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Food regulates the Serengeti wildebeest: a 40-year record

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Summary

1. The migratory wildebeest (*Connochaetes taurinus* (Burchell)) population of Serengeti has been monitored for 40 years (1958–1998). The population increased from 1963 to 1977, stabilized from 1977 to 1993 and declined during drought in 1993–94. These changes provided a significant contrast in densities and the opportunity to determine the life history stages where survival was density dependent and their causes.

2. There was a delay in age of maturity and a decline of both yearling and adult pregnancy rates at higher densities. Changes in yearling pregnancy had minimal effect on number of calves born. Adult pregnancy rate dropped from 95% to 88%.

3. The greatest absolute mortality occurred in newborn calves (0–4 months old). The most variable survival was in dry-season calf mortality (5–11 months old).

4. Density dependence was clearly present in adult mortality and this appeared to be the regulating life stage. Density dependence was also found in dry-season calf mortality. The drop in pregnancy rate was only weakly density dependent.

5. The main cause of mortality (75% of cases) was undernutrition. Bone marrow condition showed that more animals died in extremely poor condition as the population increased and predators did not cause these deaths.

6. Predation played only a minor role in limiting the wildebeest population. Predators caught animals in moderate condition during the increase phase and increasingly healthy condition during years of high population density. The main predators were lion [*Panthera leo* (Linnaeus)] and hyaena (*Crocuta crocuta* Erxleben).

7. Adult mortality was significantly negatively related to food per capita. This could be viewed either as curvilinear density dependence, or as two phases of mortality. The first phase was during population increase when mortality was inversely density dependent and may have been caused by a constant predation rate. The second was during stability and decline and comprised the additive effects of undernutrition and predation.

8. Rainfall in the dry season was the most important extrinsic determinant of food supply for the wildebeest population but food was related to mortality only when population density was incorporated.

9. At present the wildebeest population appears regulated by natural causes through food supply. Human-caused mortality appears to be a minor factor. However, if the number of wildebeest killed by humans increases as human population increases, then there could be a permanent decline in wildebeest, and a major change in the whole ecosystem, because wildebeest are the keystone species. Continued monitoring is essential for conservation of the Serengeti ecosystem.

Key-words: food, rainfall, regulation, Serengeti, wildebeest.

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Introduction

The Serengeti wildebeest [*Connochaetes taurinus* (Burchell)] population is perhaps the best known of the large migratory grazing systems of the world. It is the keystone that determines the rest of the Serengeti ecosystem (Sinclair 1979a; Sinclair & Arcese 1995a) and consequently its viability is the major management goal for conservation in this region of Tanzania. Information on its population ecology has accumulated for 40 years, and although analyses have been conducted at intervals, a complete synthesis has yet to be published. In this paper we present a synthesis of the available information on its population dynamics.

The migratory wildebeest have been monitored since 1958 (Grzimek & Grzimek 1960) with censuses every few years (Fig. 1) and estimates of reproduction, recruitment and mortality at various intervals (earlier publications are cited below). Prior to 1963 the population experienced recurrent annual mortality of calves from the exotic viral disease, rinderpest (Talbot & Talbot 1963). However, in 1963 the disease died out, probably as an indirect result of vaccination campaigns with the surrounding cattle herds. The evidence for the disappearance of this disease comes from serum antibody samples collected in the late 1950s, throughout the 1960s, and at intervals subsequently (Sinclair 1977a,b; Plowright 1982; Dobson 1995 and references therein). Following the disappearance of rinderpest the population, at nearly 0.24 million, increased steadily until 1977 at which time it reached 1.4 million (Sinclair & Norton-Griffiths 1982). Thereafter the population fluctuated between 1.1 and 1.4 million until at least 1991 (Dublin *et al.* 1990; Campbell & Borner 1995;

Sinclair 1995). In 1993 a drought, more severe than any since records began in 1938 (Mduma 1996), occurred in the Serengeti region and the wildebeest population dropped in that year to 0.9 million and has remained at that level subsequently (Farm & Woodworth 1994; Mduma, Hilborn & Sinclair 1998; Tanzania Wildlife Conservation Monitoring, personal communication).

These long-term records, the dramatic change in abundance, and the events which affected the wildebeest numbers, have allowed a determination of the life stages where survival fluctuates the most and where density dependence occurs (the regulating stage). We analyse first the life stages at which the main mortalities occur to identify where fluctuation and regulation take place (Sinclair 1989). We then present the evidence for the causes of these mortalities.

The life stages for which we obtained data were fertility loss, newborn calf mortality occurring in the wet season (March–June, ages 0–4 months), dry season calf mortality (July–December, 5–10 months), yearling mortality (ages 11–24 months) and adult mortality (> 24 months). Causes of mortality were lumped into predation and non-predation, the latter representing undernutrition and associated diseases (Sinclair 1977a, 1979b; Sinclair, Dublin & Borner 1985; Sinclair & Arcese 1995b).

Methods

STUDY AREA

We define the Serengeti-Mara ecosystem as that covered by the migratory wildebeest population (34–36°E, 1°15' to 3°30'S) and details are given in

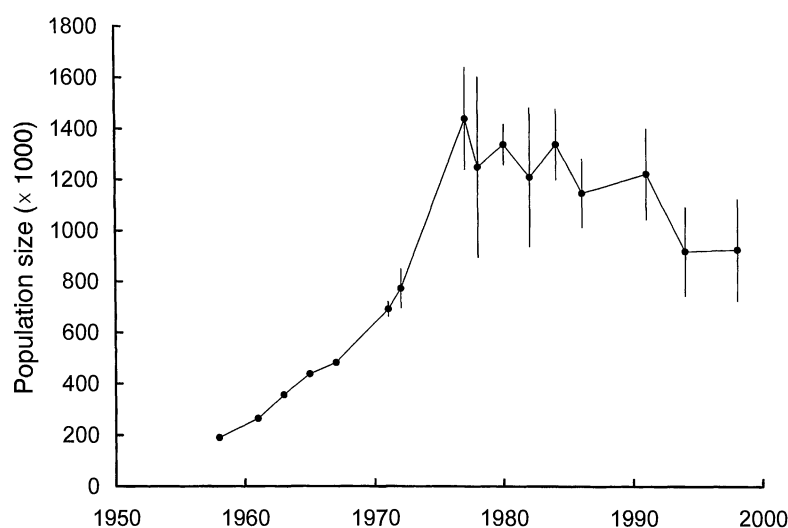


Fig. 1. Wildebeest population numbers in the Serengeti ecosystem from 1958 to 1998. The decline in 1993–94 was a result of severe starvation during a prolonged drought in 1993. Vertical lines indicate 1 standard error (sources are Farm & Woodworth 1994; Campbell & Hofer 1995; Sinclair 1995; Tanzania Wildlife Conservation Monitoring, personal communication).

Sinclair & Norton-Griffiths (1979) and Sinclair & Arcese (1995a). This system lies in northern Tanzania and southern Kenya, covering 25 000 km². It is bounded in the west by the agriculture of the Wasukuma, Wakoma and Wakuria tribes. In Kenya the Loita plains delimit the northern boundary and the forested Loita hills form the north-eastern boundary. Further south in Tanzania the Loita hills merge with the Gregory Rift escarpment and the Ngorongoro Crater highlands to form the eastern boundary. The edge of the Serengeti Plains delimits the southern extent of the system. These boundaries effectively prevent emigration and immigration of animals. There are separate wildebeest herds in Ngorongoro Crater, and on the Loliondo and Loita plains but these do not overlap with the migratory wildebeest. The ecosystem includes the administrative areas of the Serengeti National Park, Ngorongoro Conservation Area, Maswa Game Reserve, Ikoma and Ikorongo Game Control Areas, Masai Mara Game Reserve, and the Loliondo Game Control Area.

The major climatic influence is rainfall. There is a gradient from the north-west (mean annual rainfall 1100 mm) to south-east (500 mm). The rainfall is seasonal with rain beginning in November and continuing to May or June. There is a dry season from July to October and sometimes in January–February. Temperature is relatively constant year-round with a mean of 22 °C. The daily maximum is around 30 °C with a minimum of 15 °C. The vegetation is composed of short grass plains in the arid south-east turning to longer grassland further west. Plains become Acacia savannah at a sharp boundary near the centre of the park. The savannah extends west to Lake Victoria and north to the Loita plains. The north-west of Serengeti National Park has broad-leaved *Terminalia* woodland. The migratory wildebeest use the plains in the wet season, moving west and north at the beginning of the dry season. Some reach the far northern Mara Reserve by the end of the dry season, while others remain in the far west. Movements are dictated by local rainfall events and differ from year to year. Zebra (*Equus burchelli* Gray) migrate with the wildebeest and Thomson's gazelle (*Gazella thomsoni* Gunther) follow them. There are 28 ungulate species in the ecosystem. Five large carnivores feed on the wildebeest.

PREGNANCY RATES

For the years 1992–94 pregnancy rate was determined by radioimmunoassay of fecal samples using the method developed by T. Gross (personal communication, Gross 1992). Calibration for this technique used animals of known reproductive status from autopsies, and the results for these data are published elsewhere (Mduma 1996, S.A.R. Mduma,

A.R.E. Sinclair & T.S. Gross, unpublished information). The method, employed here on wildebeest for the first time, measures the progesterone hormone levels in fecal samples.

Fecal samples were collected from non-pregnant adult females, pregnant adult females, nulliparous yearling females and males to provide baseline calibration values. These allowed us to identify the level of progesterone hormone in the fecal sample that indicates pregnancy, this level being 8 ng g⁻¹ dry weight or higher (Mduma 1996). In order to estimate pregnancy rates in the population, fecal samples were collected randomly from adult females between September and December at which time females were more than 4 months pregnant, and their progesterone levels were higher than those of non-pregnant females. Fecal samples were obtained by observing herds, locating defecating animals of known sex and age, and obtaining a sample immediately. These samples were dried at 38–42 °C for 24 to 36 h, packaged and sent to the Centre for Biotechnology Research, University of Florida for progesterone analysis (Gross 1992). Horn shape and size were used to determine age and sex classes of the animals (Watson 1967; Attwell 1980; Sinclair & Arcese 1995b).

Prior to 1992 we used the previously published pregnancy rates obtained from autopsy samples (Watson 1967, Sinclair 1977). Since fecal samples were calibrated by autopsy the two data sets can be compared over the whole time period.

MORTALITY OF JUVENILES

Births are synchronized, with most occurring during February to March (Watson 1967, Sinclair 1977a). Mortality in newborn calves from March to June, in later calves from June to December, and in yearlings, was estimated by changes in the ratios of young animals to adult females (> 2 years old). Because there is sampling error in the counts of both young animals and females we used the log-likelihood method to obtain the best estimate of survival from changes in these ratios (Appendix 1). Adult mortality was estimated directly by measuring the density of carcasses and relating this to the density of live animals. With these estimates a life table was constructed using population censuses as independent data. We describe each of these measures below.

Estimates of mortality from age and sex counts

The population age and sex ratios were obtained at different times of the year by following the migrating population. Non-permanent transects were conducted from a vehicle by driving through large herds of wildebeest during their migration. Transect

lines were chosen after mapping the distribution of migratory herds during reconnaissance flights approximately every 2 weeks. In western Serengeti four transects each 20–22 km long were surveyed at an average interval of 2 weeks while wildebeest were in the area during the dry season.

Animals were counted at points along a transect, the points usually 0.5–1.0 km apart, the interval depending on the dispersion of the animals. At each point animals were counted from a stationary vehicle within a semi-circular area of 100 m radius in front of the observer, the radius being judged by eye after training with a range finder. Transects were set at least 2 km apart and this avoided double counting.

Unlike calves, yearlings (11–24 months) mixed freely with both nursery and male groups, and would even form groups of their own. Therefore, changes in the monthly yearling per adult ratio were used to estimate the yearling survival rate. Survival was estimated for wet (January–June) and dry (July–December) seasons. Calf and yearling survival were estimated (Appendix 1) from the monthly ratios.

MORTALITY OF ADULTS

Carcass counts

The large herds of wildebeest move daily and they leave behind the carcasses of those that died. Generally deaths occur at night, from predation or other causes. Predators leave their kills the next morning to find shade as the temperature rises. We surveyed in the early morning before predators left their kills or scavengers completely destroyed the remains. Carcasses were counted along the same transects as those used for age ratios. They were sighted directly from vehicles, and their distance from the transect was recorded together with age, sex and cause of death. Only carcasses less than 24 h since death were considered. The ratio of carcasses located per live animals counted each day along transects was used to estimate mortality rate.

Estimating the most likely daily mortality rate

Transect length and effective sighting distances were used to estimate the area searched. Perpendicular sighting distances from the transect to the carcass were estimated in five classes of 100 m interval and one class for those beyond 500 m (centred at 1000 m). We assumed that carcasses were randomly distributed with respect to distance from the transect. We used the program DISTANCE[®] v. 2.2 to calculate the effective sighting width and carcass density (Buckland *et al.* 1993; Laake *et al.* 1994). Each transect was analysed separately (cumulative distance and carcasses per sighting distance classes).

Pooled estimates of effective search width and density were used if transect estimates were not significantly different. The estimates for daily adult mortality were calculated from the observed distribution of deaths recorded on the transects. This estimated mortality rate was then used to calculate the expected daily number of deaths for each transect and day, as explained in Appendix 2.

LIFE TABLE ANALYSIS

A life table was constructed using censuses as the starting point. Censuses were conducted at intervals from 1960 to 1998 and the methods are described elsewhere (Norton-Griffiths 1973, 1978; Sinclair & Norton-Griffiths 1982). In years with no census the population size was interpolated with the smoothing function using EXCEL, except in 1992 and 1993. In those years the population was calculated from survival estimates. In 1993 a severe drought resulted in a large dry season mortality which was measured directly, as described above. This mortality was used, together with the 1994 census, to calculate the 1993 population size.

The sex ratio of adults was estimated directly by random vehicle transects when the whole population was on the Serengeti plains in 1971, 1972, 1980 and 1992–94 combined. Because the sex ratio was very close to equality for most of this period we used it for other years so that the values for 1971–72 were used for 1973–1979, that for 1980 used for 1981–90, and that for 1992–94 was used for 1991. The number of females in the population was calculated from the sex ratio, proportion of calves and yearlings, and the census.

At intervals from 1960 the calves and yearlings at various ages were sampled and ratios of calves/female and yearlings/adult were calculated. In the years with sufficient monthly data the estimated ratios were computed for various ages as explained above. For other years where only one monthly estimate was available, the simple ratio from observed data was used. In these cases the mean and standard error of the age and sex ratios used standard formulae (Cochran 1977; Krebs 1989). The number of adult females was used as the value for the maximum potential birth rate. The measured value for pregnancy was used to compute the actual birth rate. The steps in the calculations for the life table are detailed in Appendix 3. With these measures the population was started with the census of 190 000 animals in 1958 (Swynnerton 1958; Grzimek & Grzimek 1960) and followed until 1994.

Life stage mortalities (k-factors)

The annual change in numbers could be divided into five stages. These stages were loss of fertility (*k*-

1), neonatal mortality (k -2), dry season mortality of calves (k -3), and annual mortality of yearlings (k -4) and adults (k -5). At each stage the proportional loss relative to the initial number was calculated in log form (Appendix 4).

POPULATION REGULATION

Density dependence was detected by regression of the k -values for each stage against log of the initial population size before the mortality occurred. The ensuing slope (b), intercept (a) and coefficient of determination (r^2) of the regression were used to determine the relative impact of mortality at each life stage in the regulation of the Serengeti wildebeest population.

CAUSES OF MORTALITY

Carcasses less than 24 h following death were examined for cause of death. Evidence for predation came from the presence of predators. In addition predation was recorded from signs of struggle, blood on the ground, and evisceration, with the rumen some distance from the carcass. Scavenged carcasses from non-predation deaths did not show such signs, the rumen remaining within the body. Otherwise non-predation deaths produced carcasses that were intact.

For adult ruminants the last stores of fat are those in the bone marrow (Ransom 1965; Anderson, Medin & Bowden 1972; Sinclair & Duncan 1972; Hanks 1981; Anderson, Bowden & Medin 1990). Therefore, the body condition of dead wildebeest was determined by marrow fat from its long bones. Three categories of bone marrow condition were scored according to texture and colour judged by visual criteria, their marrow fat content having been calibrated previously (Sinclair & Duncan 1972; Sinclair 1977a; Sinclair & Arcese 1995b). These were: solid white fatty (SWF) with fat content $88.5\% \pm 0.9(\text{SE})$, white opaque gelatinous (WOG) ($55.7\% \pm 2.4\%$ fat), and translucent gelatinous (TG) ($15.9\% \pm 2.1\%$ fat). We refer to these categories below as healthy, moderate and poor.

We used chi-square (χ^2) and log-likelihood ratio (G) tests (Zar 1984) to analyse the frequency distributions of age, sex, marrow condition and causes of mortality. The William's or Yates' correction (χ^2_c or G_c) was used where appropriate. We assumed equal chances of locating a carcass regardless of age class, sex and causes of mortality except for calves and these were excluded from the analysis.

Rainfall and food limitation

Wildebeest are grass feeders and the most important environmental variable affecting grass production in

the Serengeti is rainfall (McNaughton 1979, Sinclair 1979b). The amount of grass growth, and hence food supply to grazers, depends on the amount and distribution of rainfall. A typical wet season receives sufficient rainfall to provide food for the wildebeest and food is not limiting then (Sinclair 1977a, 1979b; Maddock 1979). In contrast, the above studies have shown that food supply was sometimes inadequate during the dry season and so could be a cause of mortality. Therefore, grass production during the dry season was estimated using the regression equation for grass growth on monthly rainfall modified from that given in Sinclair (1979b) by being constrained to go through the origin as in Mduma *et al.* (1998).

$$G_y = 1.25R_y \quad \text{eqn 1}$$

where G_y is the amount of grass produced in northern Serengeti measured in kilograms per hectare per month ($\text{kg ha}^{-1} \text{ month}^{-1}$) (data in Sinclair 1977a), and R_y is the dry season (July–October) rainfall measured in mm from monthly storage gauges and averaged over the northern Serengeti region.

The amount of food per animal (F_y) is the total grass grown per month per hectare, times the number of hectares utilized in the dry season (approximately $0.5 \times 10^6 \text{ ha}$), divided by the total number of wildebeest in that year (T_y).

$$F_y = (G_y 0.5 \times 10^6) / T_y \quad \text{eqn 2}$$

Results

REPRODUCTION

Early studies obtained pregnancy rates from autopsies (Watson 1967; Sinclair 1979b). Adult fertility rates always exceeded 80% and were higher in the 1960s and 1970s ($\geq 88\%$) compared to the 1990s (Table 1). Between 1992 and 1994 116 fecal samples were collected from females. During these years pregnancy rates did not differ ($\chi^2 = 0.911$; $P = 0.634$, d.f. = 2). The lowest adult fertility rate (81%) was recorded in 1994 following the drought. One of the five yearling females had a progesterone level of 8.94 ng g^{-1} suggesting a 20% yearling pregnancy rate in 1993, a rate similar to that found in 1969.

Wildebeest pregnancy rates declined significantly from the early 1960s to 1994 (Fig. 2). Adult pregnancy rate declined from 94.6% to 83.5% ($\pm 9.8\%$ asymptotic standard error, logistic regression $P = 0.003$). The yearling pregnancy rate changed dramatically from 83% in 1960 to slightly over 20% in 1964 and remained low thereafter. This decline was significant but with a larger error margin than that for adults; from 34% in the 1960s to 5.6% in

Table 1. Wildebeest pregnancy rates between 1960 and 1994. Sample sizes are shown in parentheses

Year	Yearling pregnancy rate	Adult pregnancy rate	Source
1960	0.83 (6)	0.95 (51)	Watson (1967)
1964	0.22 (9)	1.00 (32)	Watson (1967)
1965	0.44 (9)	0.95 (40)	Watson (1967)
1968	0.04 (26)		Sinclair (1979b)
1970	0.11 (11)	1.00 (14)	Sinclair (1979b)
1971	0.06 (18)	0.88 (41)	Sinclair (1979b)
1991		0.82 (22)	S. Boutin (pers. com.)
1992		0.83 (35)	This study
1993	0.20 (5)	0.89 (44)	This study
1994		0.81 (32)	This study

the 1990s ($\pm 17.4\%$ asymptotic standard error, logistic regression $P = 0.005$).

CALF SURVIVAL

The calving season began in mid-January and covered 6 weeks with a peak in its third week (Watson 1967; Sinclair 1977a). While births were still in progress during the first 2 months, the data were not used in the calculations of calf survival because births confounded the survival estimates. From March to June (wet season) newborn calf mortality occurred. Dry season calf mortality occurred from July to December.

From July 1992 to December 1994 monthly samples of the population were obtained from the sum of 3 to 17 transects ranging in length from 10 to 70 km. The observed and estimated ratios of calves per female are illustrated in Fig. 3. Similar estimates were obtained for other years where sufficient monthly data were available. For calves these were

1965, 1966 (Watson 1967) 1971–1973 and 1984 (A.R.E. Sinclair, unpublished data), and for yearlings 1992–1994 (S. Mduma, unpublished data).

The seasonal calf survival model (Appendix 1, equations A5 and A6) showed different survival rates for the wet and dry seasons. For the 8 years of calf data, on average survival rates were higher dur-

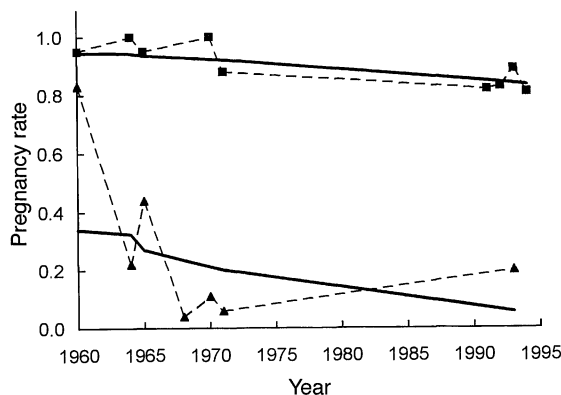


Fig. 2. The adult (■) and yearling (▲) pregnancy rates declined significantly between 1960 and 1994 [$P \leq 0.005$; logistic regression (solid lines). Dotted lines interpolate missing data points.]

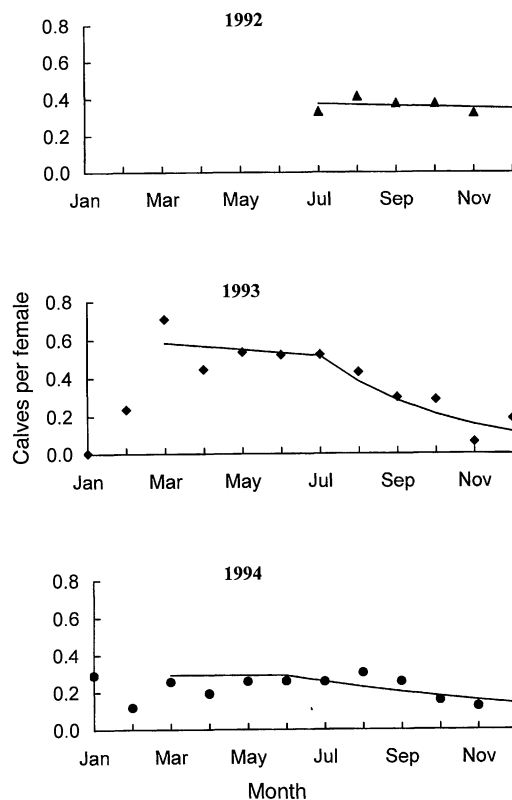


Fig. 3. Estimated monthly change in calves per female ratio calculated using the seasonal log normal model. Data for January and February were not included in the model fits. Observed ratios are shown as triangles (1992), diamonds (1993) and circles (1994).

Table 2. Proportion of wildebeest calves at 4 months and 1 year of age. The estimates in brackets are from Sinclair (1979b) and beside them are proportions calculated using the log normal model

Year	Calf:adult ratio at 4 months	Calf:adult ratio at 1 year	Source†
1960	0.180	0.080	a
1962		0.230	a
1963	0.220	0.160	a
1964	0.190	0.170	a
1965	0.125 (0.13)	0.093 (0.09)	a
1966	0.129 (0.12)	0.112 (0.11)	a
1967	0.160	0.100	b
1968	0.190	0.130 (0.125)	b
1969	0.170		b
1970	0.140	0.110	b
1971	0.175 (0.17)	0.139 (0.12)	b
1972	0.200 (0.18)	0.139 (0.125)	b
1973	0.164 (0.18)	0.097 (0.13)	b
1976		0.140	b
1977	0.170	0.146	b
1978		0.114	c
1980		0.094	c
1982		0.145	c
1983		0.103	c
1984	0.346	0.111	c
1986		0.109	c
1989		0.156	c
1990		0.135	c
1992	0.192	0.173	d
1993	0.211	0.062	d
1994	0.131	0.073	d

†Sources: a, Watson (1967); b, Sinclair (1979b); c, A.R.E. Sinclair (unpublished information); and d, this study.

ing the wet season (March–June) than during the dry season (July–December). In 1992, monthly survival rate was estimated for the dry season only and this was 96%. In 1993 the monthly calf survival rate dropped sharply from 98.5% to 73% between the wet and dry seasons. Although this drop was not statistically significant (log likelihood ratio test $P = 0.125$, d.f. = 1), it was consistent with the drought conditions in that year. Survival rates also

declined between seasons in 1994 (from 99.9% to 89.9%) (log likelihood ratio test $P = 0.016$, d.f. = 1) but less than that in 1993.

Proportions of calves per adult did not differ markedly between 1960 and 1994 (Table 2), suggesting that calf survival rates were relatively constant. Results from 8 years of ground counts where yearlings could be distinguished, suggested that between 1962 and 1989, yearlings aged 20 ± 2 months constituted $9.8\% \pm 2.3\%$ CL of the population (sample sizes = 3229 yearlings, 32 713 adults). Thus, we assumed yearlings constituted 10% and adult females 45% in years when yearlings were not counted. Using these estimates the log normal model was used to calculate the monthly change in ratio of calves per adult female if there were more than 5 months of data in a year. The ratios were estimated using the seasonal log normal model. The observed ratios given by Sinclair (1979b) were recalculated using the log normal model and the estimated ratios were similar. Table 2 summarizes the complete record (1960–1994) of calf per adult ratios when calves were approximately 4 and 12 months old.

YEARLING SURVIVAL

For practical reasons, we assumed that calves became yearlings in January of their second year, when the next cohort of calves was about to be born. Compared to the ratio of calves per female, the monthly ratio of yearlings to adults fluctuated widely, particularly in the wet season of 1993. In 1994 the yearling to adult ratio was small and varied over a narrow range.

As with calves, the seasonal log normal survival model indicates that yearlings usually survived better during the wet season than during the dry season (Table 3). In 1993 and 1994 monthly survival was 96% and 95%, respectively, during the wet season (January–June). The dry season monthly survival rate for 1992 was 73.4%, that in 1993 was 73.6%

Table 3. Seasonal survival rates of wildebeest yearlings estimated from the seasonal log normal model. First month (Y1) refers to July in 1992 and January for other years

Year	1992	1993	1994
Yearlings per 1000 adults month 1 (Y1)	148	207	65
Wet season yearling survival rate (<i>sYw</i>)	no data	0.959	0.948
95% CL		(0.85–1.0)	(0.84–1.0)
Dry season yearling survival rate (<i>sYd</i>)	0.928	0.736	0.959
95% CL	(0.84–1.0)	(0.65–0.83)	(0.87–1.0)
Monthly adult survival rate			
wet season	no data	0.980	0.995
dry season	0.973	0.946	0.994
log likelihood	–0.395	0.677	0.912

(log likelihood ratio test for between-season differences $P = 0.017$, d.f. = 1). However, in 1994 the dry season monthly survival rates remained high at 96% (log likelihood ratio test $P = 0.897$, d.f. = 1).

ADULT MORTALITY

A total of 373 wildebeest carcasses were recorded from July 1992 to December 1994. Sixty-four percent of recorded deaths occurred during the four dry-season months (July to October). Perpendicular sighting distances from transects ranged from 0 to 1500 m. Estimates of effective sighting distances were similar across transects and a pooled estimate of search width was used. This was 226 m (196–259 m 95% CI) on each side of the transect and was rounded to 250 m; hence the effective search width was 500 m. The effective searched area varied with transect length, ranging from 5 to 35 km² per transect. The density of carcasses was similar across transects and the pooled estimate was 0.2 carcasses km⁻² (0.16–0.25, 95% CI).

The carcass data for adults were used to estimate adult mortality rates (Appendix 2, equations A8 and A9). The results suggest lower adult mortality during the wet season (Table 3). Seasonal survival rates varied substantially between years, being lowest (28.1%) during the extended dry season of 1993 consistent with the lowest rainfall (25.2 mm) received over the last 35 years. The highest monthly mortality rate was in November of 1993 (9.7%) during the peak of the drought. About 0.34% (≈ 3000) of the adult population died every day during that month. Three other months with heavy mortality rates during the dry season were October 1992, October 1993 and September 1992 in decreasing order.

The 1993 mortality rate was the highest recorded since the late 1960s (Table 4). Survival rates were higher during the wet season in all years except 1971 and 1972, years that received abnormally high dry season rainfall (> 200 mm; Sinclair 1979b; Table 4).

LIFE TABLE ANALYSIS

Population trends

The complete life table data are given in Table 5. In years when censuses were not conducted, population size was estimated either by interpolation or in 1992 and 1993 from survival data. The average instantaneous rate of increase r shows three main phases over the last 40 years. First, between 1960 and 1977 the population increased from 0.25 to about 1.3 million. The mean instantaneous rate of increase was 0.103 year⁻¹. The second phase, covering 16 years (1977–1992), exhibited an approximately stationary population fluctuating between 1.1 and 1.4 million, and r was -0.008 year⁻¹. Finally, between 1993 and 1994 the population declined to 0.9 million following severe dry season mortality in the drought of 1993 and it has remained at that level subsequently (Fig. 1). The merged estimates post-drought from 1994 and 1998 [weighted by the reciprocal of the variances as in Norton-Griffiths (1978)] gives a population size of 920 463 (+ 95% CL 260 554). This is significantly below ($P < 0.05$) the merged estimate of the seven censuses pre-drought, being 1 296 295 (+ 95% CL 108 016).

The life stage producing fluctuation in population

The lifestage contributing most to the total annual fluctuation is referred to as the 'key factor' (Royama 1996). It has been a tradition to use the mortalities in log form (k -values) to analyse their contribution to the total mortality, K (the sum of k -values, Varley & Gradwell 1960; Podoler & Rogers 1975). The mean of each k -value shows the contribution to the overall annual mortality. Newborn mortality ($k-2 = 0.401$) was the greatest absolute mortality with dry season calf mortality next ($k-3 = 0.221$). Both adult mortality ($k-5 = 0.04$) and fertility loss ($k-1 = 0.039$) were relatively small. The regression slope of each k -value against K (Fig. 4)

Table 4. Adult wildebeest survival rates from 1967 to 1994. The annual monthly survival rates are not shown in years where only the dry-season mortality was measured

Year	Wet season monthly survival	Dry season monthly survival	Average annual monthly survival	Source
1967	99.2	98.4	98.9	Sinclair (1979b)
1968	99.3	98.2	98.9	Sinclair (1979b)
1969	99.5	98.8	99.3	Sinclair (1979b)
1971	99.1	99.2	99.1	Sinclair (1979b)
1972	99.1	99.6	99.3	Sinclair (1979b)
1982	–	97.3	–	Sinclair <i>et al.</i> (1985)
1983	–	97.9	–	Sinclair <i>et al.</i> (1985)
1992	–	97.3	–	This study
1993	98.0	94.7	96.3	This study
1994	99.6	99.4	99.5	This study

Table 5. Wildebeest life-table showing population estimates used in *k*-value analysis. For the March census (column 3) figures in bold face represent censuses, those in parentheses are calculated from survival (see Methods) and the others are fitted by interpolation. With the exception of interpolated adult survival, estimates for other demographic parameters were measured independently

(1) Year (adults + recruits)	(2) Population in January estimates	(3) March census (December)	(4) Adult population (January)	(5) Yearlings (June)	(6) Yearlings (December)	(7) Yearlings females	(8) Potential pregnant (Jan–Feb)	(9) Calves born (March)	(10) Calves (June)	(11) Calves (December)	(12) Calves
1959	–	212 220	203 597	–	–	–	91 619	–	–	–	–
1960	234 227	232 368	224 884	–	–	–	–	87 038	–	41 372	17 991
1961	–	263 362	–	–	–	–	–	–	–	–	–
1962	–	306 789	–	–	–	–	–	–	–	–	64 864
1963	361 302	356 124	342 784	111 028	108 053	59 473	–	–	–	77 357	54 845
1964	405 800	402 916	373 725	–	–	–	168 176	–	–	74 659	63 533
1965	445 266	439 124	423 431	–	–	–	190 544	168 176	70 224	54 229	39 379
1966	464 616	461 219	436 962	–	–	–	–	181 017	74 759	58 435	48 940
1967	488 476	483 292	471 749	–	–	–	–	–	–	76 706	47 175
1968	522 480	519 959	502 006	–	–	–	–	–	–	97 642	65 261
1969	574 188	570 299	550 451	–	–	–	–	–	–	95 813	–
1970	633 805	629 506	619 780	–	–	–	278 901	–	–	87 675	68 176
1971	694 914	692 777	672 266	66 364	65 295	32 941	302 520	278 901	179 477	120 028	93 445
1972	777 474	773 014	772 592	–	–	–	–	266 217	154 355	154 575	107 390
1973	897 250	897 156	853 204	–	–	–	–	–	155 044	144 691	82 761
1974	–	1 057 890	–	–	–	–	–	–	–	–	–
1975	1 222 212	1 221 879	1 170 854	–	–	–	–	–	–	–	–
1976	1 346 779	1 335 785	1 262 060	–	–	–	–	–	–	–	147 895
1977	1 455 723	1 440 000	1 149 711	–	–	–	–	–	–	204 787	170 945
1978	1 303 652	1 248 934	1 170 912	–	–	–	–	–	–	–	143 875
1979	1 310 003	1 293 457	1 198 561	–	–	–	–	–	–	–	–
1980	1 357 933	1 337 979	1 197 204	–	–	–	–	–	–	–	108 073
1981	1 302 201	1 273 345	1 106 276	–	–	–	–	–	–	–	–
1982	1 242 225	1 208 711	1 144 925	–	–	–	–	–	–	–	–
1983	1 328 740	1 315 111	1 227 856	–	–	–	–	–	–	–	169 782
1984	1 356 328	1 337 879	1 139 468	–	–	–	539 352	–	–	–	123 452
1985	1 254 186	1 214 961	1 050 777	–	–	–	–	–	466 105	446 099	132 890
1986	1 179 166	1 146 340	1 061 649	–	–	–	–	–	–	–	–
1987	1 179 230	1 161 429	1 059 453	–	–	–	–	–	–	–	120 584
1988	1 197 716	1 176 517	1 073 085	–	–	–	–	–	–	–	–
1989	1 213 106	1 191 606	1 059 224	–	–	–	–	–	–	–	–
1990	1 233 699	1 206 694	1 092 463	–	–	–	–	–	–	–	178 608
1991	1 245 399	1 221 783	1 099 598	–	–	–	–	–	–	–	165 761
1992	1 240 779	(1 215 627)	1 050 209	–	170 972	122 626	660 892	–	–	–	–
1993	1 242 517	(1 209 471)	936 808	244 677	208 280	43 952	609 451	544 643	–	222 252	181 784
1994	967 457	917 204	876 746	76 178	63 641	58 906	615 757	509 522	386 938	235 768	65 822
1995	501 333	–	–	–	–	–	614 483	551 952	178 366	147 557	77 340

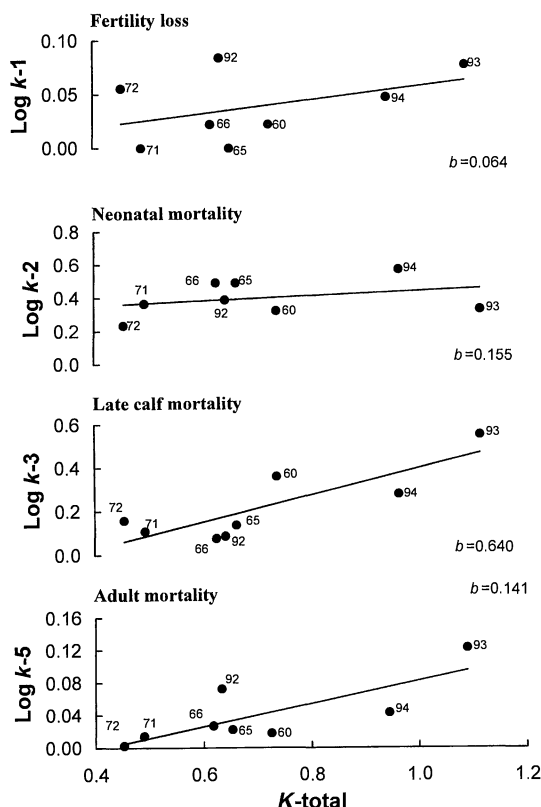


Fig. 4. Wildebeest age class mortalities (k -values) plotted against total mortality (K -total). Dry season calf mortality (k -3) had the highest regression coefficient ($b = 0.640$) and accounted for most of the variability. The yearling mortality (k -4) was omitted because data were insufficient. Data labels show years by their last two digits.

illustrates how each contributes to changes in total annual mortality. The mortality with the highest slope was dry-season calf mortality (k -3) followed by adult mortality (k -5).

POPULATION REGULATION

The role of each life stage in the regulation of the Serengeti wildebeest was examined by plotting the k -values for each stage against \log_{10} of the population size prior to the mortality (Fig. 5). Density dependence is shown if the relationship is positive and relatively significant statistically.

The adult mortality (k -5) and fertility loss (k -1) were both significantly related to population size (k -5: $P = 0.0009$ and k -1: $P = 0.031$) indicating density dependence. Neonatal (k -2) and dry-season calf (k -3) mortalities were positively related to population increase but were not statistically significant (k -2: $b = 0.011$, $P = 0.954$ and, k -3: $b = 0.175$, $P = 0.335$). Although yearling mortality (k -4) had a steep slope, it was not statistically significant (k -4: $b = 0.57$, $P = 0.52$).

The problem with calculating k -values by difference between $\log I$ and $\log F$, is that an error in either parameter (e.g. too small $\log I$), will automatically mean that k will be too large. Since k is plotted against $\log I$, the same error may exist on both axes. This was tested by plotting both $\log I$ against $\log F$, and $\log F$ against $\log I$. If the slopes of both regressions are less than unity then there is no bias in estimates of the k -values (Varley & Gradwell 1968). This test showed that there could be some dependence in adult mortality (k -5) values ($\log F$ on $\log I$ slope = 1.057 and $\log I$ on $\log F$ slope = 0.927). Thus, the results for adult mortality stage should be considered tentative. The test of independence was necessary for adult mortality data (k -5) because its estimates were obtained by difference from sequential censuses. Other k -values were obtained from independent measurements of mortality.

Adult mortality showed curvilinear density dependence with the strength of regulation accelerating at

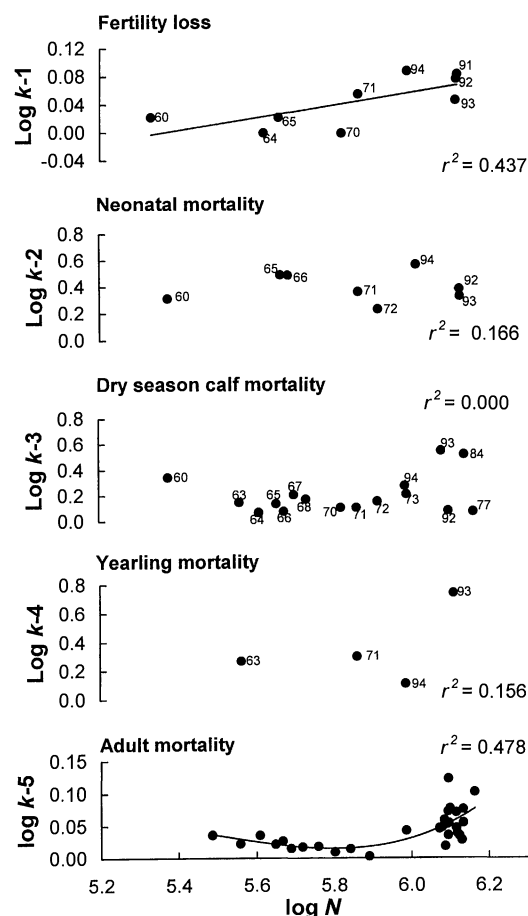


Fig. 5. Regression of $\log k$ -values on \log initial population size (I) of the Serengeti wildebeest. Density-dependent mortality was shown in adult mortality (k -5: $0.3619 I_5^2 - 4.1718 I_5 + 12.036$, $P = 0.0009$) and fertility loss (k -1: $-0.505 + 0.094 I_1$, $P = 0.031$). Numbers represent years shown by their last two digits.

higher densities (Fig. 5). This mortality comprises two groups of points. The first group (Phase 1) represents the population increase from 1962 to 1972. The second (Phase 2) occurred largely when the population was above a million and relatively stable or declining (1975 to 1994). When the population was increasing adult mortality was inversely density dependent ($b = -0.073$, $P = 0.0004$). During Phase 2 the linear slope was positive with a suggestion of delayed density dependence: k -5 regressed against density in the previous year produced a better relationship ($b = 0.336$, $P = 0.086$) than that with density in the same year.

CAUSES OF MORTALITY

Effects of age

Table 6 presents data on the age-distribution of the live population in the 1970s and those of carcasses in three phases of the population dynamics, namely increase phase (1967–73, the ‘1970s’), stationary phase (1977–1991, the ‘1980s’) and decline phase (1992–94, the ‘1990s’). Calves were underrepresented in the collections and so are not included in this analysis. In general, the age-distribution of the combined natural mortality (i.e. non-human causes) was older than that of the live population. The age of death became progressively older from the 1970s to the 1990s, as would be expected from an ageing population.

The age-distribution of predator kills did not differ from that for non-predator deaths. Predator kills were attributed to lion [*Panthera leo* (Linnaeus)] (33.8%), hyaena [*Crocuta crocuta* (Erxleben)] (30.4%) and cheetah [*Acinonyx jubatus* (Schreber)] (3.3%), while 33.3% were caused by unidentified predators. Age distribution of kills by lions and hyaenas (combined over the 1980s and 1990s) showed that the two predators did not differ strongly in their selection of age classes. Lions tended to kill proportionately more middle-aged animals, while hyaenas tended to kill young and old animals, as would be expected for a pursuit predator (for 1990s $G = 31.148$, d.f. = 4, $P < 0.001$). Non-predation deaths during the 1970s accounted for some 70% of the natural mortality and in the 1990s it represented 74%. It was significantly higher than predation in all age classes ($G_c > 5.024$, d.f. = 1, $P < 0.025$) except in very old adults because of the small sample size.

Effects of body condition

Bone marrow provides the best information on the condition of wildebeest when they die (Sinclair & Duncan 1972; Hanks 1981). Bone marrow data for the three time periods are presented in Table 7. Marrow in the live population in the 1970s was in significantly better condition than that of predator kills or non-predation deaths in any of the time periods ($G = 128.99$, d.f. = 4, $P < 0.001$). The frequency of adult marrow categories differed significantly

Table 6. The numbers and percentage of carcasses by age shown in relation to causes of mortality. All natural mortality includes predation, non-predation and other non-human causes. Data are divided into the three time periods of population increase (1970s = 1967–76), stationary numbers (1980s = 1977–91), and population decline (1990s = 1992–94). (Data for the 1970s and 1980s from Sinclair & Arcese 1995a, 1990s this study)

Cause	Period	Yearling	Young adult	Mid-age adult	Old adult	Very old	Total
Live	1970s	36	45	27	19	7	134
	Total (%)	(27)	(34)	(20)	(14)	(5)	(100)
All natural	1970s	36	52	56	28	20	192
	1980s	19	63	90	64	50	286
	1990s	35	26	70	67	15	213
	Total (%)	(14)	(20)	(31)	(23)	(12)	(100)
Predation	1970s						
	1980s	10	42	48	34	22	156
	1990s	11	6	17	14	3	51
	Total (%)	(14)	(19)	(32)	(25)	(10)	(100)
Non-predation	1970s	9	8	11	9	3	40
	1980s	9	21	42	30	28	130
	1990s	24	20	48	52	11	155
	Total (%)	(15)	(16)	(30)	(27)	(12)	(100)
Lion	1980s	3	14	20	15	5	57
	1990s	5	3	12	9	0	29
	Total (%)	(11)	(18)	(38)	(29)	(4)	(100)
Hyaena	1980s	3	16	9	4	11	43
	1990s	3	1	3	6	0	13
	Total (%)	(15)	(22)	(22)	(28)	(13)	(100)

Table 7. Numbers and percentage of wildebeest carcasses found with bone marrow in healthy, moderate or poor amounts of fat in the three time periods defined in Table 6, in comparison to a sample of the live population. Non-predation includes all natural (non-human) causes except predation. (Data from Sinclair & Arcese 1995b, this study)

Cause	Period	Healthy	Moderate	Poor	Total
Live	1970s	104	54	0	158
	Total (%)	(66)	(34)	(0)	(100)
Non-predation	1970s	27 (30)	30 (33)	33 (37)	90
	1980s	13 (14)	38 (41)	42 (45)	93
	1990s	23 (15)	53 (36)	72 (49)	148
	Total (%)	(20)	(37)	(43)	(100)
Predation	1970s	6 (17)	28 (78)	2 (5)	36
	1980s	40 (30)	75 (56)	18 (14)	133
	1990s	18 (39)	18 (39)	10 (22)	46
	Total (%)	(29)	(58)	(13)	(100)

between non-predation deaths and predator kills ($G = 11.623$, d.f. = 2, $P < 0.01$). Considering non-predation first, there were always more animals dying in poor condition than in other condition classes. Furthermore, the poor condition class increased proportionately from the 1970s to the 1990s, while those that died in good condition decreased.

In contrast, the majority of predator kills were in moderate condition in the 1970s (increase phase) and were in progressively better condition in the 1980s and 1990s (Table 7). These results are consistent with earlier conclusions (Sinclair & Arcese 1995b) that wildebeest were exposed to greater risks of predation as the population became food limited, and thus were caught earlier in the dry season and so in better condition (the rationale is explained in Sinclair & Arcese 1995b). A minority of predator kills were in poor condition, but this proportion increased steadily from the 1970s to the 1990s (5.6% to 21.7%). Thus, predators were catching more animals in poor condition as the population density increased, indicating some compensatory effect (predation of animals that would have died from undernutrition anyway). However, there was a far greater increase in the proportion of healthy animals caught as density increased (from 16.7% to 39.1%), indicating that predation and non-predation causes tend to be additive.

FOOD LIMITATION AND RAINFALL

Rainfall

The mean wet and dry season rainfall for the Serengeti between 1960 and 1994 was 679 mm and 139 mm, respectively, and mean annual rainfall was 781 mm. These values are similar to those reported by Norton-Griffiths, Herlocker & Pennycuik (1975) for rainfall data collected between the 1930s and early 1970s. Figure 6 presents the dry season rainfall

in northern Serengeti. This is the area used by wildebeest in the dry season. From this rainfall the grass biomass ha⁻¹ (food) and per capita food ha⁻¹ were calculated (eqns 1 & 2) (Fig. 6).

In 1993 the area experienced the lowest dry season rainfall in 34 years (25 mm) with reduced rainfall starting in April and continuing to December. This resulted in the lowest estimated amount of dry season food per hectare and available food per individual, and this low food availability coincided with very high mortality between April and December 1993. Figure 7 shows the estimated monthly mortality rate of adults (Appendix 2) before, during and after the drought. Mortality increased in the dry season delayed by one month. In 1993 some 30% of the population died during this dry period.

Food limitation

The 1993 record low rainfall, and hence food supply, provided a natural perturbation experiment that enabled us to understand the influence of reduced amounts of food on high levels of wildebeest density. Age-specific mortalities (k -values) are plotted against per capita food supply in Fig. 8. Adult mortality (k -5) was significantly negatively related to per capita food supply during the dry season ($b = -0.053$, $P = 0.0005$), and this relationship persisted even when 1993 was excluded from the regression equation ($b = -0.036$, $P = 0.039$).

The reduced amount of food per animal during the dry season also significantly influenced the dry season calf mortality (k -3: $b = -0.322$, $P = 0.002$). However, this relationship was not significant if 1993 was excluded from the regression fit ($b = -0.301$, $P = 0.153$). There was a weak inverse relationship between dry season food supply and the annual yearling mortality (k -4: $b = -0.410$, $P = 0.063$). Although pregnancy loss (k -1) and neonatal mortality (k -2) showed a negative relationship with the dry season per capita food supply, these

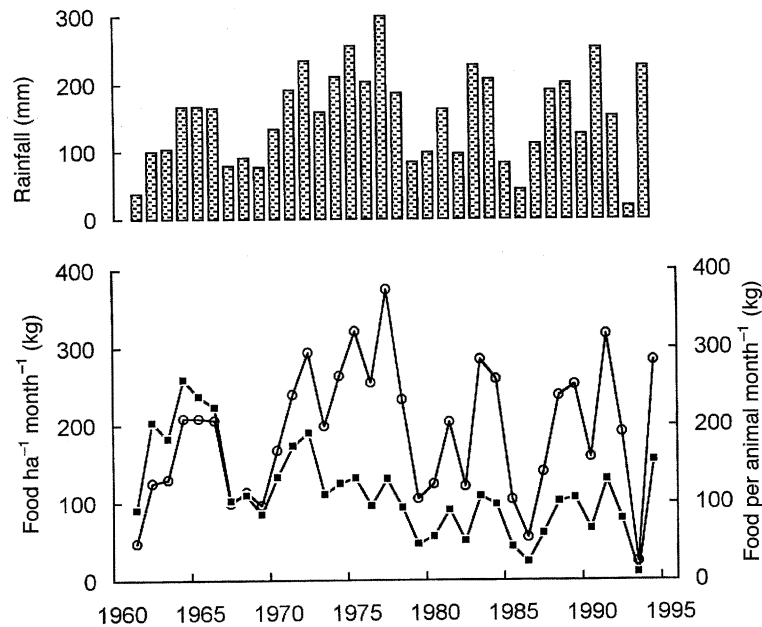


Fig. 6. The northern Serengeti dry season rainfall pattern (top) used to estimate the amount of grass (food) produced (bottom, ○) and, the per capita food available (bottom, ■) for the years 1961–1994.

were not statistically significant ($k-1$: $b = -0.100$, $P = 0.34$ and, $k-2$: $b = -0.017$, $P = 0.617$). Thus, adult mortality ($k-5$) and dry season calf mortality ($k-3$), in particular, were consistent with food being the limiting factor. Regression of these mortalities against dry season food ha^{-1} (not per capita) showed no significant relationship at any life stage over the last 30 years.

Discussion

POPULATION FLUCTUATION

Key factor analysis has its limitations when applied to ungulates as a result of overlapping generations, non-independence of estimates and covariance of k -factors (Royama 1996). The problems raised by Royama are nicely illustrated in our data; for exam-

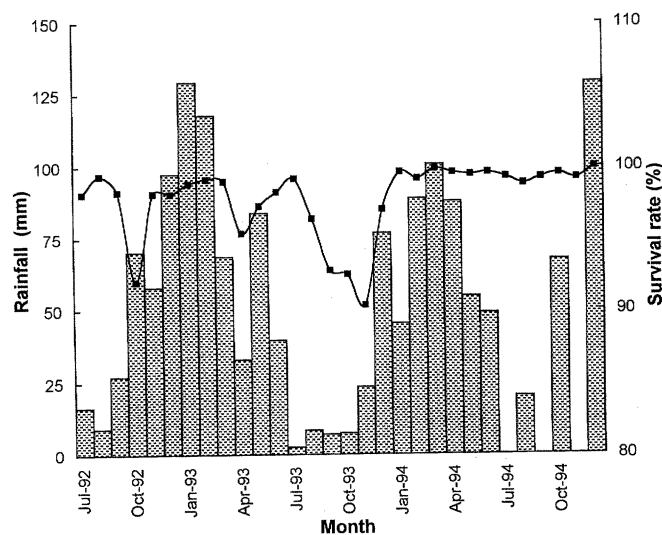


Fig. 7. Monthly adult survival rates (■) estimated from a model relating daily counts of adult carcasses to numbers of live animals. The survival curve follows the rainfall regime (bars) with about one month time lag. Rainfall data for July and September 1994 are missing.

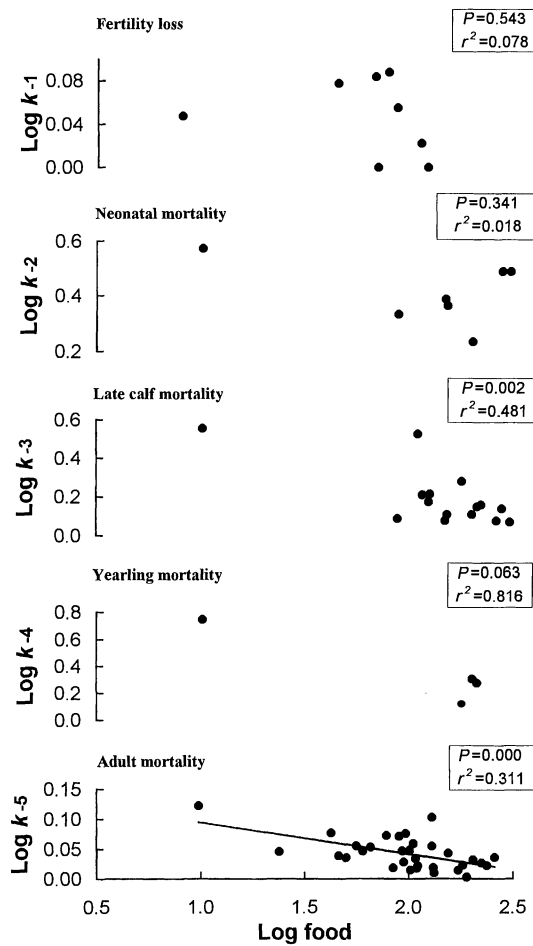


Fig. 8. The age class mortalities (k -values) regressed against dry season per capita monthly food supply in 1967–94. Late calf ($k-3$) and adult ($k-5$) mortalities were significantly negatively related to the dry season food availability (Bonferroni corrected $P < 0.01$).

ple, dry-season calf mortality ($k-3$) had the strongest relationship with total annual mortality (K) (highest regression slope) and would be described as contributing most to annual change in population. This conclusion would be consistent with many other studies of large herbivores in Africa (Sinclair 1977a; Spinage 1982; Owen-Smith 1990) and elsewhere (e.g. Clutton-Brock, Guinness & Albon 1982; Houston 1982; Boyce 1989; Skogland 1990; Clutton-Brock *et al.* 1991; Milner-Gulland 1994; Coughenour & Singer 1996; Saether *et al.* 1996). However, adult survival is much more important in determining the rate of population increase or population size. Because of the high adult survival, a 1% increase in adult survival would make about a 10-fold bigger change in population size (or rate of increase) than a 1% increase in calf survival.

Neonatal mortality constituted the highest proportional loss compared to other life cycle stages. This stage was neither correlated with dry-season food availability, nor was it the 'key factor', that most related to K . Rather neonatal mortality was sensitive to many different mortality agents, a conclusion also reached in other ungulate studies (Houston 1982; Skogland 1990; Clutton-Brock *et al.* 1992; Linnell, Aanes & Andersen 1995). Nutrition sometimes influences the size, vigour, and survival of newborn calves, and undernourished calves become more susceptible to diseases and predation. Other studies on ungulates have shown a strong relationship between reproductive success and the female's nutritional status (Verme 1963, 1967, 1969, 1977; Wegge 1975; White 1983). Thus, neonatal mortality is highly sensitive to many causes and is likely to be density independent.

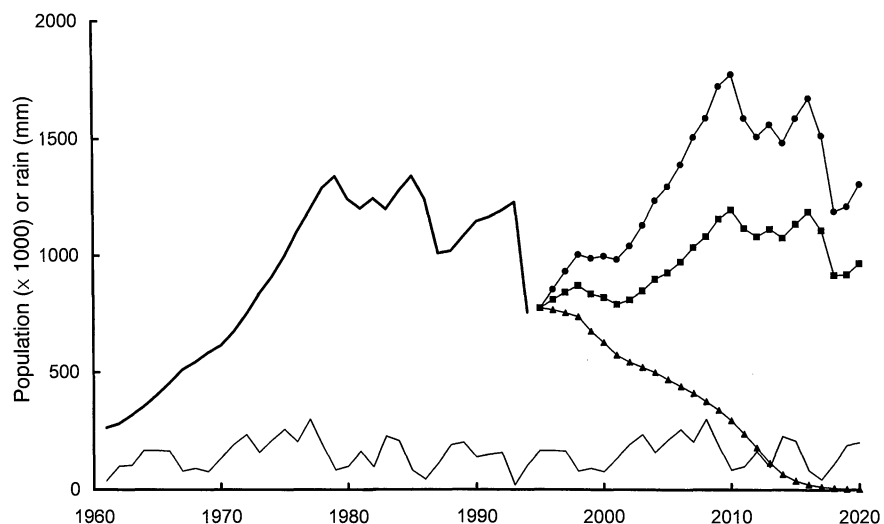


Fig. 9. Predicted wildebeest population trajectory from 1960 to 1994 estimated from the available data using relationships of dry season rain, food, and adult and calf survival (solid line) (Mduma *et al.* 1998). This model predicts the population from 1994–2020 under three levels of human harvesting, no harvest (\bullet), 40 000 animals yr^{-1} (\blacksquare), 80 000 animals yr^{-1} (\blacktriangle). Dry season rainfall (thin line) after 1993 is assumed to repeat the 1963–1989 pattern.

The decline in yearling pregnancy rate from 34% to 5.6% suggests a delay in sexual maturity. In most ungulate species the attainment of maturity is determined by size rather than by age. Growth is determined by nutrition, derived from food quality and quantity (Geist 1971; Grimsdell 1973; Sinclair 1977a; Laws 1981; Clutton-Brock *et al.* 1982; Skogland 1983; Saether & Haagenrud 1985; Clutton-Brock, Albon & Guinness 1988; Leader-Williams 1988; Owen-Smith 1990; Choquenot 1991; Gaillard *et al.* 1992; Saether & Heim 1993; Festa-Bianchet, Urquhart & Smith 1994; Langvatn *et al.* 1996). Hence, at high population densities less food per individual could result in reduced growth rate and therefore delayed maturity. However, our results produced no significant correlation between the change in yearling pregnancy rate and food available per individual. This was largely because the major change in yearling fertility took place early in the wildebeest population increase, before we could detect changes in per capita food supply. Despite the seemingly large change in fertility of this age-group, its effect on the total number of calves born per year was minor: yearlings contributed only 3% compared to 14% by 2-year-olds and 83% by adult females.

The decline in adult female fertility was density dependent and consistent with other studies of ungulates (Laws 1968; Caughley 1970; Geist 1971; Clutton-Brock *et al.* 1982; Houston 1982; Swenson 1985; Albon, Clutton-Brock & Guinness 1987; Milner-Gulland 1994; Clutton-Brock *et al.* 1997). In several published studies there is a relationship between fertility, nutrition and density (Caughley 1970; Geist 1971; Grubb 1974; Clutton-Brock *et al.* 1982; Loudon, McNeilly & Milne 1983; Albon *et al.* 1986; Leader-Williams 1988; Owen-Smith 1990; Clutton-Brock *et al.* 1991; Jorgenson *et al.* 1993; Saether *et al.* 1996). However, in the wildebeest the change in fertility was relatively small and it did not appear to be clearly related to food supply.

REGULATION

The life stage which showed the most statistically significant density-dependent response was adult mortality, most of which occurred in the dry season. Neonatal mortality, calf mortality in the dry season and yearling mortality all showed some (non-significant) suggestion of density dependence. Adult mortality can be interpreted either as a curvilinear response with negative feedback accelerating at high densities, or as two processes, one during population increase as a constant low value, and the other at high densities with a possible one-year delayed effect. A curvilinear response is consistent with earlier propositions that this is the mode of regulation in large mammals (Fowler 1981, 1987; Sinclair 1989,

1996; Saether 1997). Such curvilinear density dependence leads to a highly stable population with a monotonic approach to equilibrium and rapidly dampened fluctuations from environmental perturbations provided that the shape of the relationship at high density is less than unity, which it is in this case. With slopes greater than unity overcompensation can occur resulting in cycles or destabilizing oscillations (Grenfell *et al.* 1992; Clutton-Brock *et al.* 1997).

Adult mortality was inversely density dependent in the years of rapid population increase (Fig. 5). This mortality appears to be some constant whose proportional effect declines as population increases. A predator population that is not responding to the wildebeest increase could cause such a constant mortality. In fact, the main predators of wildebeest, lion and hyaena, did not increase in numbers as the wildebeest population grew (Hanby & Bygott 1979) consistent with our suggestion. In contrast, as the wildebeest population neared its carrying capacity it experienced undernutrition (as indicated by the bone marrow data, Table 7). The consequent mortality was added to the earlier mortality and this resulted in regulation and stability.

CAUSES OF POPULATION CHANGE

Food supply

Food supply appears to be the primary cause of mortality both limiting and regulating this migratory population consistent with other studies of migrants (Skogland 1985; Fryxell 1987; Fryxell & Sinclair 1988; Albon & Langvatn 1992). Adult mortality was negatively related to per capita food supply in the dry season throughout the period of study. As a result of the 1993 drought dry season calf mortality was also related to food supply, and yearling mortality tended in this direction. Neither pregnancy rate nor neonatal mortality were related to dry season food supply, which may be expected because both are influenced largely by events in the wet season.

Food supply affected the fat reserves in animals. The last reserves to be used before starvation sets in are those in the long bones (Ransom 1965; Sinclair & Duncan 1972; Hanks 1981). In dead animals the marrow class with lowest fat (translucent gelatinous) occurred most frequently in the dry season in non-predation cases. In addition, this class increased in frequency as the population density increased from the 1970s to 1990s (this study and Sinclair 1979b; Sinclair *et al.* 1985; Sinclair & Arcese 1995).

Rainfall in the dry season was the most important extrinsic determinant of food supply for the wildebeest population. Earlier studies documented the relationship between rain and dry season grass growth (Sinclair 1977a, 1979b; McNaughton 1979). The

drought of 1993 produced the lowest rainfall yet recorded and extended the dry season by several months. This resulted in extremely low food availability and it allowed us to detect the major stages producing fluctuation and regulation. Other large die-offs resulting from starvation and dehydration are not unusual in ungulates (e.g. Klein & Olson 1960; Caughley 1970; Reimers 1983; Leader-Williams 1988; Owen-Smith 1990; Clutton-Brock *et al.* 1991, 1997; Saether 1997). It is noteworthy that none of the lifestage mortalities in Serengeti wildebeest were significantly correlated with absolute amounts of food available (i.e. food per hectare). Food was related to mortality only when population density was incorporated (food per hectare per individual). In other studies food-limited populations appear to fluctuate when fecundity is not density dependent (Clutton-Brock *et al.* 1997; Saether 1997) but we have not yet detected such influences in the wildebeest population of Serengeti.

Predation

Predation played only a minor role in limiting the wildebeest population. First, less than 3% of adult females died from predation so its effect on the number of births was small. One reason for this small impact was long distance migration (Hilborn & Sinclair 1979; Maddock 1979; Fryxell & Sinclair 1988; Fryxell, Greever & Sinclair 1988). Migration creates a temporary refuge because predators have difficulty in adjusting their reproductive needs for denning sites to the mobility of their prey. Because of the temporary absence of migrating prey, the numerical response of predators is limited by the less numerous resident prey species. Even hyaena, which can commute for longer distances (Hofer & East 1995), cannot follow the wildebeest throughout their migration; hyaenas do not commute into northern Serengeti where there are also very few resident hyaenas. Hence, migrant wildebeest experience very low predation rates when they are in northern Serengeti in the dry season.

A second reason for low predation is the aggregation of herds on the plains in the wet season and the synchrony of births at that time. Wildebeest show extreme birth synchrony (Watson 1967; Estes 1976; Sinclair 1977a,b) as do caribou (*Rangifer tarandus* Linnaeus) (Bergerud 1974; Dauphine & McClure 1974), moose [*Alces alces* (Clinton)] (Van Ballenberg & Miguella 1993) and other ungulates (Spinage 1973; Rutberg 1987). Such synchrony may be providing protection through predator swamping (Estes 1976); predators' functional and numerical responses are constrained by the short time that newborn calves are vulnerable.

IMPLICATIONS FOR CONSERVATION

The Serengeti wildebeest population has apparently reached its environmental carrying capacity under the present rainfall regime. We have estimated the trajectory of the population using the relationships of rainfall, food, and adult and calf survival up to 1991 (Fig. 9), the equations being given in Mduma *et al.* (1998). No downward trend was detected before 1993. The drop in 1993 was predicted from the parameters estimated up to 1991 and did not require a revision of the food and rainfall dynamics. Using this model and a return to pre-1993 rainfall conditions we predict the trajectory of the wildebeest population subsequent to 1994 under three regimes of human harvesting. Illegal harvesting (poaching) is analysed in Mduma *et al.* (1998) where we considered both a putative but unlikely maximum offtake (80 000 animals yr⁻¹) and the upper confidence bound of our measured offtake (40 000 animals yr⁻¹). These are compared to a no harvest regime. With a harvest of 40 000 animals the population should return to about 1.2 million animals in about 15 years. The census of 1998 obtained subsequent to the model calculations gave 923 000 which is consistent with an offtake of 20 000 animals yr⁻¹, close to our most likely estimated value (Mduma *et al.* 1998). With no harvest we predict the population should rise to an unprecedented level of 1.6 million. However, with an offtake of 80 000 animals yr⁻¹ the harvest is unsustainable and the population will collapse.

Although illegal harvesting of this population has been a conservation concern since the 1970s (Dublin *et al.* 1990; Campbell & Hofer 1995; Mbano *et al.* 1995), our combined results here and in Mduma *et al.* (1998) suggest that poaching offtake has played a minor role in limiting population size. We do, however, add the caveat that if human populations continue to increase at the park boundary as they have in the past 20 years, or if rainfall decreases, the effect of human hunting could cause the collapse of the wildebeest population. Such a change would alter the whole Serengeti ecosystem (Sinclair 1979a, 1995).

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Appendix 1

ESTIMATES OF CALF AND YEARLING SURVIVAL

Calf and yearling survival was estimated from the changes in the calf/female or yearling/adult ratios by fitting a model of wet and dry season survival to observed counts of females and calves. This estimate was possible only for years when at least 5 months of monthly ratios were available (9 years, see text).

The underlying method assumes that in each month (m) the herd of wildebeest contained (F_m) adult females and calves (C_m), and the monthly survival rates of adult females was s_F and calves s_C . The temporal dynamics for females and calves, and their expected ratio (R_m) are therefore:

$$F_{m+1} = F_m s_F \quad \text{eqn A1}$$

$$C_{m+1} = C_m s_F \quad \text{eqn A2}$$

$$R_m = C_m / F_m \quad \text{eqn A3}$$

The adult female survival rate (s_F) was assumed to be known from adult mortality data (described below) (Tables 3,4). When the same survival is assumed for wet and dry season the model estimated two parameters, the calf survival rate (s_C), and the ratio in the first month (R_1). For purposes of calculation an arbitrary number of females in month 1 is specified, the number of calves in the whole population is then calculated from R_1 , and all future R s are predicted using equations A1, A2 and A3. For all months the expected number of calves seen in the transect counts $E(Y_m)$ is obtained from the observed number of females seen in the transect counts (X_m) and the predicted ratio (R_m):

$$E(Y_m) = X_m R_m \quad \text{eqn A4}$$

Thus we can use equations A1–A4 to predict the observed number of calves seen in each month's transect counts (Y_m) from the observed number of females seen in the transect counts (X_m), by estimating two parameters, the calf/female ratio in month 1 (R_1), and the calf survival rate (s_C).

The log-likelihood method

We assumed that the difference between observed and predicted number of calves was log normally distributed (and exploratory analysis of the data indicated that the variance increased with the magnitude of the observed calf count). The likelihood of the predicted calves seen ($E[Y_m]$), given the observed number seen (Y_m) and the model parameters (R_1 and s_C) given a log normal likelihood (Hilborn & Mangel 1997) is:

$$L[Y_m | R_1, s_C, X - m] = \frac{1}{\sigma \sqrt{2\pi}} \frac{1}{Y_m} \exp \left\{ - \frac{\ln(Y_m) - \ln(E[Y_m])^2}{2\sigma^2} \right\} \quad \text{eqn A5}$$

The standard deviation (σ) is estimated as:

$$\hat{\sigma} = \sqrt{\frac{\sum [\ln(O) - \ln(P)]^2}{n - p}} \quad \text{eqn A6}$$

where n is the number of months, and p is the number of parameters estimated.

We considered two nested models, one where the calf survival was the same in both wet and dry season, and another in which wet-season survival was different from dry-season survival. In the former case $p = 2$ (R_1 and one calf survival), while $p = 3$

when we allow for a difference between wet and dry season survival of calves.

Calculation of yearling survival was made in a similar manner.

Confidence bounds for calf and yearling survival

Confidence bounds on the estimated calf (or equivalent yearling) survival rates s_C were estimated by the likelihood profile (Hilborn & Mangel 1997) as follows. First, the maximum likelihood estimates for wet and dry s_C were calculated using equations A5 and A6. Then the negative log-likelihood (negative log of values from eqn A5) was computed. The 95% confidence bounds were obtained by using the likelihood ratio test (Hilborn & Mangel 1997).

The maximum likelihood (or minimum negative log-likelihood, L_{best}), computed from equation A5, gave the best estimate of calf survival $s_{C(best)}$. Incremental values either side of $s_{C(best)}$ were then taken and associated negative log-likelihood values calculated to obtain a likelihood profile. The 95% 'support limits' for the parameter $s_{C(best)}$ (analogous to the 95% confidence interval, Zar 1984) includes all values having negative log-likelihood values less than ($L_{best} + 1.96$) units (Zar 1984, p. 94).

Appendix 2

ESTIMATES FOR ADULT MORTALITY

The estimates for daily adult mortality were calculated from the observed distribution of deaths recorded on the transects in the following way. The probability of an animal dying on a given transect and day is small and should follow a Poisson distribution (Steel & Torrie 1980, p. 395). Thus, the probability of k deaths in the Poisson distribution is:

$$\Pr(X = k) = e^{-u} u^k / k! \quad \text{eqn A7}$$

where $\Pr(k)$ is the probability of k deaths, given the expected number u from such a distribution. The number of carcasses found (k) is known from data. The object was to find the 'most likely' daily mortality rate (m_d) that is most consistent with the observed data. The expected number of carcasses (u) is the number of animals in the area searched (n_t), times the daily mortality rate (m_d). For a single transect, the mortality rate that maximizes the probability [$\Pr(k)$] is the number of carcasses (k) divided by the number of animals (n_t) in the area searched. Within a month we have a variable number of transects and days, and the log-likelihood method was used to calculate the 'most likely' adult daily mortality rate m_d over all days and transects. This was achieved by minimizing the negative log-likelihood [$-l(u/k)$] using the non-linear function SOLVER in

Microsoft® EXCEL V. 5. The negative log-likelihood of u given the number of carcasses found in a particular transect k is obtained from the Poisson distribution such that:

$$-l(u/k) = u - k \ln(u) + \ln(k!) \quad \text{eqn A8}$$

The estimated mortality rate m_d found by minimizing equation A8 was used to calculate the expected daily number of deaths for each transect and day ($u_{T,D}$) from:

$$u_{T,D} = N_{T,D} \cdot m_d \quad \text{eqn A9}$$

where $u_{T,D}$ is the expected number of carcasses to be found on transect T and date D , $N_{T,D}$ is the number of live individuals in the searched area for that transect T and date D , m_d is the 'most likely' daily mortality rate over all transects and days.

Finally, daily mortality rate was averaged for the whole area but for each month separately.

Appendix 3

CALCULATIONS FOR THE WILDEBEEST LIFE TABLE (TABLE 5)

The following assumptions were made in constructing the life table: (i) all censuses were conducted in March and do not include the number of neonates; (ii) estimates of potential pregnancy rate refer to June which is the end of the rutting season; and (iii) estimates of realized (measured) pregnancy rates refer to March which is the end of the calving season. We also assumed that all calves are born in March.

We use the following notation:

$N_{c,m,yi}$ number of calves (< 1 year) in month mi and year yi .

$N_{y,m,yi}$ number of yearlings in month mi and year yi .

$N_{ad,m,yi}$ number of adults (> 2 years) in month mi and year yi .

$N_{pp,yi}$ number of potentially pregnant adult (> 2 years) females in year yi .

$N_{op,yi}$ number of pregnant females in year yi .

$C_{mi,yi}$ proportion of the population that is calves (< 1 years) in month mi and year yi as shown in Table 2 and estimates from the seasonal log normal model.

$Y_{mi,yi}$ proportion of the population that is yearlings ($1 \leq 2$ years) in month mi and year yi from data in Mduma (1996).

T_{yi} total wildebeest population in March, from censuses and interpolation.

$m_{a,yi}$ adult annual mortality rate (< 2 years) in year yi .

$s_{m,yi}$ adult monthly survival rate in year yi .

$p_{p,yi}$ potential pregnancy rate which refers to all adult (> 2 years) females in year yi . We assumed that adult females constituted 45% and 58% before 1990 and after 1990, respectively, based on measures of adult sex ratio.

$p_{o,yi}$ adult pregnancy rate in year yi (Table 1).

STEPS

Columns indicated below refer to those in Table 5.

1. The starting point was the wet season census assumed to occur in March. Where a census was not conducted we used a smoothing curve to interpolate population size in March (T_y) (column 3).

2. The number of yearlings in January of year yi was obtained by multiplying the March population size of year yi by the proportion of calves in the December of year $yi-1$, that is:

$$N_{y,yi} = T_{yi} \cdot C_{Dec,y-1} \quad \text{eqn A10}$$

3. Thus, in January the population is composed of adults (> 2 years) and yearlings (column 2). The adult population is obtained by subtracting the yearlings from the March population size (**Note:** the March population size does not include young of the year) to give column 4:

$$N_{ad,yi} = T_y - N_{y,yi} \quad \text{eqn A11}$$

4. The annual adult mortality rate is 1 minus the ratio of adults in year yi to adults plus yearlings in year $yi-1$:

$$m_{a,yi} = 1 - [N_{ad,yi} / (N_{ad,yi-1} + N_{y,yi-1})] \quad \text{eqn A12}$$

which in Table 5 is simply computed by (column 2 - column 4) / column 2 for year yi .

5. The monthly adult survival rate is therefore:

$$s_{m,yi} = \sqrt[12]{(1 - m_{a,yi})} \quad \text{eqn A13}$$

Thus the adult monthly population size is reduced by monthly survival rate (assuming equal mortality). The estimated survival rate covers the period from March to February.

6. From the estimated adult population size in June, the number of potentially pregnant females (column 8) in year yi is given by:

$$N_{pp,yi} = N_{ad,yi} \cdot p_{p,yi} \quad \text{eqn A14}$$

7. The realized pregnancy and hence calves born in March (column 9) of year yi is:

$$N_{op,yi} = N_{ad,yi} \cdot p_{o,yi} \quad \text{eqn A15}$$

8. Estimates of calves alive in March (column 10) were obtained from the proportion of calves in the March population census:

$$N_{c,Mar,yi} = T_{yi} \cdot C_{Mar,yi} \quad \text{eqn A16}$$

9. Estimates of calves alive in June and December (columns 11 and 12) were obtained by multiplying the proportion of calves in June and December by

the adult population size in those months:

$$N_{c,m,yi} = C_{mi,yi} N_{ad,m,yi} \quad \text{eqn A17}$$

10. The numbers of yearlings in January, June and December (columns 5, 6 and 7, respectively) were obtained by multiplying the proportion of yearlings in January, June and December by the number of adults in their respective months:

$$N_{y,m,yi} = Y_{mi,yi} N_{ad,yi} \quad \text{eqn A18}$$

Appendix 4

The life table mortalities (k -values) were calculated in terms of the population size before (I) and after (F) the reduction occurred:

$$k\text{-value} = \log(I) - \log(F) \quad \text{eqn A19}$$

i) *Fertility loss* ($k-1$). The decrease in fertility was measured from the proportion of adult females that did not become pregnant in year t_i relative to the potential maximum. For wildebeest, the potential maximum included all females 2 years and older (Sinclair 1977a). The fertility rate was obtained over 8 years from autopsies and faecal samples in the present study (1992–1994) and published records (Watson 1967; Sinclair 1977a). The number of potential mothers (I_1) was:

$$I_1 = N_i p_{Ad} r_s \quad \text{eqn A20}$$

and the number of adult females which were pregnant (F_1) was:

$$F_1 = I \cdot r_p \quad \text{eqn A21}$$

where N_i = population size in year i (census estimate), p_{Ad} = proportion of adults in year i , r_s = proportion of females (> 2 years) in the adult population, i.e. Females/(Females + Males); and, r_p = pregnancy rate.

For book-keeping purposes we assumed all pregnancy measures were taken in March and represent the birth rate because resorption and abortion of fetuses was negligible (Sinclair 1977a).

ii) *Neonatal mortality* ($k-2$). Neonatal mortality refers to the number of calves that died before they were 4 months old, i.e. those that did not survive to June. This period provided estimates of wet-season survival rates. Neonatal loss ($k-2$) was calculated as the difference between number of calves born (I_2) (from the pregnancy rate) and those which survived to June (F_2) calculated from the June calf/female ratios. Eight years data were available.

iii) *Dry-season calf mortality* ($k-3$). Dry-season calf mortality represented the proportion of calves dying during the dry season in their first year (July–December). The initial number (I_3) was the number of calves in June and final number F_3 was the number of calves in December from the calf ratio at that time, and 16 years data were available.

iv) *Yearling mortality* ($k-4$). This is the proportion of yearlings that died between the ages of 11 months and 24 months. The number of yearlings at the beginning of each year (I_4) was estimated from the number of calves alive in December of one year, and F_4 was the number of yearlings in the following December. Only 4 years data were available.

v) *Adult mortality* ($k-5$). Adult mortality was calculated as the difference between adults plus 24-month yearlings in January (I_5) and the adults (F_5) in the following December. The estimated annual mortality was then expressed on a monthly basis and used to calculate life table schedules. Some 34 years data were available. To verify the mortality rate from the life table we compared these estimates with independent measurements from the carcass counts described above and previously published data (Sinclair 1979b).