The decline of the Serengeti Thomson's gazelle population

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Summary. The population of Thomson's gazelles in the Serengeti National Park, Tanzania has declined by almost two thirds over a 13 year period. In the early 1970s, numbers stood at 0.66 million animals but had decreased to less than 0.25 million animals in 1985 as estimated by 5 different censuses using two different counting techniques. Predation, interspecific competition and disease are all factors that could have contributed to this decline, and at least one of these factors, predation, could now prevent the Thomson's gazelle population from increasing.

Key words: Thomson's gazelles – Serengeti population decline – Predation – Interspecific competition – Disease

Monitoring changes in East Africa's ungulate community is an important enterprise because, when conducted in relatively undisturbed conditions, it increases understanding of how savannah ecosystem diversity is maintained, and provides the opportunity to detect a species' decline and to devise appropriate management policies. In the Serengeti ecosystem, aerial censuses of selected ungulates have been conducted on an increasingly regular basis since 1961. Two main findings emerge from these counts: wildebeests (*Connochaetes taurinus*) have increased from below 0.3 million animals in 1961 to between 1.3 and 1.5 million animals in 1977, but since then have levelled off at just below this figure (Sinclair et al. 1985). Zebras (*Equus burchelli*) however, have remained at approximately 0.2 million animals in all five censuses conducted since 1961 (Sinclair and Norton-Griffiths 1982). A third, more tentative finding has been a decline in the population of Thomson's gazelles (*Gazella thomsoni*) since 1972 but, because significant differences could only be found between 1972 and 1980, and not between 1978 and 1980, there was always a possibility that the apparent decrease could have been attributable to changes in bias errors as noted by Sinclair and Norton-Griffiths (1982). In the first part of this paper, we extend these data by presenting the reults of aerial censuses conducted in 1982 and 1985 using the same counting technique. Furthermore,

the census made in 1985 was repeated four more times, using more sensitive counting techniques, in order to confirm and strengthen the results. Together, these observations show the Serengeti Thomson's gazelle population has declined markedly.

The fact that numbers of some of the Serengeti ungulate species have changed considerably in the last 20 years, while others have changed little, has led to a number of theories on the processes that regulate migrant ungulate populations (e.g. Sinclair and Norton-Griffiths 1982). These include predation, interspecific competition and disease. In an ambitious exercise, Sinclair (1985) attempted to tease apart these theories using a natural disturbance, namely the influx of wildebeests into the northern part of the Serengeti ecosystem in the dry season. On the basis of predictions made as to what changes might occur after wildebeests moved into an area; in terms of use of short green grass, habitat overlap and herd distances from wildebeests, he concluded that both Thomson's gazelles and Grant's gazelles (*Gazella granti*) were strongly influenced by predation in the Masai Mara Game Reserve, and that interspecific competition was unlikely to regulate their populations. Some of Sinclair's predictions of anti-predator benefits that animals might gain from associating with wildebeests (see Bertram 1978) are based only on general hypotheses of the advantages derived from group membership. Until the vigilance and anti-predator behaviour of individual gazelles temporarily residing in mixed species herds of known composition are better understood, and changes in the probability of predatory attack in these aggregations are known, it may be impossible to make accurate statements about the benefits that species derive from associating with wildebeests. Moreover, the use of indirect evidence to infer the importance of predation, without close observation of individual gazelles and their herds (FitzGibbon, unpublished work), their anti-predator behaviour (Caro 1986), the behaviour of their predators (Kruuk 1972; Schaller 1972), and at least rough estimates of killing rates by different predator species, is unlikely to provide an adequate description of the processes of population regulation.

In the second part of the paper, therefore, we discusss the major factors that could have brought about the decline in the Thomson's gazelle population in recent years. By presenting the available information on each one, it is possible to begin to assess their relative importance. It also suggests the most important avenues for future research on this topic.

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Methods

Gazelle censuses 1972, 1978, 1980, 1982

Weekly reconnaissance flights were carried out to determine the time when wildebeests were out on the Plains (see Sinclair 1979 for a general description), and when they were spread out evenly. When this had occurred, a preliminary survey was flown to mark the boundaries of the wildebeest distribution on a 1:250,000 map. Aerial transects were flown within this area, usually 4 km apart. Vertical aerial photographs of gazelles were taken with a motor-drive, longbacked F1 Nikon camera with 180 mm lens clamped to the outside of the aircraft door. Flying height was about 1200 feet above ground, controlled by radar altimeter. As a check on pilot, and hence census, accuracy, the front seat recorder noted the altitude using the radar altimeter about once every min. To obtain a subsample of the transect, photographs were taken at intervals which varied according to the distribution of the wildebeests (between 5 and 30 s). Gazelles were counted from the frames and analysed according to Jolly's method No. 2 for unequal-sized sampling units (see Norton-Griffiths 1978; Sinclair and Norton-Griffiths 1982).

Gazelle censuses 1985: systematic reconaissance flight method (SRF)

In 1985, a new method of censusing gazelles was initiated. This was done in order to be sensitive to the particular pattern of distribution of gazelles, in order that Thomson's gazelles and Grant's gazelles could be distinguished from the aircraft, and so that results could be analysed immediately.

Weekly reconnaissance flights were carried out to determine when all the gazelles were out on the Plains and were evenly distributed. Note that the wildebeest distribution, which differs somewhat from the Thomson's gazelle distribution in the wet season (Maddock 1979), was not taken into account in these new censuses. A preliminary survey was flown to determine the boundaries of the gazelle distribution on the Plains. This was marked on a 1:250,000 map and aerial transects were flown within this area, 4 km apart. Strip width was marked with streamers and two experienced observers counted Thomson's and Grant's gazelles separately be speaking into tape recorders. Flying height was 300 feet and strip width (nominal) was 150 m on each side of the aircraft. The front seat observer noted radar altitude at 1 min intervals to allow accurate calculation of actual transect widths. The areas of the census zones were 2508 km^2 and 3260 km^2, the number of transects were 11 and 29, and the numbers of possible transects were 156 and 435, respectively for March and May 1985 censuses.

"Brown animal" censuses: 1985

In addition to these gazelle censuses, two additional censuses were made of all the ungulate species, using the SRF method. Both censuses were conducted in May 1985, one covering the Plains only, while the other covered the Plains and woodlands. Flying height was a nominal 300 feet with a nonimal strip width of 150 m on each side of the aircraft. All species except elephant (*Loxodonta africana*), rhinoceros (*Diceros bicornis*) and buffalo (*Syncerus caffer*) were counted. Analyses of Thomson's and Grant's gazelle counts were carried out according to Jolly's method No 2.

Table 1. Predation rates on adult Thomson's gazelles after Schaller (1972) and Kruuk (1972); see Appendix for methods of calculation. Lion, leopard and spotted hyaena rates are shown reduced by a third in the 1970s and two thirds in the 1980s

Predator species	Adult Thomson's gazelles killed per predator per year					
	Plains			Woodlands		
	1960s	1970s	1980s	1960s	1970s	1980s
Lion	0	0	0	3.34	2.22	1.10
Cheetah	27.90[a]	27.90[a]	27.90[a]	–	–	–
Leopard	0	0	0	4.88– 5.85	3.25– 3.90	1.63– 1.95
Hunting dog	6.69[a]	4.46[a]	2.23[a]	–	–	–
Spotted hyaena	1.28– 3.90	0.85– 2.60	0.43– 1.30	0.45– 1.37	0.30– 0.91	0.15– 0.46

[a] Both plains and woodlands

Gazelle census 1985: photographic count

In order to link the SRF counting method to censuses in previous years, a photographic census of the Plains was also made in March 1985. Methods employed here were as in the 1972–1982 censuses except that flying height was approximately 400 feet an the camera lens was 55 mm, which provided approximately the same area per picture frame as in counts of previous years. The lower altitude was chosen so as to gain a better view of whether Thomson's gazelles were in the frames. If none were, no picture was taken, but the hypothetical frame was counted as zero gazelles. The pictures taken in this count represent only a subsample of the transect area. The total number of animals in a transect was therefore calculated by multiplying the animals found on the photographs by the ratio of transect area to the area photographed.

Estimating predator pressure on the Thomson's gazelle population

Predation rates on adult gazelles. To assess the impact of predators on the Thomson's gazelle population, we need to compare the number of adults killed by predators to the number of juveniles recruited into the adult population. Schaller (1972) assessed the effects of the five major predators (lion *Panthera leo*, cheetah *Acinonyx jubatus*, leopard *Panthera pardus*, hunting dog *Lycaon pictus*, and spotted hyaena *Crocuta crocuta*) on Thomson's gazelles in various parts of the ecological unit during the late 1960s. In general, the number of animals taken were based on "known killing rates coupled with the availability of gazelle in various parts of the ecological unit" (Schaller 1972:401), in an effort to correct for the annual temporal and spatial changes in gazelle distribution relative to their predators (see Table 1 and Appendix).

Since Schaller's study, no comparable estimates have been made of the relative proportions of the various prey species in the diets of these predators; unfortunately, Frame's (1986) analysis did not provide annual killing rates across the entire ecosystem. In the absence of more recent data, the rates used by Schaller have been assumed to apply

to the predator and prey propulations of the mid 1970s and 1980s.

Strictly speaking, the assumption of fixed predation rates through time should apply only if diet selection by the different predators and their killing rates on gazelles remain unchanged in response to changes in the abundance of their prey species. How realistic is this assumption? In the absence of reliable functional response models (see Hilborn and Sinclair 1979) incorporating gazelles and other prey species, we can, at present, only speculate about the quantitative changes which might have occurred in predator diets. On the Serengeti Plains, cheetahs specialize on Thomson's gazelles, and their diet has changed relatively little since the 1960s (T.M. Caro, unpublished work). Hunting dogs, because of their low and declining population size, have had relatively little impact on the gazelles at any point in recent time, and the number killed in the 1970s and 1980s can be considered almost negligible.

Lions, spotted hyaenas, and leopards prefer wildebeests, zebras and woodland ungulates, with adult Thomson's gazelles comprising only 1.5%, 2.5–7.5%, and 6% of their annual meat consumption respectively in the late 1960s (calculated from Schaller 1972; Kruuk 1972). By comparison, wildebeests made up 20–25% and zebras 30% of lions' diets (Schaller 1972). The diets of these larger predators could have shifted further from gazelles to alternate prey if the populations of the latter increased and/or gazelles declined in number. During the mid 1970s, absolute gazelle numbers remained relatively constant, so their availability to predators would not have changed, but wildebeests increased twofold, altering *relative* abundances. The larger predators might thus have taken relatively more of this alternate prey (but see Sinclair and Norton-Griffiths 1982, who report lions' predation rates on zebras to have remained constant from the 1960s and 1970s). By the mid 1980s, gazelles had declined by a factor of three (see below), while the wildebeest population remained at its mid 1970s level. For the sake of argument, we suggest a liberal figure for a decrease in gazelle killing rate of one third in the 1970s, and two thirds in the 1980s of the 1960s levels for these three predator species.

Predator populations and numbers of gazelles killed. Since Schaller's study, accurate censuses or population estimates of large predators have been confined to the Serengeti Plains and its margins: predator censuses were carried out in May 1977 (S.N.P. Report No 52) and May 1986, while demographic studies followed the trends in lion (e.g. Pusey and Packer 1987), cheetah (e.g. Caro and Collins 1986) and hunting dog (e.g. Frame et al. 1979) numbers. There is little reliable information as to whether woodland predator numbers have increased appreciably; resident prey populations have remained relatively stable in the northern and central regions (Hanby and Bygott 1979; Hilborn and Sinclair 1979) or have increased only slightly (M. Borner, unpublished work), but appear to have increased significantly in the western corridor and Plains areas (Hilborn and Sinclair 1979; M. Borner, unpublished work). Lion populations on the Plains and in the woodlands along the northwest margin of the Plains are known to have changed, the latter by a factor of 1.37 (1970s) and 1.67 (1980s) over the 1967 level (C. Packer and A. Pusey, unpublished work). In the absence of extensive data on woodland lion numbers, no comparable increases outside the study area can neces-

Table 2. Changes in numbers of predators in the Serengeti ecosystem. Also shown are estimated numbers of adult Thomson's gazelles killed per annum, assuming no change in killing rates since the 1960s

	Predator numbers			Adult Thomson's gazelles killed
	Plains	Non-Plains	Ecosystem	
1960s				
Lion	25[a]	1975–2375	2000–2400[b]	6597– 7933[c]
Cheetah	–	–	200–250[b]	5501– 7251[b]
Leopard	0	800–1000[b]	800–1000	3900– 5850[b]
Hunting dog	–	–	250–300[b]	1673– 2007[b]
Spotted hyaena	2100[d]	900[d]	3000[d]	3871–11701[bd]
			Total:	21628–34742
1970s				
Lion	79[e]	2003–2403[f]	2082–2482	6690– 8026
Cheetah	251[g]	–	500[h]	13955
Leopard	0	800–1000[b]	800–1000	3900–5850
Hunting dog	42[i]	–	42	281
Spotted hyaena	3393[g]	900	4293	4746–14461
			Total:	29572–42573
1986				
Lion	110[j]	2025–2425[k]	2135–2535	6764– 9100
Cheetah	464[l]	–	564[m]	15736
Leopard	0	800–1000[b]	800–1000	3900– 5850
Hunting dog	46[n]	–	46	308
Spotted hyaena	4261[o]	900	5161	5857–17846
			Total:	32565–48840

[a] 1967 figure (C. Packer and A. Pusey, unpublished work); [b] Schaller (1972); [c] recalculated from Schaller (1972) if Plains lions take no gazelles (Packer and Pusey, unpublished work); [d] Kruuk (1972); [e] Mean of 1974–1979 figures (Packer and Pusey, unpublished work); [f] recalculated from 1960s figure using woodland-edge population (= 75 in 1967) increase of 1.37 (Packer and Pusey, unpublished work); [g] 1977 predator census; [h] Frame, cited in Hanby and Bygott (1979); [i] Mean of 1974–1977 Figs. of Malcom (1979), (J. Fanshawe, unpublished work); [j] 1986 figure (Packer and Pusey, unpublished work); [k] recalculated from 1960s figure using woodland population increase of 1.67 (Packer and Pusey, unpublished work); [l] recalculated from Caro and Collins (1986) to include cub equivalents (see Schaller 1972); [m] 100 added as a conservative estimate for the woodlands (TMC); [n] calculated from 1986 sightings by J. Fanshawe (see text); [o] 1986 predator census

sarily be assumed. Thus lion and spotted hyaena population changes have been estimated by combining recorded increases on the Plains with Schaller's (1972) figures for the non-plains segments of the ecosystem. Estimates of lion population sizes in the woodlands were additionaly increased by incorporating the rates of increase for the woodland study area (see Table 2).

The bulk of the cheetah population is considered to occupy the Plains and its margins, as the few recent surveys of the woodlands (Caro and Collins, unpublished work) suggest that densities there are lower than on the Plains.

Cheetah numbers for the 1970s were taken from the 1977 Plains predator census (251) and from Frame (cited in Hanby and Bygott 1979) as 500 for the entire ecosystem. This figure is double Schaller's (1972) estimate for the 1960s and may reflect differences in methodology rather than a genuine increase. The 1980s figure was taken from Caro and Collins (1986) as 309 adult animals. Using Schaller's age structure (2/3rds of the population were adult), this number was corrected upwards to give a total estimate of 464. A conservative estimate of 100 woodland cheetahs were added to this figure.

Leopards are found only in the woodlands (but see Frame 1986) and populations are thought to remained stable. The hunting dog population has been recorded chiefly on the Plains. Numbers in the 1970s were calculate by taking an average of the years 1974–1977 (from Fig. 1.8, Malcolm 1979). Numbers in the 1980s were estimated by multiplying 22 (total number of individuals in two packs in early 1986) by the percentage of the population that these packs represented between 1974 and 1977. Areas on the plains from which dogs are now believed absent were excluded; woodland numbers are unknown (J. Fanshawe, unpublished work).

The estimated number of gazelles taken by predators in given year was calculated by multiplying predator population estimates by the derived predation rates Table 1. For the purposes of this analysis, predator population age structures and social group sizes were assumed to have remained similar to Schaller's estimates.

Estimating recruitment of Thomson's gazelles. During each calendar month, Bradley (1977), in the 1970s, and CDF, in 1985, counted the relative proportions of different age-sex classes of Thomson's gazelles in order that the number of animals entering the population could be calculated, unbiased by the wet season birth peak. Animals were counted by driving transects through the main gazelle concentrations each month, stopping at 0.25 km intervals, and recording the age and sex of Thomson's gazelles within 200 m of the vehicle and in a 180° arc of the front of the vehicle (Bradley 1977). Gazelles were categorised as fawns and half-grown animals (0–4.5 months), adolescent females (4.5–8.5 months), adolescent males (4.5–12.5 months), subadult and adult females (>8.5 months), and subadult males and adult males (>12.5 months) in each group (Bradley 1977). In 1985, recording was terminated when over 1000 subadult and adult females had been counted each month (1527–3493 total animals per month). In both studies, the total number of individuals that were found in the fawn, adolescent female and adolescent male classes over the course of the year were then divided by the number of months individuals remained in those classes, 4, 4 and 8 months respectively, giving a monthly relative occupance by age class (Bradley 1977). For adults, the total number counted was devalued by the number of adolescent females and males likely to have entered the adult age class during that year. A female entering the adolescent age class in the first 1/3 of the year would have spent up to 8 months as an adult, whereas a female entering in the last 1/3 would spend as little as 0 months as an adult. Therefore, we assumed that adolescent females could be counted as adults in an average of 4 months of the year. As males spent 8 months as adolescents, they could be adults for 0–4 months, or an average of 2 months. We then multiplied the monthly relative age

class figure as calculated above, by 4 and 2 respectively for females and males, summed them and subtracted this figure from the total number of adults counted. This corrected adult total was then divided by 12 to give the monthly relative occupance for this age class.

The relative totals for adolescent females and males were summed and divided by the corrected adult total to give an estimate of percent annual recruitment into the adult population. Two years of data were available from Bradley (1977) and a mean annual recruitment rate for the mid-1970s was calculated.

Ground counts of gazelles and wildebeests. From July 1983 until February 1985, the presence of Thomson's gazelles and wildebeests was recorded at 99 points on the Serengeti Plains and plains-woodland border. Counts were made from specific points, usually more than 4 kms apart, from rises affording a good all-round view of an area known to be utilised by Thomson's gazelles. Every calendar month, each point was visited and the presence of absence of these two species within a 1 km radius was recorded by observers (TMC and DAC) (see Caro and Collins 1987) using 10 × 40 binoculars standing on the bonnet of the vehicle. A minimum of 19 days was set between repeated observations at the same point because it was found that gazelle numbers started to change appreciably after this period.

Collection and analysis of faecal parasites. To make a preliminary assessment of the condition of the Thomson's gazelle population, faecal samples from 44 individual Thomson's gazelles were collected on the Serengeti Plains in February and March 1986 because animals in poor condition are likely to have elevated faecal parasite loads. A vehicle was driven near a group of gazelles, and when an animal defaecated, its age-class, sex and reproductive condition were noted. Faeces were then collected within less than 5 minutes of being voided and were examined within 24 h. A 5 g sample of faeces was mixed with 30 ml of saturated salt solution and 0.3 ml of this slurry was pipetted into two chambers of a McMaster counting slide. The number of parasite eggs seen under the marked area was then counted.

Results

Size of the Serengeti gazelle populations

The number of gazelles counted in 1982 was $292,175 \pm 86,484$ (refers to 95% confidence limits throughout) (M. Borner, unpublished data, see Fig. 1).

Table 3 shows the results of the gazelle censuses for 1985. March and May SRF censuses of Thomson's gazelles on the Plains were remarkably similar, and when results were merged (Norton-Griffiths 1978), it was clear that there were less than 0.25 million Thomson's gazelles. The "Brown Animal" census on the Plains indicated this may have been somewhat of an overestimate; nevertheless the total population may number 0.275 million when Thomson's gazelles on areas of plains in the Western Corridor were included. The photographic census conducted in March was 83% of the SRF census for that month, suggesting that counts conducted in previous years may have underestimated the population size.

Table 3. Gazelle censuses 1985. Censuses apply to the Plains area only, except where indicated. Counts were merged according to the method described in Norton-Griffiths (1978)

Count	Method	Estimate	95% Confidence Limits
Summary of Results: Thomson's Gazelles			
March	SRF	238,879	29.0%
May	SRF	226,755	29.6%
March & May results merged	SRF	232,816	22.3%
March	Photographic	198,022	16.6%
May (Brown Animal)	SRF	201,280	24.0%
May (Brown Animal including corridor)	SRF	275,350	23.0%
Summary of Results: Grant's Gazelles			
March	SRF	18,277	43.0%
May	SRF	24,198	24.7%
March & May results merged	SRF	21,976	22.7%
May (Brown Animal including corridor)	SRF	31,877	25.0%
Merged Gazelle Estimates			
Thomson's Gazelles		232,816	22.3%
Grant's Gazelles		21,976	22.7%

Grant's gazelles were found to number $21,976 \pm 4989$ when March and May censuses were merged. However, there were 45% more Grant's gazelles counted when animals in the Westen Corridor were included.

When the merged Thomson's gazelle censuses for 1985 were plotted with earlier population estimates (Fig. 1), a clear decline is evident in Thomson's gazelle numbers over the last 13 years. The 1982 and 1985 census figures were significantly lower than all previous estimates ($P < 0.001$, d-tests, see legend), but were not significantly different from each other. The figure for each census was lower than the previous one, and indeed numbers in 1985 were only 36% of the numbers in 1972.

Factors affecting the Thomson's gazelle population

Predation. One factor which might have influenced the decline in the Thomson's gazelle population is the effect of predation. Table 2 shows the number of adult Thomson's gazelles that Schaller estimated were taken by predators per annum during his study period (1966–1969) in the whole ecosystem (21,600–34,700, Schaller 1972, p 402). Schaller also estimated the Thomson's gazelle population to be 180,000, (70.0%–71.1% of which may have been adults, Table 4) so if recruitment into the adult population in the late 1960s was similar to the 1970s (16.7%, see below), or 1985 (25.4%, see below), 21,000–32,500 animals respectively, would have been entering the adult population. In this case, predators would have accounted for 66.5%–165.5% of the adult recruitment. However, if a more realistic population estimate of Thomson's gazelles made in 1972 was used (0.66 million, Sinclair and Norton-Griffiths 1982), adult recruitment could have been
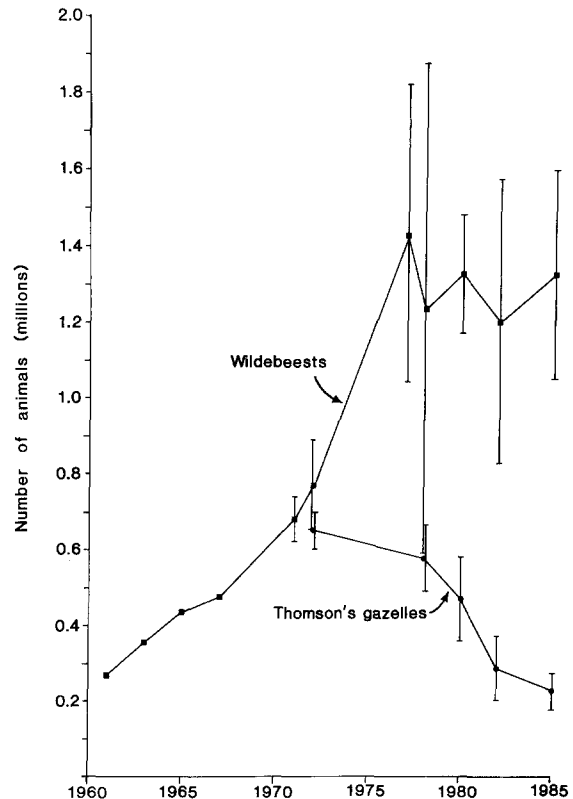

Fig. 1. Changes in the Serengeti Thomson's gazelle population (*Gazella thomsoni*); means (circles) and 95% confidence limits are plotted against time. Gazelle numbers for 1972–1980 replotted from Sinclair and Norton-Griffiths (1982), except that the 1.086 correction factor for undercounting fawns was excluded. d-test values between years were as follows: 1972 v 1978, d = 1.385, NS; 1972 v 1980, d = 2.860, $P < 0.02$; 1972 v 1982, d = 7.191, $P < 0.001$; 1972 v 1985, d = 11.649, $P < 0.001$; 1978 v 1980, d = 1.486, NS; 1978 v 1982, d = 4.661, $P < 0.001$; 1978 v 1985, d = 6.768, $P < 0.001$; 1980 v 1982, d = 2.543, $P < 0.02$; 1980 v 1985, d = 3.845, $P < 0.001$; 1982 v 1985, d = 1.153, NS. Wildebeest (*Connochaetes taurinus*) numbers (squares) are also shown; 1961–1982 replotted from Sinclair et al. (1985); 1984 census from Borner ($1,337,849 \pm 275,597$ unpublished work)

78,600–118,600 animals, and only 18.2%–44.2% of this recruitment would have been lost through predation.

More accurate calculations are possible for the mid 1970s because of Bradley's (1977) work on Thomson's gazelle recruitment rates, and the predator census conducted in May 1977 (SNP Report No 52). Table 2 shows that predators may have taken as many as 29,600–42,600 adult Thomson's gazelles for the population. Using Bradley's figures for the age structure of the Thomson's gazelle population (Table 4), recruitment rate was estimated (see Methods) as 16.7%, or 69,500 animals entering the adult population (when total population was 0.59 million in 1978 (Sinclair and Norton-Griffiths 1982)). Predators are thus estimated to have taken a number of adult Thomson's gazelles equivalent to 42.5%–61.3% of the adult recruitment, a higher proportion than in the late 1960s. If it is argued that leopards, lions and spotted hyaenas were taking one third less Thomson's gazelles than formerly, predators are estimated to have accounted for 35.2%–47.7% of the adult recruitment at this time.

Table 2 shows that the increased numbers of carnivores based on the May 1986 predator census and other sources

Table 4. Thomson's gazelle population age structure; percentages in backets.

Adult and subadult males	Adult and subadult females	Adolescent males	Adolescent females	Fawns and half-growns	Total number counted
Bradley (1977) 1st year of study: raw data					
10170	19297	1682	697	2107	33953
(30.0)	(56.8)	(5.0)	(2.1)	(6.2)	
corrected for age class occupance (see text)					
9750	18600	2523	2091	6321	
(24.8)	(47.3)	(6.4)	(5.3)	(16.1)	
Bradley (1977) 2nd year of study: raw data					
7446	13723	1090	604	1756	24619
(30.2)	(55.7)	(4.4)	(2.5)	(7.1)	
corrected for age class occupance					
7174	13119	1635	1812	5268	
(24.7)	(45.2)	(5.6)	(6.2)	(18.2)	
Mean age class percentages for Bradley's two years					
(24.8)	(46.3)	(6.0)	(5.8)	(17.2)	
This study: raw data					
8534	17829	1505	1337	1437	30642
(27.9)	(58.2)	(4.9)	(4.4)	(4.7)	
corrected for age class occupance					
8158	16492	2258	4011	4311	
(23.2)	(46.8)	(6.4)	(11.4)	(12.2)	

Table 5. Number of scan-points on the Serengeti Plains and plains-woodland border in which Thomson's gazelles and wildebeests were found together or separately from July 1983 to February 1985. November to May were wet season months, June to October were dry season months. Probability values (two-tailed) associated with binomial tests comparing the number of scan-points where Thomson's gazelles were found with or without wildebeests are shown (because scan-points were preselected on the basis of where Thomson's gazelles were likely to be found)

Month	Gazelles and wildebeests	Gazelles only	Wildebeests only	Neither	P value
July	1	50	0	48	<0.0001
August	0	49	0	50	<0.0001
September	7	43	0	49	<0.0001
October	8	68	0	23	<0.0001
November	22	57	6	14	<0.0002
December	21	57	5	16	<0.0001
January	29	26	5	36	NS
February	15	41	4	36	<0.002
March	18	56	4	17	<0.0001
April	31	38	2	25	NS
May	13	68	0	15	<0.0001
June	2	66	0	28	<0.0001
July	4	61	0	31	<0.0001
August	0	53	0	43	<0.0001
September	6	61	0	29	<0.0001
October	6	57	0	33	<0.0001
November December	No data				
January	19	45	2	33	<0.002
February	29	20	5	6	NS

(see Methods) could have taken 32,500–48,800 adult Thomson's gazelles. Using the age structure of the population in 1985 (Table 4), recruitment was estimated at 25.4%, or 41,400 animals entering the adult population. Thus predators are estimated to have taken adult Thomson's gazelles equivalent to 78.7%–118.0% of the recruitment into the adult population. This is changed to 51.9%–65.2% of the annual recruitment if the same three predators are judged to have reduced their Thomson's gazelle killing rates by two thirds of 1960s levels.

In short, the increase in predator numbers and concomitant decrease in gazelle numbers is likely to have resulted in a growing predation impact on the Thomson's gazelle population over the last 20 years, even if predators' diets shifted substantially in response to these changes.

Interspecific competition. A second factor which could be affecting the numbers of Thomson's gazelles in the Serengeti is competition over grazing with other herbivore species. Sinclair and Norton-Griffiths (1982) suggested that the most likely species that has sufficient overlap of range and diet to bring this about is the wildebeest.

Overlap in range use is the first of three conditions necessary to demonstrate that feeding competition between wildebeests and Thomson's gazelles was occurring. Overlap during the dry season, which is the limiting time for ungulates (Sinclair 1975), would constitute the strongest evidence but, as Table 5 shows, dry season overlap between the two species on the Plains was negligible. Maddock (1979) described the clear separation which also occurs on a broader

scale of the ecosystem; in dry seasons, the bulk of the wildebeest population concentrates in the northern woodlands while the gazelles remain on the Plains-woodland margins and in the western woodlands. Moreover, during the wet season months of 1983–1985, when wildebeests occupy the Plains in large numbers, gazelles were consistently found in areas from which wildebeests were absent (Table 5). Nevertheless, despite their apparent lack of direct range overlap through much of the year, there may be overlap in their use of critical grazing areas through time. It is possible that as wildebeests leave the Plains in May, they consume much of the grass on the Plains-woodland boundary which would provide dry season grazing for the gazelles when they arrive in the same area later in July.

A second condition necessary to demonstrate competition between wildebeests and gazelles in the few areas where their ranges do coincide is dietary overlap in the species and plant parts which they consume. We have no data to support or refute this condition.

Finally, the third condition necessary to demonstrate competition would be numerical changes in the relative population sizes of the two species. In this instance numbers of Thomson's gazelles have continued to decline steeply after 1978 despite a levelling off of wildebeest numbers (Fig. 1), suggesting that effects of any direct dietary competition may be negligible or delayed.

Disease. A third factor which could have contributed to the decline in the Thomson's gazelle population is disease. In a preliminary investigation of this possibility, faeces of

adult Thomson's gazelles were examined for parasite eggs. In February and March 1986 adult Thomson's gazelles on the Plains had relatively low numbers of parasite eggs, the families *Strongyloidea* and *Trichostrongyloidea*, in their faeces (males, $N=20$, $\bar{X}=9.2$ parasite eggs in each faecal sample, SD $=9.2$; females, $N=19$, $\bar{X}=11.9$, SD $=17.0$). As in many species, lactating females showed consistently elevated parasite burdens compared to non-lactating females ($N=5$, $\bar{X}=17.6$, SD $=10.7$).

Two adult Thomson's gazelles were found dead on the Plains (and a third by M. Murray in September 1986, unpublished work). TMC had found only one dead adult Thomson's gazelle between March 1980 and December 1983 but found two dead in February 1986; suggesting increased adult mortality independent of predation, albeit of slender evidence. On post-mortem examination both animals were found to be in a similar, emaciated, condition. Gross pathological changes were confined to the intestines and draining mesenteric lymph nodes. These were severely congested, and inflamed, with mutiple ulcerated nodules in the wall of the small intestine. Histological examination showed that each nodule contained several adult male and female nematodes of the species *Paracooperia* and numerous rod-shaped bacteria, surrounded by an infiltration of chronic inflammatory cells. The bacteria were shown to be both Gram negative and Ziehl-Naelson negative, and therefore possibly either of the genus *Escherichia* or *Salmonella*.

Emigration. The "Brown Animal" count conducted in May 1985 covered the whole of the Serengeti but only increased the total numbers of Thomson's gazelles counted by 37%. No new aggregations or migratory routes of this species have been noticed by scientists over the last 14 years. For these reasons emigration is not thought to be responsible for the decline in numbers of Thomson's gazelles.

Poaching. It is unlikely that poaching could have been responsible for the fall in Thomson's gazelle numbers. There is virtually no poaching on the Serengeti Plains where Thomson's gazelles spend the wet season (MB, unpublished work). A large, though unknown proportion of Thomson's gazelles migrate to the plains-woodland border and stop there during the dry season (Maddock 1979); little poaching for meat occurs in these areas either (MB, unpublished work). The remainder which move into the Western Corridor during the dry season could be subject to poaching from snares or possibly pit traps but this activity is most frequent north of the Grumeti River, to where only a small percentage of the population move (at least during the 1970s). Moreover, populations of larger resident ungulates, which poachers prefer, have increased in this area over the last decade (M. Borner, unpublished work). Thus, although poaching could remove some animals from the southern part of the Western Corridor, the level of poaching in this area over the last 14 years is almost certainly insufficient to have been an important factor in bringing about the decline in the population.

Discussion

Results presented here demonstrate that the Serengeti Thomson's population has declined by roughly two thirds in the last 13 years. These results are based on censuses employing similar techniques conducted in 1972, 1978 and 1980 (Sinclair and Norton-Griffiths 1982) and by M. Borner in 1982 and 1985. Furthermore, an additional four, more sensitive, censuses in 1985 all confirm that the population currently stands at approximately 250,000 animals. Additional censuses are required to confirm whether the decline is levelling off as the lack of significant difference between 1982 and 1985 counts might suggest.

A number of factors could be responsible for this decline. One of these is the increased predator population in the Serengeti. Although there are difficulties in obtaining accurate estimates of predator numbers (Bertram 1976), two carefully conducted censuses in May 1977 and 1986, using the same methods, indicate a substantial increase in spotted hyaena numbers, and demographic studies have shown that lions have increased at least on the Plains and the fringing woodlands. The increase in the first species is thought to have occurred partially in response to the 500% rise in wildebeest numbers, resulting primarily from the disappearance of rinderpest after 1962 and secondarily from a 70% increase in dry season rainfall between 1971 and 1976 (Sinclair et al. 1985). The second factor may have brought about an increase in the number of resident prey on the Plains (Hanby and Bygott 1979) which has allowed lions and hyaenas to increase there. Together these increases in the number of predators, and consequently numbers of gazelles killed, could have swamped recruitment into the adult Thomson's gazelle population. This effect is exacerbated because predators would have taken a greater proportion of the now reduced Thomson's gazelle population than previously. At the very least, predators may now prevent the population from increasing, if their diet has not changed drastically, given that they could be taking an amount equivalent to 80%–120% of the adult recruitment. Even if diets have changed to some degree (see Methods), we have shown that predation should still be a major factor in limiting gazelle numbers now accounting for as much as 65% of the annual recruitment. This conclusion is similiar to that reached by Schaller (1972), and also by Sinclair (1985) working in the Masai Mara Game Reserve in Kenya, but is based on estimating the number of prey animals taken by predators, rather than in the latter case on inferences derived from associations between different ungulate species. Our estimated predation rates are admittedly crude, and more up to date figures on annual predator diets under current prey densities are clearly needed.

Thomson's gazelles were found in areas where wildebeests were absent, and support casual observations that the bulk of the wildebeest and Thomson's gazelle populations are found in slightly different areas on the Plains during the wet season (see also Maddock 1979). During the dry season, when food is likely to be limiting, there was extremely little overlap between the two species on the Plains and its margins. However, lack of such direct habitat overlap does not necessarily imply that species are not in competition. Species could be feeding on the same plant species in the same area but at different times. However, whether such range overlap, separated in time, actually results in competition depends on whether ungulates are eating the same food items and on the plants' response to grazing. Grazing by one species may facilitate the growth of plants common to the diet of both of them (McNaughton 1976), or it could reduce available forage later on in the

year. In short, the importance of interspecific competition can be clearly demonstrated or refuted only by examination of what is eaten in the presence and absence of other ungulate species in the area and rates of nutrient intake in these circumstances. Our results suggest that Thomson's gazelles do not overlap greatly in range use with wildebeests, but the effects of wildebeests on gazelles' energy intake at different times of year require critical examination. At present, we cannot exlude interspecific competition as a factor contributing to the Thomson's gazelle population decline.

Thomson's gazelles are known to suffer from anthrax, sarcoptic mange, haemonchus, lungworm, pleuritis, nephritis and orchitis (Schiemann, cited in Kruuk 1972), but the incidence of these diseases in past and current populations is unknown. The two dead animals autopsied had ulcerated small intestines and bacterial infections. However a small sample of apparently healthy adults had low parasite counts in their faeces. Whether disease caused the population's decline in the past is an open question, but its possible effect in the future demands further investigation.

This paper has shown that the Serengeti Thomson's gazelle population has fallen by nearly two thirds in 13 years, and has examined the factors that could have been responsible for this decline. Although it is difficult to determine what caused the decrease in numbers, there are three likely candidates. First, the increasing wildebeest population may have preciptated and contributed to the decline in Thomson's gazelles through interspecific competition over food. Second, increasing numbers of predators, resulting from the rise in the wildebeest and resident prey populations, may have been an important source of adult mortality, increasing in intensity as gazelle numbers decreased. New data are required to verify the assumption that predators' diets and killing rates have not altered dramatically since Schaller made his calculations in the 1960s. If they have not, we have estimated that predation is now sufficient to prevent the lowered Thomson's gazelle population from increasing. Finally, diseases may also have brought about the decline, and could be affecting the population now, but both suppositions require further research.

The numerical responses of the wildebeest and gazelle populations suggest that these factors may have acted sequentially or in combination. One possible scenario is that interspecific competition initiated the Thomson's gazelle population decline (if they were not already falling before 1972; see for example Hendricks (1970) who estimated the population as 980,000 in 1967–1968), but the effects were ameliorated by the run of wetter dry seasons between 1971 and 1976 (Sinclair and Norton-Griffiths 1982) resulting in a period of relative stability. Since 1977, when dry season rainfall returned to its former pattern, the effects of wildebeest competition may have been increasingly felt. At this time, the rising predator populations may have had an additional impact on the declining Thomson's gazelle population and exacerbated its decline.

Appendix

Schaller employed a variety of assumptions and methods of calculation for estimating the number of gazelles killed by the different predator species, with the exception of spotted hyaenas. For the latter species, Schaller cited Kruuk's (1972) data on prey consumption rates.

Lions. The "average lion" (summing across age classes and their relative requirements, Schaller 1972:278–279) was estimated to consume 2468 kg of prey biomass per year. Of this, 2.5% was Thomson's gazelles (p 219) of average weight 12 kg (p 453), giving a rate of 5.14 gazelles/lion/year. The relative proportion of adult gazelles (all animals greater than 12 months old, p 312) in the kill was 65% (calculated from the table on p 402), and thus each lion killed 3.34 adult Thomson's gazelles per year. C. Packer and A. Pusey (unpublished work) note that Schaller's data referred to lions inhabiting the woodlands or the plains-woodland fringe. They suggest that lions living exclusively on the Plains have negligible success in capturing adult gazelles.

Cheetahs. The cheetah population, numbering 200–250, one third of which were cubs, was composed of solitary individuals (28%) and group members (72%). Solitary individuals killed 150 prey/year, while members of between 54 and 72 groups (thus calculated to consist of 2.67–2.50 animals respectively, $\bar{X}=2.59$) killed 341 prey/group/year (pp 313–314). As 60% of all prey were Thomson's gazelles (pp 313–314), individuals killed 90.0 and each group member 79.0, for a total of 82.1 gazelles killed per year by the average population member. Some 34% of the gazelles taken were adults (p 394), giving a rate of 27.9 adults killed by each cheetah per year. This rate of predation on adults is likely to be an underestimate however (T.M. Caro, unpublished work).

Leopards. An adult leopard was thought to consume 1000–1200 kg of prey biomass per year, 10% of which was Thomson's gazelles at 12 kg average weight, giving a killing rate of 8.33 to 10.00 gazelles per year (p 401). Twenty per cent of the leopard population were cubs (<1 year old), which consumed 0.5 of an adult ration, so the effective "consuming adult" population was 90% of the total population size (p 292). Adult gazelles made up 65% of the total kill (p 292). Thus, at a consumption rate of 1000 kg/year, an "average leopard" would kill $8.33 \times 0.9 \times 0.65 = 4.88$ adults, while at 1200 kg, the kill would be 5.85 adults per year.

Hunting dogs. Each hunting dog appeared to kill 36.5 prey/year; although a rate of 55 per year is also mentioned (p 337), the former is more consistent with Schaller's text and final table (p 402). Of these, one third, or 12.17, were Thomson's gazelles. The relative proportion of adult gazelles in the kill was 55% (p 394), giving a consumption rate of 6.69 adults per hunting dog per year.

Spotted hyaenas. Kruuk's (1972) estimates of prey consumption rates by spotted hyaenas were based on dry season faecal samples taken from the Plains and woodlands of the Western Corridor (pp 63–81). The two sets of samples give widely differing predation rates, a possible reflection of differential gazelle abundance or vulnerability in the two habitats. However, as many of the roughly 2100 hyaenas in his study area included both plains and woodlands in their annual ranges, Kruuk felt that the different figures could represent maximum and minimum consumption rates over the whole area. Kruuk suggested that the total hyaena population of the Serengeti could number 3000 (pp 301–302), with some 900 individuals inhabiting the northern, central, and peripheral woodlands. Dividing total kill figures by 3000 gives a killing rate of 1.28–3.90 adult gazelles per hyaena per year. As Thomson's gazelles occupy only some 35% of the northern and central woodlands on an annual basis (calculated from Maddock 1979:111), the gazelle predation rates for the (900) hyaenas in these areas should be reduced by this factor. Kruuk's analysis did not distinguish between Grant's and (the much more numerous) Thomson's gazelles. Using his figures will give a slight overestimate of predation rate on the latter species alone.

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