* 80:2539–2554
- Maddock L (1979) The “migration” and grazing succession. In: Sinclair ARE, Norton-Griffiths M (eds) *Serengeti: dynamics of an ecosystem*. University of Chicago Press, Chicago, Ill., pp 104–129
- Mduma SAR, Sinclair ARE, Hilborn R (1999) Food regulates the Serengeti wildebeest: a 40-year record. *J Anim Ecol* 68:1101–1122
- Ménard C, Duncan P, Fleurance G, Georges J-Y, Lila M (2002) Comparative foraging and nutrition of horses and cattle in European wetlands. *J Appl Ecol* 39:120–133
- Mills MGL, Shenk TM (1992) Predator-prey relationships: the impact of lion predation on wildebeest and zebra populations. *J Anim Ecol* 61:693–702
- Mills MGL, Biggs HC, Whyte IJ (1995) The relationship between rainfall, lion predation and population trends in African herbivores. *Wildl Res* 22:75–88
- Moehlman PD (ed) (2002) *Equids: zebras, asses and horses*. Status survey and conservation action plan. IUCN/SSC Equid Specialist Group. IUCN, Gland, p 190
- Ogutu JO, Owen-Smith N (2003) ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecol Lett* 6:412–419
- Pluhacek J, Bartos L (2000) Male infanticide in captive plains zebra, *Equus burchelli*. *Anim Behav* 59:689–694
- Prins HHT (1996) *Behaviour and ecology of the African buffalo: social inequality and decision making*. Chapman and Hall, London
- Redfern JV, Grant R, Biggs H, Getz WM (2003) Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* 84:2092–2107
- Schaller GB (1972) *The Serengeti lion*. University of Chicago Press, Chicago, Ill.
- Sinclair ARE (1974) The natural regulation of buffalo populations in East Africa. IV. The food supply as a regulating factor, and competition. *East Afr Wildl J* 12:291–311
- Sinclair ARE (1977) *The African buffalo. A study of resource limitation of populations*. University of Chicago Press, Chicago, Ill.
- Sinclair ARE (1985) Does interspecific competition or predation shape the African ungulate communities? *J Anim Ecol* 54:899–918
- Sinclair ARE (1997) Fertility control of mammal pests and the conservation of endangered marsupials. *Reprod Fertil Dev* 9:1–16
- Sinclair ARE, Arcese P (1995) *Serengeti II: dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago, Ill.
- Sinclair ARE, Norton-Griffiths M (1979) *Serengeti: dynamics of an ecosystem*. University of Chicago Press, Chicago
- Sinclair ARE, Norton-Griffiths M (1982) Does competition or facilitation regulate migrant ungulate populations in the Serengeti? A test of hypotheses. *Oecologia* 53:364–369
- Sinclair ARE, Dublin HT, Borner M (1985) Population regulation of Serengeti wildebeest: a test of the food hypothesis. *Oecologia* 65:266–268
- Sinclair ARE, Mduma SAR, Arcese P (2000) What determines phenology and synchrony of ungulate breeding in Serengeti? *Ecology* 81:2100–2111
- Smuts GL (1976) Reproduction in the zebra mare *Equus burchelli antiquorum* from the Kruger National Park. *Kodoe* 19:89–132
- Smuts GL (1978) Interrelations between predators, prey, and their environment. *BioScience* 28:316–320
- Spinage CA (1972) African ungulate life tables. *Ecology* 53:645–652
- Treisman M (1975) Predation and the evolution of gregariousness. I. Models for concealment and evasion. *Anim Behav* 23:779–800
- Van Wieren SE (1996) Digestive strategies in ruminants and non-ruminants. PhD thesis. Agricultural University, Wageningen
- Watson RM (1967) *The population ecology of the Serengeti wildebeest*. PhD thesis. Cambridge University, Cambridge
- Watson RM (1969) Reproduction of wildebeest, *Connochaetes taurinus albojubatus* Thomas, in the Serengeti region, and its significance to conservation. *J Reprod Fertil [Suppl]* 6:287–310