

APPRAISAL OF TWO COUNTING METHODS AND
THE POPULATION DYNAMICS OF FOUR HARVESTED
ANTELOPE SPECIES IN A KENYAN GAME RANCH

by: ABDELWAHAB S. M. SINNARY

A THESIS

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I, ABDELWAHAB S.M. SINNARY, declare that the work presented in this thesis is the results of my own investigations and has neither been accepted nor is being submitted for any other degree.

-----*AS*-----

-----12/5/88-----
Date

This thesis has been submitted for examination with my approval as University supervisor.

-----*Warui Karanja*-----

DR. WARUI KARANJA

-----12/5/88-----
Date

This thesis has been submitted for examination with my approval as University supervisor.

-----*Luis Malaret*-----

DR. LUIS MALARET

-----12/5/88-----
Date

DEDICATION

To those who dream of seeing an end to the degradation of the African Environment and to those who actively work towards that end.

ABSTRACT

Wildlife Ranching and Research Ltd., Athi River (WRR) is a privately owned mixed game and cattle ranch, with the aim of demonstrating the environmental and economic viability, as well as social acceptability of game ranching. The field work for this research was carried out at WRR between October 1986 and September 1987. The emphasis was on economically important species.

Monthly total ground counts made it possible to evaluate levels of harvesting that could be accommodated by Grant's gazelle, kongoni and wildebeest. Wildebeest and kongoni could accommodate 32.6% and 14.0% average annual offtake rates, respectively without the population declining. Grant's gazelle, on the other hand, could only accommodate 0.05% annual offtake rate. The highly skewed sex ratio in favour of females was only partly responsible for the low recruitment in this species. An unknown mortality factor was considered responsible for the major part of the low recruitment value. Ground counts carried out in the wet season were more accurate than the ones carried out in the dry season for Thomson's gazelle, but not for Grant's gazelle and kongoni. Total ground counts were more accurate than aerial counts when applied to the small antelopes, i.e Thomson's and Grant's gazelles and impala combined.

No significant differences could be detected between results of the two methods when applied to the WRR ungulate community as a whole. Total ground counts were recommended as the counting method that best suits the WRR situation.

Results of road counts were disappointing. The results exhibited high variations, and two species, i.e. Thomson's gazelle and wildebeest were found to prefer the road side, resulting in overestimated population sizes.

Ageing and sexing in the field indicated that Thomson's and Grant's gazelles, and kongoni breed throughout the year with possible birth peaks in the cases of Thomson's gazelle and kongoni.

A correction factor was used when calculating the incidence of pregnancy in wildebeest for the bias resulting from WRR harvesting strategy of not harvesting pregnant and lactating females. The correction factor could not be extended to the other species. Equations describing the rate of foetal growth in wildebeest were given. Environmental factors affecting rate of foetal growth, variation in the rate of growth and the timing of the mating season were discussed. It was argued that a harvesting strategy of avoiding the killing of pregnant and lactating females may introduce artificial selective pressures that tend to increase the birth rate. Rates of pregnancy were low in young kongoni and

wildebeest and high in old ones. Recommendations were suggested related to harvesting timing of the different age and sex classes of the different species.

Subjective age classes based on eruption sequence and wear pattern of the maxillary molars provided an accurate ageing criterion up to the age of 28 months in the case of wildebeest. Crown heights exhibited high variation in animals of the same age. The linear regression model provided a better fit than the exponential to the pattern of decrease of crown heights with age.

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1. INTRODUCTION AND LITERATURE REVIEW

The advantages of game ranching are obvious enough to make it one of the alternative land use systems in semi arid Africa (Crawford 1972, Hopcraft 1975, 1980, Stelfox 1985, Sinnary 1987). Game ranching has emerged as an economically profitable land-use system in South Africa and Zimbabwe (Buar 1983). Its advancement in East Africa has been slow however, a number of reasons contributing to this unfortunate situation. Early investigations in the subject stressed the fact that game animals should provide the poor African with a cheap source of meat. Most subsequent investigations and experiments on the subject were carried out with this goal in mind. The results were either frustrating or were not promising (Eltringham 1984, Spinage 1986).

In contrast to these experiments, Wildlife Ranching and Research Ltd., Athi River (WRR), has been a notable exception. The operations of WRR considered game ranching as an alternative land use system in semi arid Africa and were also aware that for game ranching to emerge as an alternative land use system its economic returns should be higher than those of the 10 thousand years old traditional cattle ranching. One of the major problems encountered by WRR during the beginning of its operations was the establishment of a market for game meat. To fetch the highest prices the name of game meat was changed from bush meat into venison,

which is indicative of a delicacy, a matter that enabled WRR to sell game meat to first class hotels and butcheries. This was one of the factors that led to the early success of WRR.

It seems that the initial goal of game ranching (to provide a cheap source of meat) needs to be changed and the emphasis laid on the economic and conservation aspects of the system. It appears that game ranching is not going to be of significant importance in the national parks and other conservation areas, at least in the near future. Substantial numbers of animals, on the other hand, are found in private and tribal lands. These animals are considered pests because of their negative economic values. These very pests can be changed into economic resources when utilised, and this shift in focus is the greatest challenge facing game ranching.

With this goal in mind WRR has been a site of research examining the various aspects of the system. My own work is one effort in support of achieving the goal of having game ranching emerge as an alternative land use system in the semi arid Africa. The research was carried out with the following specific objectives in mind:

1. compare the applicability of total ground counts and road counts in the WRR situation;
2. provide information on the age and sex structure of harvested animals;
3. provide data on age specific birth rate of the harvested populations;

4. investigate the effect of a skewed sex ratio in favour of the females on birth rate of the harvested populations; and
5. discuss the relevance of the results to the management of the ranch.

The focus of this study was on the quantitative parameters of the populations that influence annual harvest quotas of the economically important species. The work, however, was only a first step towards understanding the population processes that affect offtake rates and more work needs to be done. More information is needed to understand the effects of the environment on mortality and reproduction rates. The age and sex composition that maximises economic returns is only barely understood. Little is known about the species composition that maximises the economic returns. The relationship between reproduction levels and the annual offtake rates of the various species is only barely understood though it is an important aspect of the economy of any ranching venture. The powerful tool of computer simulation may be needed to study the joint effect of these complex variables on the annual offtake rates.

The choice of any counting method is a compromise between a number of factors including the species counted, size of the census zone, nature of the terrain, type of the vegetation and availability of resources (Norton-Griffiths 1978). Various authors investigated different aspects

of ground sampling techniques and designs (Hayne 1949, Dasmann and Mossman 1962, Eberhardt 1968, Gates 1969, Hirst 1969, Robinette *et al.* 1974). A large body of theoretical work has also started to accumulate since the last decade (Anderson *et al.* 1979, Burnham 1979, Seber 1986). Many authors agree that the fixed transect width provides the best design if a reasonably large transect width can be covered and all the animals within that transect can be detected (Norton-Griffiths 1978). The fixed transect method also has got the advantage of a simple sample design. There is no robust method of relating sampling intensity to precision, though some attempts have been made (Sinclair 1973, Norton-Griffiths 1975, 1978). To develop such a method the factors that affect the precision of the sample counts must be identified and an equation, or a series of equations must be derived that describe the relationship between these factors, sampling intensity and precision. Until such an equation is developed more frustrations, more expenses and valuable time will be wasted in unsuccessful sample counts.

Seasonality of reproduction in Thomson's gazelle has been previously discussed. Brooks (1961) found that peak birth periods showed great local variations among adjacent populations and related the variations to the emergence of fresh grass. Robinette and Asher (1971) found year round breeding with peaks coinciding with the wettest months. Hopcraft

(1975), however, found that the peaks were one or two months before the rains. Although the above studies agree that birth takes place throughout the year with apparent peaks, it is doubtful whether these peaks indicate seasonality in breeding because the birth peaks of adjacent populations show large variations, and the peaks are not clearly related to rainfall.

The temporal distribution of reproduction of African ungulates varies widely, both between different species within the same area and in the same species between different areas (Jarman 1976, Leuthold and Leuthold 1975). Brooks (1961) found a local correlation between time of birth and availability of fresh fodder in adjacent populations of Thomson's gazelle. Estes (1966, 1976) attributed the synchronised calving season in wildebeest to predation pressure. Leuthold and Leuthold (1975) could relate seasonality in breeding to the feeding habits of the 10 species they studied. Fryxell (1985, 1987) attributed seasonality in reproduction of the white-eared kob (*Kobus kob leucotis*) to resource limitation. However, the factors that shape the temporal pattern of reproduction in African ungulates are not clearly understood.

Crown height as an ageing criterion has received much attention in the last decade to the extent that a number of models have been proposed to describe the pattern of decrease of crown height with age. The first attempts were made by Spinage (1971, 1973). Spinage's (1971, 1973)

model states that crown height is reduced by a certain percentage of the initial crown height at a specific age. The age is taken as a percentage of the age at which crown height becomes zero. The percent decrease of crown height is a function of the exponent $1/2$. Klein *et al.* (1981) proposed a linear model for predicting age of ungulates, but later on the authors shifted to a curvilinear model (Klein and Cruz-Uribe 1983, Klein and Cruz-Uribe 1984). Models developed so far are not without problems and ecologists use ageing data in the analysis of population dynamics, (e.g. constructing life tables), or to construct models that investigate the effect of specific incidences on the population, (e.g. harvesting). Most of these models assume that age is accurately estimated. Caughley (1967) argued that when a population with a stationary age distribution is sampled and the percentage error in ageing is the same for all age classes, the following errors in the construction of life tables would normally result:

1. age-specific life expectancies are overestimated;
2. maximum sampled longevity is overestimated;
3. the differences between mortality rates over different age intervals are decreased; and
4. the distribution of age frequencies is smoothed.

The utility of the available ageing models to ecologists is questionable.

2. STUDY AREA

WRR is a privately owned, mixed game and cattle ranch owned and directed by Dr. David Hopcraft. WRR was initiated to demonstrate the economic and environmental viability as well as the social acceptability of game ranching. The ranch occupies an area of 81 Square km., and is located 40 km southeast of Nairobi on the Athi-Kapiti plains. Altitude varies between 1600 and 1700 m a. s. l., latitude is $01^{\circ}30'$ south and longitude is $37^{\circ}02'$ east (Stelfox 1985).

WRR falls within the fourth ecoclimatic zone (semi-arid zone) according to the Pratt and Gwynne (1977) classification of the East African range lands. Rainfall is bimodal and exhibits considerable seasonal as well as year to year variation. The long rainy season falls between March and May; followed by a cool, cloudy and dry season from June to September. The short rainy season extends from October through December and is followed by a hot and sunny dry period which continues to the middle of March. Average rainfall for seven years starting in 1981 was 455.7 mm (Table 1).

WRR soils have the same origin as those of the Athi-Kapiti plains, which originated in the Tertiary era, and consist of volcanic deposits indicated by the Basalt rocks visible along topographic depressions (Saggerson in Stelfox 1985). The topography is dominated by a gently

Table I. Rainfall (mm) At Wildlife Ranching And Research Ltd. (WRR).

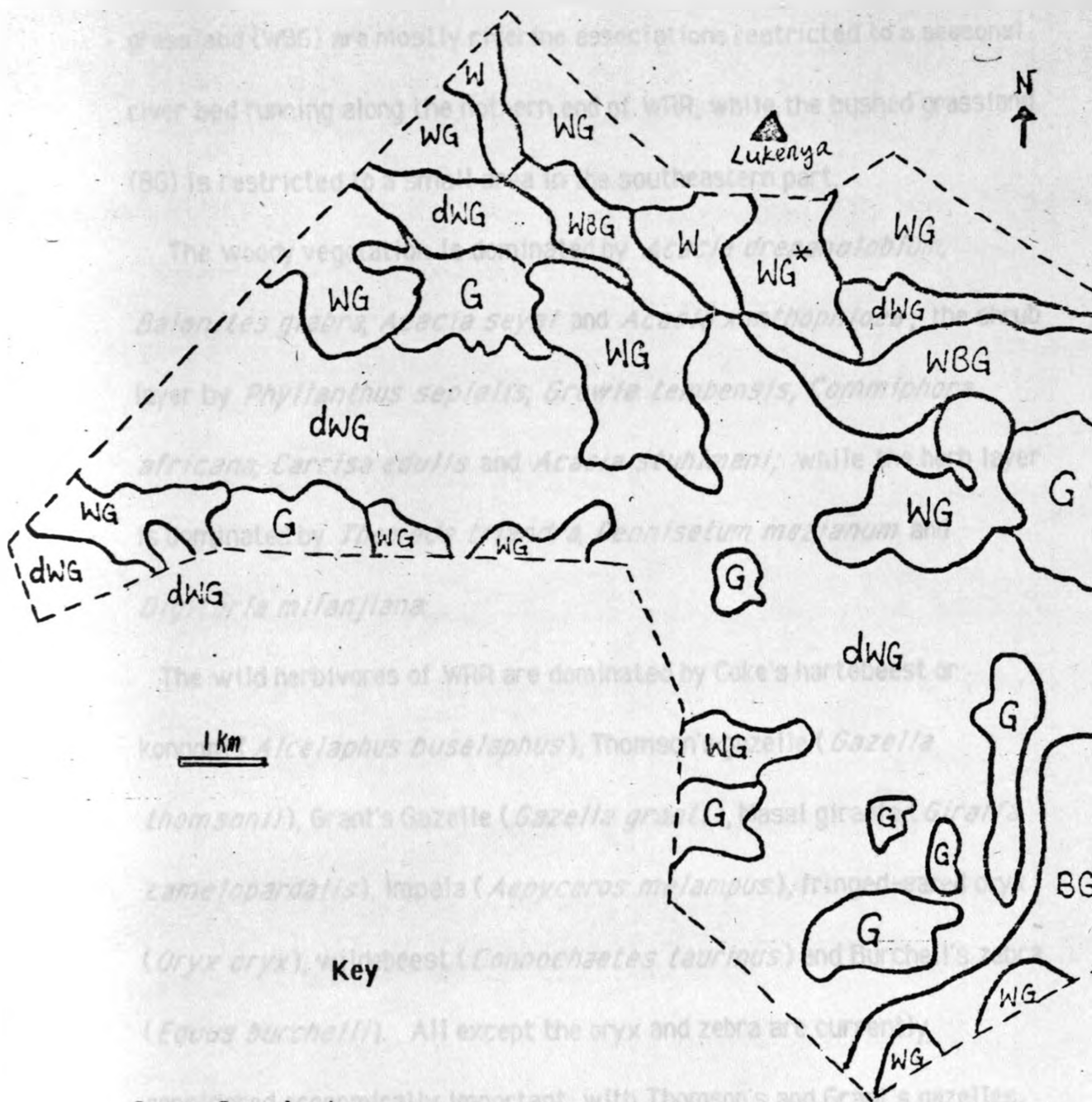
	1981	1982	1983	1984	1985	1986	1987
JAN	0	0	5	10	9	35	56
FEB	0	0	72	0	314	0	10
MAR	111	55	30	18	25	24	38
APR	118	32	81	73	184	204	35
MAY	99	55	14	0	27	0	31
JUN	12	11	20	0	0	0	93
JUL	1	6	2	0	0	0	0
AUG	0	6	0	0	0	0	0
SEP	18	20	18	21	0	0	46
OCT	21	64	15	70	19	0	0
NOV	13	112	39	37	75	145	88
DEC	24	112	139	37	75	60	7
TOTAL	417	473	435	266	728	468	404

undulating terrain occasionally interrupted by riverine depressions. This has led to the formation of predictable soil patterns along the undulations. The effect, commonly referred to as the catena effect, is a result of water runoff and the differential soil erosion and formation factors. In the ranch the catena effect is such that the soils on top of the ridges are sandy, well drained and light grey in colour. The depressions, on the other hand, are characterised by black, poorly drained and grey black alluvial soils (Reed 1983, Stelfox 1985).

The dominant soils are the montmorillonitic vertisols, commonly known as the black cotton soils. They are characterised by high cation exchange capacity, high base saturation, poor drainage and black colour. They typically swell when wet, while they crack and become rock hard when dry. Nitrogen is the major limiting factor to plant growth (Kuria in Stelfox 1985).

Topographic relief strongly influences species composition, leaf height, phenological stage and tree density (Stelfox 1985). This has also resulted in habitat types being closely associated with the topographic level. Moving from the hilltop downwards the following vegetation types are most often encountered (Figure 1): Grassland (G); *Balanites glabra* or *Acacia seyal* wooded grassland (WG); and *Acacia drepanolobium*

Figure 1. Habitat types at WRR (Taken from Reed 1983).



G Grassland

WG *Balanites glabra* wooded grassland

WG* *Acacia seyal* wooded grassland

DWG *Acacia drepanolobium* dwarf tree wooded grassland

BG Bushed grassland

WBG Wooded bushed grassland

W Woodland

dwarf wooded grassland (DWG). Woodland (W) and wooded bushed grassland (WBG) are mostly riverine associations restricted to a seasonal river bed running along the northern end of WRR, while the bushed grassland (BG) is restricted to a small area in the southeastern part.

The woody vegetation is dominated by *Acacia drepanolobium*, *Balanites glabra*, *Acacia seyal* and *Acacia xanthophloea*; the shrub layer by *Phyllanthus sepialis*, *Grewia tembensis*, *Commiphora africana*, *Carrisa edulis* and *Acacia stuhlmani*; while the herb layer is dominated by *Themeda triandra*, *Pennisetum mezianum* and *Digitaria milanjana*.

The wild herbivores of WRR are dominated by Coke's hartebeest or kongoni (*Alcelaphus buselaphus*), Thomson's gazelle (*Gazella thomsonii*), Grant's Gazelle (*Gazella granti*), Masai giraffe (*Giraffa camelopardalis*), impala (*Aepyceros melampus*), fringed-eared oryx (*Oryx oryx*), wildebeest (*Connochaetes taurinus*) and Burchell's zebra (*Equus burchelli*). All except the oryx and zebra are currently considered economically important, with Thomson's and Grant's gazelles, kongoni and wildebeest assuming more importance in terms of the current harvesting rates. The last four species will be referred to as the economically important species throughout the thesis.

Stelfox (1985) argued that topography, by affecting ungulate mobility,

forage quality and heat balance determines the patterns of resource use among the ungulate community of WRR. The effect is such that species with similar food preferences are most dissimilar in topographic distribution. With the onset of rain, WRR ungulates exhibit an uphill movement, increasing the degree of species overlap along the topographic gradient.

The black-backed Jackal (*Canis mesomelas*), bat-eared fox (*Otocyon megalotis*), and spotted hyaena (*Crocuta crocuta*) are the resident large carnivores in WRR. Cheetah (*Acinonyx jubatus*), wild dogs (*Lycaon pictus*) and lions (*Panthera leo*) occasionally pass through the ranch. A predator control programme existed in WRR for hyaena, lion and jackal between 1981 and 1985.

Prior to 1981 WRR was operated as a cattle and sheep ranch. Following the findings of his research (Hopcraft 1975) on productivity comparison between Thomson's gazelle and cattle, and their relation to the ecosystem, Hopcraft applied to the Kenyan government for a permit to operate his ranch as a game ranch. To meet the government regulations WRR had to complete several modifications. A 50 Km chain link fence, 2.6 m in height was erected along the perimeter to ensure the existence of a closed system. A slaughter house, linked to a meat processing room was built, and two Land Rovers were modified for the purpose of harvesting and

transporting the animals to the slaughter house. The numbers of sheep and cattle were gradually reduced to minimise competition with game animals. Game animals are brain shot and slaughtered every tuesday night. The animals are immobilised, using a spotlight, before being shot. They are transported to a centrally located slaughter house within one hour of being shot, where they are eviscerated and skinned. The following day the meat is inspected by a government official. The meat is sold to selected hotels and butcheries in Nairobi. More details of the modifications as well as a detailed description of the harvesting strategy are to be found in Stelfox (1985).

3. MATERIALS AND METHODS

ROAD COUNTS

A series of road counts were carried out at WRR in January, February, April and May 1987. A transect width of 250 m on both sides of the road was chosen as a compromise between maximizing sampling intensity and ensuring that all animals, especially Thomson's and Grant's gazelles, within the circuit were seen. A road circuit covering 23 square km. and resulting in a sampling intensity of 28.4% was chosen as a compromise between maximizing sampling intensity, time required to cover the circuit and equal representation of the various habitat types. The counts were carried out between 07:00 and 13:00, using a motor-cycle, within the first third of the month, except for the April count which was carried out on the 16th. Time required to complete a count varied between 4 and 5.5 hours, with an average of 4.5 hours, and the same route was followed all the time.

Variables recorded for each group of animals encountered included time, right angle sighting distance, group size, habitat type, topographic level (catena) and location. Distance to an animal group was measured using a range finder. Measurement error of the range finder was within 10% at a 250 m distance. The catena level was classified following

Stelfox (1985). The location of each group encountered was recorded in a 0.5 X 0.5 km. grid reference map of WRR. The habitat classification system adopted was the one described by Reed (1983).

In addition to the counts described above, four series of four daily road counts were carried out in December 1986, and March, June and July 1987 with the aim of estimating the variation in road counts, expressed in terms of the standard deviation (Hirst 1969). Timing of these counts was chosen to correspond with the different seasonal conditions. The four series of counts corresponded with the middle of the short rainy season, the end of the hot dry season, the end of the long rainy season and the beginning of the cool dry season, respectively.

There are a number of potential sources of bias that may affect road counts at WRR. The road system at WRR does not provide an equal representation of the different habitat types. A large proportion of the road system falls within the upper topographic levels. These upper levels are usually associated with grassland and wooded grassland, while the lower levels are associated with the *Acacia drepanolobium* dwarf tree wooded grassland. These sources of bias, however, do not affect the results provided that a sound sampling scheme is adopted, and that the analysis is carried out in such a way that the effect of the sources of bias is excluded (Norton-Griffiths 1978) (whose method was used to calculate

population sizes). The road system also seems to affect, directly or indirectly, the distribution of some ungulate species at WRR. Thomson's gazelle and wildebeest for example, prefer the immediate vicinity of the roads resulting in overestimating population sizes of these species.

Cattle night inclosures, or bomas are characterised by a grass community dominated by *Cynodon* species, and generally receive heavier utilisation by wild ungulates (Stelfox 1985). These bomas are usually constructed near the roads.

Thomson's and Grant's gazelles were the smallest species included in the road counts. The method described by Anderson and Pospahala (1970) was, therefore, applied to check if the visibility bias was increasing with increasing distances from the middle of the road. This required dividing the transect width into 10 intervals of 25 m each from the road centre on both sides and counting the numbers of animals at each interval for all counts made. A regression equation was then fitted to the distribution. This method requires a random distribution of animals within the census zone, which requires a random selection of the sample units in census zone, but since this zone was associated with the road system which is not random, the requirements of the Anderson and Pospahala method are not met. Another approach is therefore needed.

If the visibility bias of detecting individuals of any species increases

with distance, average group size will also increase with increasing distance as a result of the inability to detect small groups at long distances. It is, therefore, expected that average group size will remain constant irrespective of the distance from the centre of the road if there is no visibility bias. This being the case, regressing group size on the right angle sighting distance should result in a slope not significantly different from zero. Both the Anderson and Pospahala method as well as the approach based on the regression of group size on the distance were applied in the cases of Thomson's and Grant's gazelles. The numbers of animals counted at 25 m intervals from the centre of the road (Anderson and Pospahala method) were smoothed by taking the running average of every three consecutive values.

TOTAL GROUND COUNTS

Monthly total ground counts were carried out at WRR between November 1986 and September 1987, except in March. WRR was divided into a number of sectors, defined by existing road systems and fence lines. Originally WRR was divided into a variable number of sectors according to the availability of investigators. After January 1987, however, more investigators became available, and the ranch was divided into the same four sectors for each count (Figure 2).

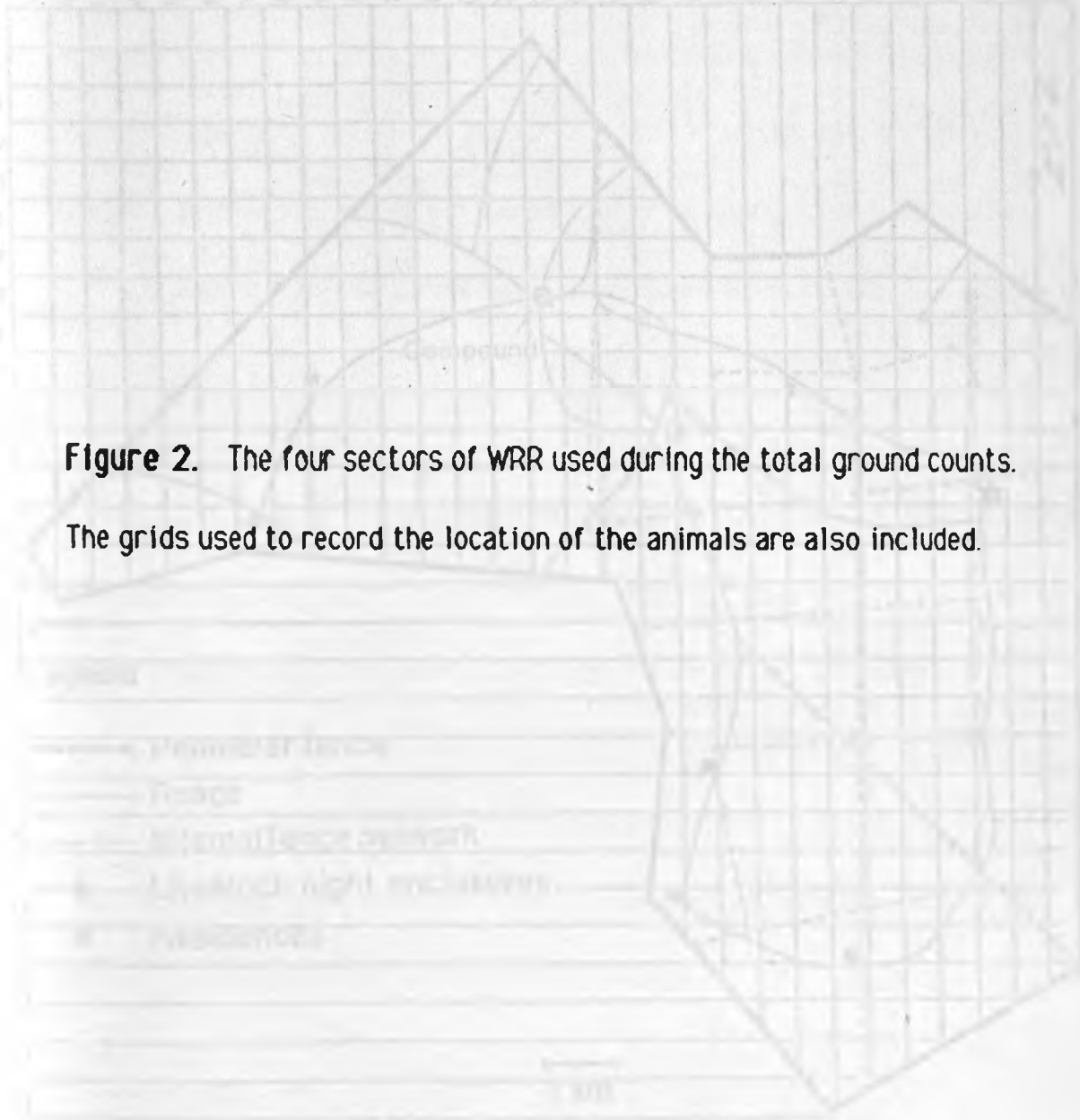
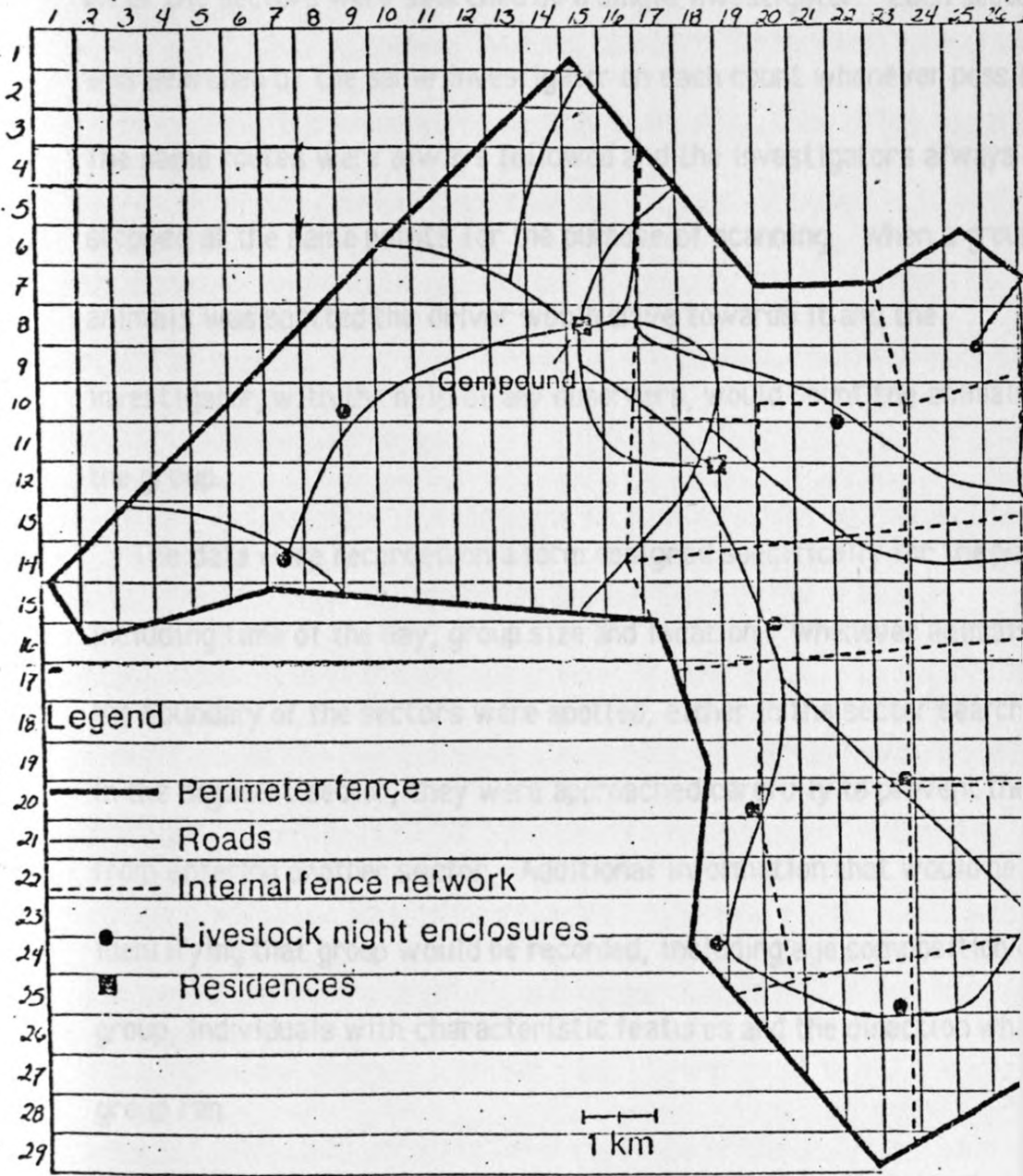


Figure 2. The four sectors of WRR used during the total ground counts. The grids used to record the location of the animals are also included.



The counts were carried out between 0800 and 1130. A driver and one investigator per sector was considered the minimum requirement for a good count. This number was not always available, in which case some or all of the sectors were searched by a single investigator. Each sector was searched by the same investigator on each count whenever possible. The same routes were always followed and the investigators always stopped at the same points for the purpose of scanning. When a group of animals was spotted the driver would drive towards it and the investigator, with the help of any observers, would count the animals in the group.

The data were recorded on a form designed specifically for the purpose including time of the day, group size and location. Whenever animals at the boundary of the sectors were spotted, either in the sector searched or in the adjacent sector, they were approached carefully to prevent them from entering another sector. Additional information that would help in identifying that group would be recorded, including age composition of the group, individuals with characteristic features and the direction which the group ran.

WRR initiated monthly total ground counts in 1981. It was not possible to carry out the counts regularly but the number of counts carried out was large enough to assess the various factors that affected the accuracy of

the method of total ground counts as applied to the WRR situation.

Accuracy of a total ground count, defined as how close the results given by any count are to the actual number of animals, was a function of a number of factors, including season, size and colour of the species, type of habitat preferred, average group size, weather conditions, time of the day and the way in which the count was carried out. It was not possible to evaluate the effect of all of these factors but it was possible to evaluate the effect of average group size and season for three species: Thomson's and Grant's gazelles, and kongoni.

It was not possible to assess the factors affecting accuracy of the total ground counts through direct comparisons of the counts as populations sizes of the various species at WRR did not remain stationary. Populations of the four economically important species increased between 1981 and 1984 (Stelfox 1985) and started to decline in 1985 and by the middle of 1986 the populations started to increase again. Counts of Thomson's and Grant's gazelles, and kongoni carried out in any one year were, therefore, grouped together. The highest count in any one year was assumed to be 100% accurate for the purpose of the analysis. This assumption was based on the fact that overestimation of population sizes of the WRR ungulates was not a serious problem compared to the problem of underestimating the sizes of these populations. Population sizes of the

WRR oryx and giraffe were known when the field work of this study was taking place. Almost 50% of the 18 total ground counts carried out at WRR between November 1986 and February 1988 underestimated population sizes of these species while no single count gave overestimated figures. Counts other than the highest count in any year were assigned percentages of the highest count accordingly. Such a practice allowed comparisons between counts carried out in different years and seasons without the need of assuming stable population sizes during the period of investigation.

The years 1981 and 1985 were not included in the analysis because counts carried out then were too few for the purpose of the analysis. Only four counts were carried out in 1981 and three in 1985. Four counts were also carried out in 1986 in January, February, November and December. The first two were excluded, while the last two were analysed together with the 1987 counts. I co-ordinated the counts carried out between November 1986 and September 1987, thus I thought it would be appropriate to treat them together. The December 1984 count was excluded because it gave results that were too low, and I suspected that the count was a bad one. The analysis was not applied to the wildebeest as wildebeest populations do not increase gradually, but rather in an abrupt way as a result of the birth-pulse pattern exhibited by this species.

Months in the period investigated were classified as either wet or dry. A wet month was defined as one that received a minimum of 30 mm of rainfall, or that was preceded by one or two months with a total of, at least, 30 mm of rainfall if the month was at the beginning of the rainy season. The Mann-Whitney U test was used to test differences in accuracy between the dry and wet season counts using the percentages of the highest count and was also applied to test differences in average group sizes between the wet and dry seasons.

Four total aerial counts were carried out at WRR; one count in August another in November 1986, and two counts in March 1987. Accuracy of the November aerial count was compared to that of the total ground count carried out in the same month. No equivalent ground counts were available for comparison with the other three aerial counts, so the average of the two ground counts carried out in February and November 1986 was compared with the August 1986 aerial count. The aerial count carried out on March ninth was compared with the February 1987 ground count and the March twenty sixth aerial count was compared to the April 1987 ground count. The Wilcoxon Matched-Pairs sign ranks test was then used to test differences in accuracy of the two methods. It was not possible to test for differences in accuracy of ground and aerial counts for individual species because the aerial counts were too few. I therefore separated

ungulates into three functional groups on the basis of the ranch economy and on the basis of equal visibility. The first group consisted of the four economically important species. The second consisted of the small antelopes, i.e Thomson's and Grant's gazelle, and impala. Included in the third group were the big plains ungulates, i.e kongoni, wildebeest, zebra and oryx. Finally, accuracy of the ground and aerial counts was tested for the species included in the three above groups plus the giraffe.

Results of the total ground counts were used to evaluate the relationship between annual offtake and recruitment of the four economically important species. If:

N_t = population size at year t ;

N_{t+1} = population size at year $t+1$;

H = number of animals harvested between year t and $t+1$; and

R = recruitment to the population between year t and $t+1$; then:

$$N_{t+1} = N_t + R - H \quad (1)$$

Where: $R = B - D$;

B = number of animals born between year t and $t+1$; and

D = number of animals that died between time t and $t+1$ (Caughley 1977). It

follows that:

$$R = N_{t+1} - N_t + H \quad (2)$$

To estimate annual recruitment of Grant's gazelle and kongoni, all total

ground counts carried out within any year were grouped together. The average of all the counts for each year was calculated. The end of June was considered to be the month corresponding with that average because the end of June divides the year into two equal halves. If counts are carried out at regular intervals, their mean, mode and median will all coincide with the end of June assuming that results of these counts are normally distributed. An average total ground count was 80.2% and 84.1% accurate in the case of Grant's gazelle and kongoni, respectively. Based on this, yearly average (corresponding with the end of June) counts were multiplied by a correction factor of 1.25 and 1.19 in the cases of Grant's gazelle and kongoni, respectively to be 100% accurate. The numbers harvested between year t and $t+1$ (H) were obtained from the WRR harvest records starting from July, t , to June, $t+1$, where the terms t and $t+1$ refer to the year. Recruitment between year t and $t+1$ (R) was calculated using equation (2). R was then expressed as a percentage of N_t .

The above analysis could not be applied to Thomson's gazelle and wildebeest. Results of the road counts suggested that total ground counts were probably underestimating population sizes of Thomson's gazelle, therefore a correction factor will not make an average total ground count be 100% accurate and annual recruitment values will be underestimated, while percentage annual recruitment will be overestimated if based on the

results of the underestimated total ground counts. The birth-pulse pattern did not allow the analysis to be applied to wildebeest, however the probability of spotting a wildebeest group is higher than that of spotting a group of the other ungulates since the WRR wildebeest form large, cohesive and conspicuous groups. If the probability of spotting any wildebeest group within any one count equals P and the number of wildebeest groups in WRR equals n , then the probability of spotting all the wildebeest groups in any one count will be P^n . The probability of spotting all the groups in any one count is at its maximum when n equals one and it decreases as n increases. Since the average number of wildebeest groups at WRR ranged between five to six it was likely to spot all the wildebeest groups in at least one count if a series of counts were carried out.

Based on this argument the wildebeest counts were arranged into eight groups, each group included all the counts carried out between May of one year and February of the next. Wildebeest calves are born between March and April (Sinnary Unpublished) with the median date of birth around the middle of March (based on the 1987 calving season data). March and April counts were excluded as a result. It was assumed that the highest count between May, t , and $\text{February}, t+1$, was 100% accurate. The number of animals harvested in the interval between the middle of the month with the highest count and the middle of March that followed was calculated

from WRR records and subtracted from the number of animals recorded in the highest count. This value is equal to the number of animals just before the middle of March or N_t . It was then calculated from WRR records as the number of animals harvested between the 15th of March of one year and the 15th of March of the next. Annual recruitment (R) and percentage recruitment were then calculated as in the case of Grant's gazelle and kongoni.

INCIDENCE OF PREGNANCY IN WILDEBEEST

Annual incidence of pregnancy (AIP), defined as the number of pregnancies an average female has each year (Sinclair and Grimsdell 1982), can be estimated by inspecting macroscopically the uteri of harvested females. This method, however, suffers from three sources of bias when applied to estimate AIP of the WRR females. The first is due to the inability to detect pregnancy at its early stages, the second and the third to the WRR harvesting strategy of avoiding killing pregnant and lactating females. Other methods of estimating AIP, through the microscopic inspection of the reproductive tract, are more technical and also more time and money consuming to be of much use to a game rancher. However, the highly synchronised mating and calving seasons in wildebeest made it possible to work out a correction factor for AIP based

on the macroscopic inspection of the uterus.

When a female is harvested, the uterus is inspected macroscopically and if found to be pregnant, the foetus and uterus are weighed. Monthly prevalence of pregnancy (MPP), defined as the percentage of pregnant females recorded every month (Sinclair and Grimsdell 1982) was calculated for the wildebeest from WRR records for the breeding cycles of 1982/83 to 1985/86. The term "breeding cycle" refers to the series of events starting at the time when the first female is serviced and ending when the last female gives birth. MPP for the breeding cycle of 1986/87 was calculated for wildebeest that were harvested from a neighbouring ranch owned by General Mulinge (Mulinge ranch).

MPP can be defined as $100n_i/N_i$, where n_i is the number of pregnant females and N_i the total number of females killed in the i th month. Since both the mating and calving seasons are highly synchronised, the MPP statistic should remain fairly constant between the time all the females were mated and the time just before the first female gives birth. This, however, was not the case for the WRR wildebeest females because of a bias resulting from the failure to detect pregnancy at its early stages and two sources of bias related to WRR harvesting strategy. The first source of bias affects the results at the early stages of pregnancy, leading to an underestimated AIP value. The minimum embryo weight recorded was 5

gm, indicating that smaller, younger embryos were missed. The second and third sources of bias are, however, rather complex ones.

The second source of bias is a compound one and is due to the active avoidance by the harvester of killing pregnant and lactating females unless the calf is considered old enough not to be adversely affected by the death of the mother. It follows that the probability of harvesting a lactating female depends on the frequency with which she is seen followed by a calf at the time of harvesting. Since a wildebeest calf becomes more independent of its mother as it gets older (Talbot and Talbot 1963), the probability of harvesting a lactating female increases with the age of the calf until it becomes similar to that of a nonlactating female. At the early stages of pregnancy the foetus is too small for the harvester to detect whether a female is pregnant and thus avoid killing her. As pregnancy progresses, the foetus grows until it reaches a weight that enables the harvester to detect pregnancy. The probability of harvesting a pregnant female, therefore, is similar to that of a nonpregnant female at the early stages of pregnancy and remains so until a minimum foetus weight is reached at which the harvester is able to detect pregnancy. At this stage, the probability of harvesting such a female decreases, till it reaches a minimum just before she gives birth.

Since the two sources of bias, due to lactation and pregnancy are

working in opposite directions, their combined effect becomes minimum at some stage during the middle of the pregnancy period, when the previous season's calf has become more or less independent of the mother and when the foetus has not reached the minimum weight at which the harvester is able to detect pregnancy. This stage corresponded with the month of November, when MPP was at its maximum (Figure 3). MPP increased gradually from a minimum in June to a maximum in November, and then declined to zero in May, marking the end of the calving season. It is assumed in the analysis that MPP in November did not suffer from the above mentioned sources of bias.

A harvesting strategy in which pregnant and lactating females are avoided, also has the effect of increasing the proportion of pregnant females in the population from the time all the females are mated, leading to overestimation of MPP due to the survival advantage the pregnant and lactating females have over the nonpregnant and nonlactating ones. The extent of this bias increases in proportion to the ratio of the harvested to the total number of live females at the beginning of the mating season. It is expected, however, that the effect of this bias was small because the calculation of MPP was based on November's data, a time when the effect of the bias had not reached its maximum. At such a time the ratio of harvested females to the total number of females at the beginning of the

Figure 3. Monthly prevalence of pregnancy (MPP) of the WRR and Mulinge wildebeest showing the effect of the WRR harvesting strategy of avoiding killing pregnant and lactating females on MPP. The figures were obtained by adding the number of pregnant females killed in the 1982/83 to 1986/87 breeding seasons in any one month (n_i) and dividing the results by the the respective numbers of females killed (N_i) and then multiplying the total by 100.

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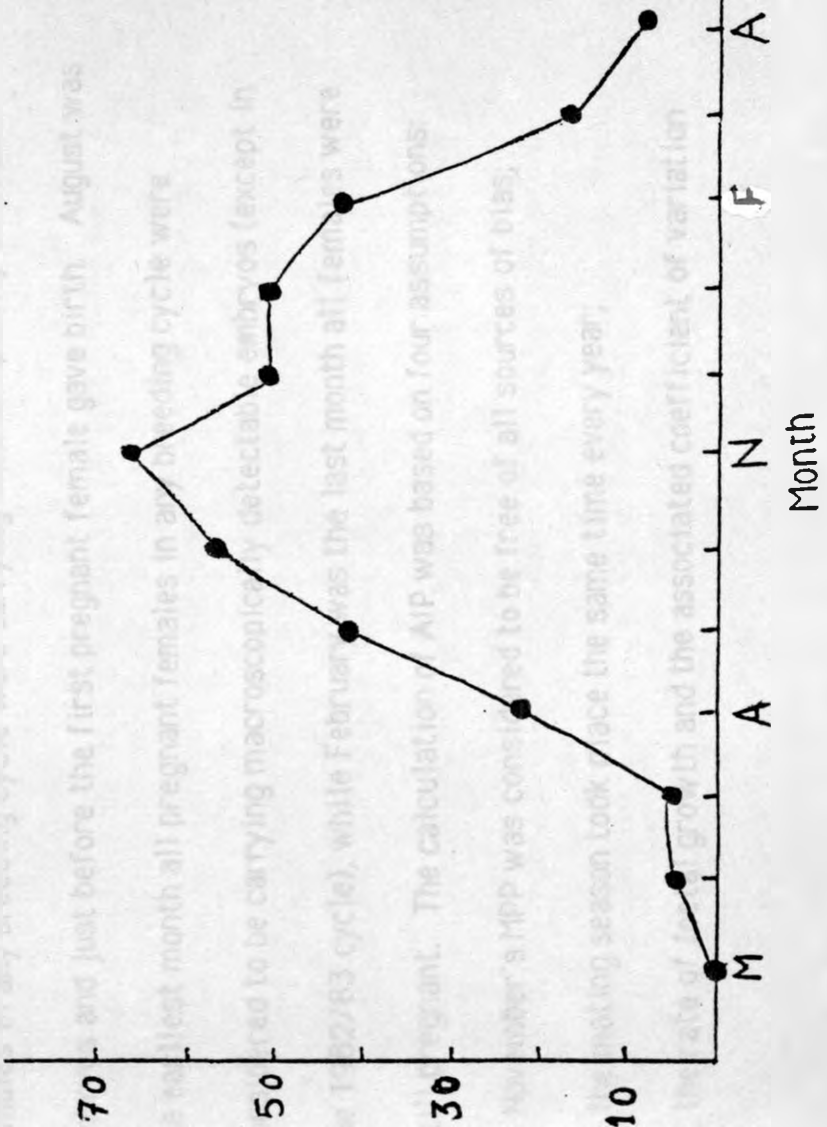
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Monthly prevalence of pregnancy (MPP)

mating season is expected not to be more than 15%. The effect of this and the probable underestimation of MPP in November may cancel each other because they have opposite effects.

AIP is defined as

$$\text{APP} \cdot t / 365 \quad (3)$$

where:

APP = annual prevalence of pregnancy (=unweighted average of MPP);

t = the length of the gestation period; and

365 = the number of days in the year (Sinclair and Grimsdell 1982). This definition, however, cannot be applied to calculate the corrected AIP as it requires unbiased estimates of the true MPP parameters. AIP is, therefore, redefined as the MPP during the interval when all the pregnant females in any breeding cycle were carrying macroscopically detectable embryos and just before the first pregnant female gave birth. August was the earliest month all pregnant females in any breeding cycle were considered to be carrying macroscopically detectable embryos (except in the 1982/83 cycle), while February was the last month all females were still pregnant. The calculation of AIP was based on four assumptions:

1. November's MPP was considered to be free of all sources of bias;
2. the mating season took place the same time every year;
3. the rate of foetal growth and the associated coefficient of variation

remained the same in consecutive years;

4. and as a result, the length of the gestation period remained the same throughout. If this is true, the percentage of pregnant females missed in any month will remain the same every year, as long as the harvesting strategy does not change.

A constant correction factor can be applied to the MPP statistic between August and February assuming that the MPP parameter was constant between August and February. The MPP statistic, as calculated from WRR records, on the other hand, is a biased estimate as a result of the failure to detect pregnancy at its early stages and the two sources of bias related to WRR harvesting strategy of avoiding killing pregnant and lactating females. The monthly correction factor will, therefore, correct the MPP statistic to be equal to that of November, assuming that MPP is free of bias in this month. The correction factor of MPP (CF_i), can be defined as $MPP_{Nov} \cdot N_i / n_i$, where: MPP_{Nov} is November's actual MPP and was obtained by adding together the n_i values in November for all the years investigated and then dividing by the corresponding N_i and multiplying by 100. The n_i and N_i figures represent the totals of n_i and N_i in any one month for all the years investigated. The following steps can then be followed to calculate the corrected annual incidence of pregnancy (CAIP) for any breeding cycle or age class.

1. Record n_i and N_i by month between August and February for the females in the particular cycle or age class.
2. Multiply the n_i values by the respective CF_i values and add the results to obtain the corrected number of pregnant females ($\sum n_i.CF_i$).
3. Obtain the total number of females killed ($\sum N_i$).
4. Calculate AIP ($100\sum n_i/\sum N_i$) and CAIP ($100\sum n_i.CF_i/\sum N_i$).

Wildebeest foetal growth equations were calculated for all years investigated making use of the synchronised mating and calving seasons to examine the effect of the environment on assumptions two, three and four underlying the new approach to estimate CAIP. This required recording age of the foetus when the mother was killed in a coded form. The first embryo was recorded on the 5th of June, and the first of June was therefore coded as day one. Excluded from the analysis were two foetuses recorded in May and July 1983, respectively because they either resulted from very late pregnancies (Coady 1974, Wishard 1981), or were being reabsorbed.

PREVALENCE OF PREGNANCY IN THOMSON'S AND GRANT'S GAZELLES, AND KONGONI

The correction factor for incidence of pregnancy in wildebeest could not be applied to other species studied because, unlike wildebeest, they do not

exhibit synchronised mating and calving seasons. An unbiased index of incidence of pregnancy will, nevertheless, help in various management aspects.

Annual prevalence of pregnancy (APP), defined as $\sum n_i / \sum N_i \cdot 100$, of Thomson's and Grant's gazelles, and kongoni was calculated from WRR records. Age-specific prevalence of pregnancy (ASPP) was only calculated for kongoni, as sample sizes for the gazelles were too small. Prevalence of pregnancy was calculated for the period between March 1984 and December 1985, for Thomson's gazelle, to show the effect of the 1984 drought on prevalence of pregnancy.

AGEING AND SEXING IN THE FIELD

Thomson's and Grant's gazelles, and kongoni were aged and sexed with the aid of a 15-40X magnifying scope to examine the animals between October 1986 and June 1987, excluding March. Individuals were classified as young or adults based on the shape and size of the horn and adults were sexed. Young of Thomson's and Grant's gazelles were classified as small (horns not visible) or large (visible horns but not reached adult shape and size) young. Young of kongoni were classified as small (no horns), medium (V-shaped horns) and large (U or crescent-like horns, which had not reached adult shape and size) young.

Age classes of Thomson's and Grant's gazelles and kongoni were based on the work of Hopcraft (1975), Spinage (1976) and Gosling (1975).

Kongoni were generally wary, and they were sometimes aged and sexed at a distance of more than 500 m, a distance too far to enable distinguishing all of the small young. Small young of this species were therefore assumed to extend between 0-2 months instead of the one month period suggested by Gosling (1975).

The equation:

$$AIP = P/L \quad (4)$$

was used to estimate AIP in the three species, where:

P = number of young of any age class as a percentage of the adult females;

L = length of the period (in years) over which a young class extends. This method assumes the following:

1. a stationary population with a stable age structure;
2. the length of the period over which an age class extends is accurately measured; and
3. mortality of the young is of negligible importance.

It is not common to find populations that satisfy the first two assumptions. However, estimation of AIP based on the small young age class only suffers from minor violations compared to estimations based on older young as the time lag when the small young are born and when they

are aged in the field is minimum compared to the older young classes. The major problem is calf mortality which is not a serious problem in WRR ungulates as annual calf mortality in WRR wildebeest was estimated to be less than 10% (Sinnary Unpublished). A 3 and 2 months' hiding period was assumed for Thomson's and Grant's gazelles, respectively. Numbers of young and males were expressed as a % of adult females, while numbers of adult females were expressed as a % of the total number of individuals. The data were summarised by calculating the unweighted averages of the total numbers of individuals in each sex class per 100 females over the whole study period.

AGEING BY TEETH, WILDEBEEST

Twelve subjective age classes were worked out for the WRR and Mulinge wildebeest, based on the sequence of tooth eruption and pattern of tooth wear of the three maxillary molars. Four criteria used to distinguish the different age classes were:

1. whether the molar tooth was above or below the jaw bone;
2. whether the cusps were fused or separated;
3. shape of anterior and posterior infundibuli; and
4. presence or absence of intermediate infundibulum.

The age classes are described below:

AGE CLASS ONE

Molar one

1. anterior cusps separated (50% or more of dentine exposed)
2. posterior cusps fused (< 50% of dentine exposed)
3. anterior infundibulum shallow U or y shaped
4. posterior infundibulum not exposed and if so, shallow U shaped
5. anterior and posterior infundibuli not separated and intermediate infundibulum not formed

Molar two below jaw bone

AGE CLASS TWO

Molar one

1. posterior cusps separated (50% or more of dentine exposed)
2. anterior infundibulum y or hat shaped
3. posterior infundibulum not exposed and if so, shallow U shaped
4. intermediate infundibulum not formed or forming but anterior and posterior infundibuli not separated

Molar two at or below jaw bone

AGE CLASS THREE

Molar one

1. anterior infundibulum hat shaped
2. posterior infundibulum shallow U or y shaped

3. intermediate infundibulum formed and anterior and posterior infundibuli separated

Molar two at or above jaw bone, cusps fused (< 50% of dentine of anterior cusps exposed) and infundibuli not separated

AGE CLASS FOUR

Molar one

1. anterior infundibulum hat shaped
2. posterior infundibulum y or hat shaped
3. intermediate infundibulum present

Molar two

1. anterior cusps separated (50% or more of dentine exposed)
2. posterior cusps fused (< 50% of dentine exposed)
3. anterior infundibulum not exposed and if so, shallow U shaped
4. posterior infundibulum not exposed or barely so
5. intermediate infundibulum not formed

Molar three below jaw bone

AGE CLASS FIVE

Molar one as in age class four

Molar two

1. posterior cusps separated (50% or more of dentine exposed)
2. anterior infundibulum shallow U or y shaped

3. posterior infundibulum not exposed and if so shallow U shaped

4. intermediate infundibulum not formed

Molar three at or above jaw bone, cusps fused and infundibuli not exposed

AGE CLASS SIX

Molar one as in age class four and five

Molar two

1. anterior infundibulum y or hat shaped

2. posterior infundibulum shallow U or y shaped

3. intermediate infundibulum formed or forming

Molar three

1. anterior cusps partially separated (< 50% of dentine exposed)

2. posterior cusps completely fused

3. anterior infundibulum not exposed or barely so

4. posterior infundibulum not exposed

5. intermediate infundibulum not formed

AGE CLASS SEVEN

Molar one as in age class four, five and six

Molar two

1. anterior infundibulum y or hat shaped

2. posterior infundibulum y or hat shaped

3. intermediate infundibulum present

Molar three

1. anterior cusps completely separated
2. posterior cusps partially or completely separated
3. anterior infundibulum shallow U or y shaped
4. posterior infundibulum not exposed or barely so
5. intermediate infundibulum forming but anterior and posterior infundibuli not separated

AGE CLASS EIGHT


Molar one

1. anterior infundibulum hat shaped
2. posterior infundibulum y or hat shaped
3. intermediate infundibulum present (sometimes a trace)

Molar two

1. anterior infundibulum y or hat shaped
2. posterior infundibulum y or hat shaped
3. intermediate infundibulum present (sometimes a trace)

Molar three

1. anterior infundibulum y or hat shaped
2. posterior infundibulum  shaped
3. intermediate infundibulum present (rarely absent)

AGE CLASS NINE

Molar one as in age class eight

Molar two

1. anterior infundibulum y or hat shaped
2. posterior infundibulum y or hat shaped
3. intermediate infundibulum present or absent

Molar three

1. anterior infundibulum y or hat shaped
2. posterior infundibulum y shaped
3. intermediate infundibulum present or absent

AGE CLASS TEN

Molar one

1. anterior infundibulum U or shallow U shaped
2. posterior infundibulum hat to U shaped
3. intermediate infundibulum absent or barely present, in which case oval in shape

Molar two as in age class nine

Molar three as in age class nine

AGE CLASS ELEVEN

Molar one

1. anterior infundibulum line or O shaped
2. posterior infundibulum U or shallow U shaped

3. intermediate infundibulum absent

Molar two and three as in age class nine and ten

AGE CLASS TWELVE

Molar one

1. anterior infundibulum completely lost, leaving a blank surface
2. posterior infundibulum U, shallow U, line, O shaped or absent
3. intermediate infundibulum absent

Molar two and three

1. anterior and posterior infundibuli y, hat, U, shallow U, line, O shaped or absent
2. intermediate infundibulum absent

Crown height of the three maxillary molars was measured to the nearest 0.5 mm at the buccal side from the base of the enamel to the tip of the cusps. Two measurements were taken from only one of the pair of the first, second and third molars, and the average of the two measurements was taken. Whenever possible the measurements were taken from the same side of the jaw. Molars with intact cusps were used, except in a few cases (< 5%), where molars with broken cusps were used if it was possible to estimate the height of the broken portion.

The base of the enamel was easy to locate in most cases, except in old animals (age class nine and above) where a layer of cementum was found

to cover the enamel. In most cases, however, the cementum could be easily chopped off to expose the base of enamel. Real difficulties were only encountered in chopping off the cementum from the first molar in very old animals (age class twelve and some in age class eleven). It was feared that chopping the cementum off might break the fragile cusps, in which case the base of the enamel was arbitrarily located.

At WWR the birth season of 1987 extended between the first of March and the middle of April, with the median date of birth around the middle of March (Sinnary Unpublished). Since wildebeest calves are born at the same time every year, animals killed in any one month will consist of discrete age groups whose mean age is spaced at intervals of one year. If crown height is a good ageing criterion its distribution for a group of animals killed in the same month, but not necessarily the same year, should be multimodal. Multimodality can be tested using normal probability transformation (Cassie 1950, 1962, 1963, Caughley 1965).

It is possible to evaluate subjective age classes as an ageing criterion by making use of the birth-pulse pattern. If it is possible to work out subjective age classes that extend over a period of less than a year, then killing dates of animals belonging to the same age class should exhibit a normal frequency distribution that covers only part of the year. The distribution should also follow a sequential pattern, such that the

distribution of animals belonging to a younger age class precedes that of the animals in the immediately older age class, with some overlap in between.

Obtaining a large sample of wild animals of known age is a difficult task. A small sample, on the other hand, may not produce acceptable results because of the high variation in crown heights of animals of the same age. It is, however, possible to evaluate the pattern of decrease of crown height of any of the three molars with time without the need of having animals of known age. This can be achieved by factorizing time and regressing crown heights of the second and third molars on the first, and the third on the second molar. The evaluation is based on the fact that crown height of any of the three molars provides a separate estimate of the age of the animal at death. There are two possible models, the linear and exponential. If two molars decrease linearly with time, then

$$M_1 = a_1 + b_1.t \quad (5)$$

$$M_2 = a_2 + b_2.t \quad (6)$$

where:

M_1 and M_2 = crown heights of the first and second molars;

a_1 and a_2 = intercepts of the regression of M_1 and M_2 on age;

b_1 and b_2 = slopes of the regression of M_1 and M_2 on age; and

t = age of the animal at death.

Note that both b_1 and b_2 have negative values since crown height decreases with age of the animal.

From (5)

$$t = (M_1 - a_1)/b_1 \quad (7)$$

Substituting the value of t from Equation 7 into 6:

$$M_2 = a_2 - b_2/b_1 \cdot a_1 + b_2/b_1 \cdot M_1 \quad (8)$$

Where:

$a_2 - b_2/b_1 \cdot a_1$ and b_2/b_1 are the intercept and the slope of the regression of M_2 on M_1 , respectively. Rearranging Equation 8:

$$a_2 - b_2/b_1 \cdot a_1 = M_2 - b_2/b_1 \cdot M_1 \quad (9)$$

And

$$a_2 = M_2 - b_2/b_1 (M_1 - a_1) \quad (10)$$

If two molars both change exponentially with time such that:

$\ln M_{(1,2)} = \ln a_{(1,2)} + b_{(1,2)} \cdot t$, it can be proved that

$$\ln M_2 = \ln a_2 - b_2/b_1 \cdot \ln a_1 + b_2/b_1 \cdot \ln M_1 \quad (11)$$

$$\ln a_2 - b_2/b_1 \cdot \ln a_1 = \ln M_2 - b_2/b_1 \cdot \ln M_1 \quad (12)$$

$$\ln a_2 = \ln M_2 - b_2/b_1 (\ln M_1 - \ln a_1) \quad (13)$$

Here again $\ln a_2 - b_2/b_1 \cdot \ln a_1$ and b_2/b_1 are the intercept and slope, respectively.

Equations 8 and 11 can be used to select the correct model by regressing crown heights of any two molars on each other. The correct model will be

the one with the highest coefficient of variation (r^2) provided that a reasonably large proportion of the variation in crown height of any of the two molars is explained by its regression on age (t) and that crown heights of the regressed molars are independent.

There was not a clear difference in the coefficient of variation for the linear and exponential models when applied to ageing data. In order to check whether the regression technique might not be sensitive enough for this type of analysis I simulated situations where the exponential model would be mistaken for the linear model and vice versa. To simulate the first option I used the values of M_2 and M_1 obtained from a subset of my data, to create a population of M_2 ranging between 15 to 65 mm at intervals of 2.5 mm (actual range of M_2 values in data set), ($n = 21$). The equation:

$$M_2 = 11.56 - 1.138.M_1 \quad (14)$$

was used to create a population of M_1 corresponding to the values of M_2 with $r^2 = 1$. The natural logarithms for each value of the two molars were obtained and regressed resulting in the equation:

$$\text{Ln}M_2 = 1.88 + 0.573\text{Ln}M_1 \quad (15)$$

$$r^2 = 0.98 \text{ and } n = 21$$

The coefficient of variation was only reduced by a very small fraction.

To simulate the case where a linear model is mistaken for an

exponential model equation (15) was used to create a population of $\text{Ln}M_1$ values corresponding to $\text{Ln}M_2$ values, with $r^2=1$. Values of $\text{Ln}M_2$ and $\text{Ln}M_1$ were then transformed into M_1 and M_2 , respectively, and regressed. The equation

$$M_2 = 15.12 + 0.971M_1 \quad (16)$$

was obtained with $r^2 = 0.98$, and $n = 21$. Again, the decrease in r^2 was very small. These results support the suggestion that the regression approach is insensitive in detecting differences between the two models when applied to ageing data.

To see the effect of mistaking the linear model for the exponential model and vice versa on the intercept values I used Equations 9 and 12 to calculate the intercepts $[(a_2 - b_2/b_1 \cdot a_1)$ and $(\text{Ln}a_2 - b_2/b_1 \cdot \text{Ln}a_1)]$. The intercept values were calculated for each of the 21 measurements of crown heights in both cases where one model was mistaken for the other. This was done by substituting the values of M_1 , M_2 (linear), $\text{Ln}M_1$ and $\text{Ln}M_2$ (exponential), and b_2/b_1 to derive the intercept values in the left hand side of Equations 9 and 12. The same value of b_2/b_1 was substituted in each case of the same regression. I then plotted each intercept value against M_2 (linear) and $\text{Ln}M_2$ (exponential), (Figures 4A and 4B). The intercept values were not randomly distributed around the average intercept values. Average intercept values as used here refer to the intercept values

Fig. 4A. The effect of mistaking the exponential model for the linear on the intercept values ($\ln a_2 - b_2/b_1 \cdot \ln a_1$). Points represent the individual intercept values obtained by substituting the value of the slope of the regression of $\ln M_2$ on $\ln M_1$ (b_2/b_1), and the individual values of $\ln M_1$ and $\ln M_2$ in equation 12. The dashed line represents the average intercept value obtained by regressing the natural logarithm of crown height of the second molar ($\ln M_2$) on that of the first molar ($\ln M_1$).

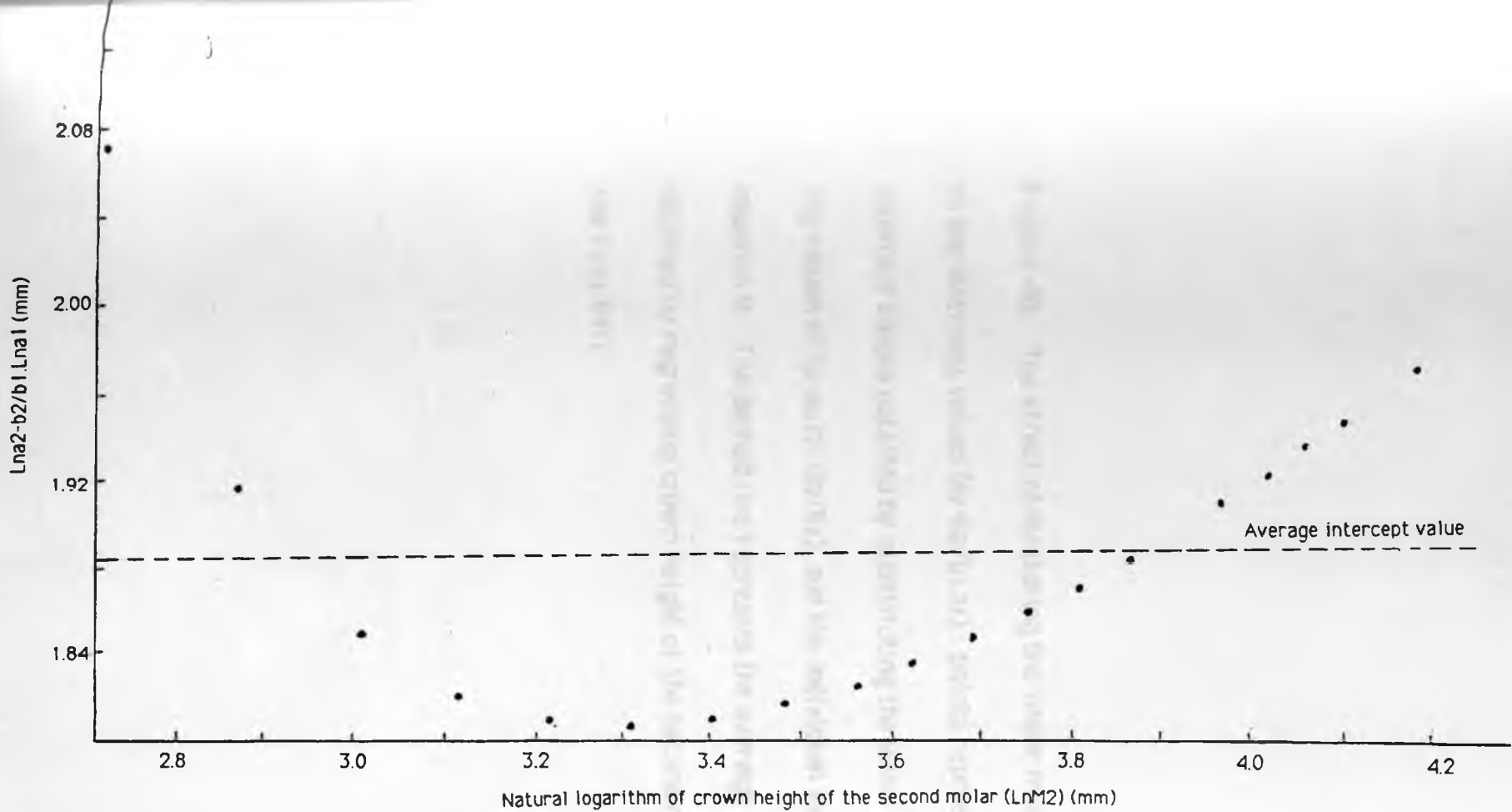
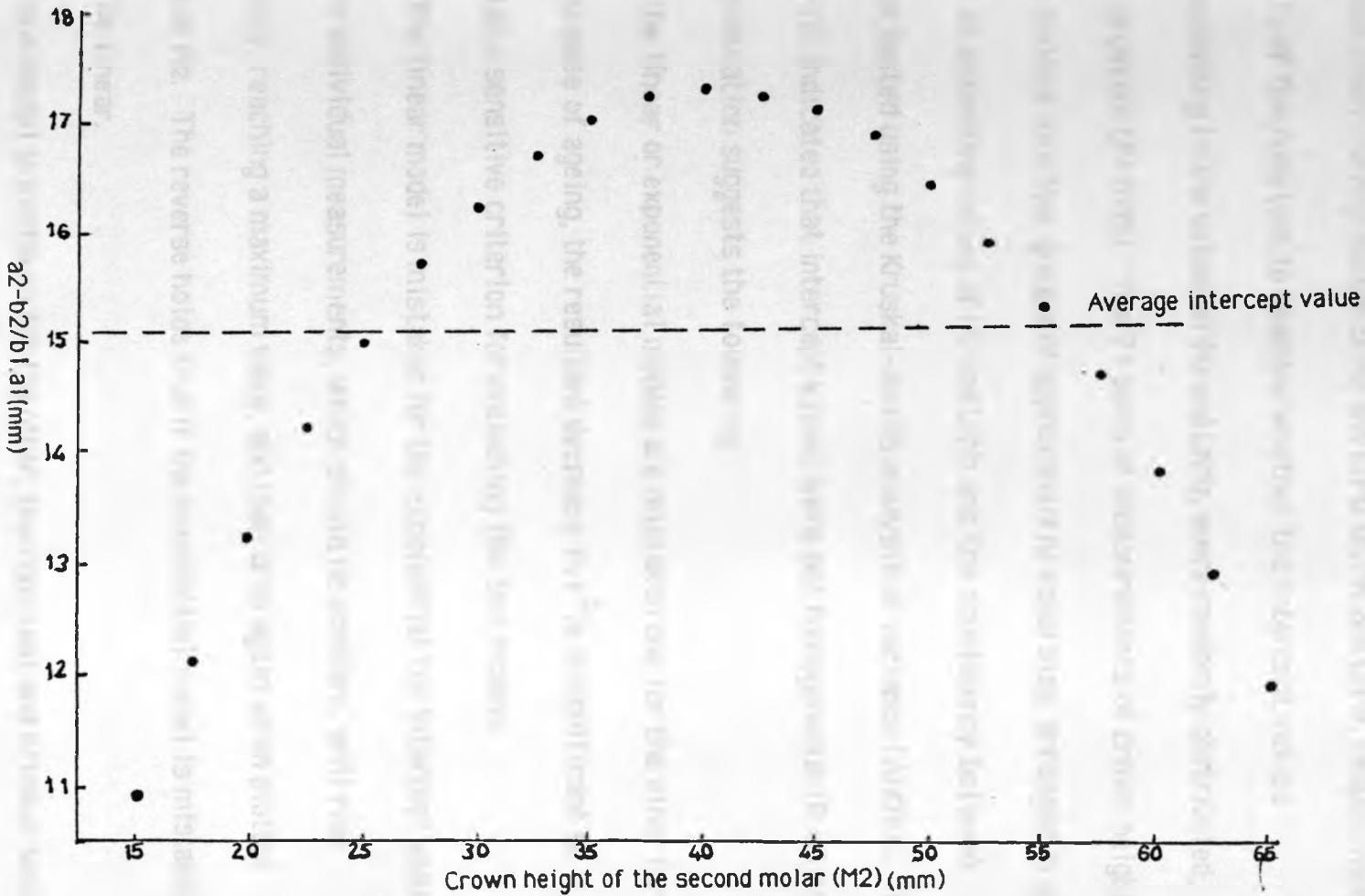


Figure 4B. The effect of mistaking the linear model for the exponential on the intercept values ($a_2 - b_2/b_1 \cdot a_1$). points represent the individual intercept values obtained by substituting the value of the slope of the regression of M_2 on M_1 (b_2/b_1), and the individual values of M_1 and M_2 in equation 9. The dashed line represents the average intercept value obtained by regressing crown height of the second molar (M_2) on that of the first (M_1).



obtained from the regression of M_2 and $\ln M_2$ on M_1 and $\ln M_1$, respectively. Results of the runs test to examine whether the intercept values corresponding to the values of M_2 and $\ln M_2$, were randomly distributed, were negative ($P < 0.05$). The 21 pairs of measurements of crown heights were divided into four groups of approximately equal size, arranged in an order of ascending values of M_2 and $\ln M_2$ and the consistency between groups tested using the Kruskal-Wallis analysis of variance (ANOVA). The analysis indicated that intercept values were not homogeneous ($P < 0.01$). The simulation suggests the following:

1. If the linear or exponential models are mistaken one for the other for the purpose of ageing, the resultant decrease in r^2 is insignificant to provide a sensitive criterion for evaluating the two models.
2. If the linear model is mistaken for the exponential the intercept values of the individual measurements, which should be constant, will rise steadily, reaching a maximum value, and then drop again when plotted against M_2 . The reverse holds true if the exponential model is mistaken for the linear.
3. If one model is mistaken for the other, the runs test and Kruskal-Wallis ANOVA can be used to test for the consistency of the intercept values.

These three procedures provide a new way of evaluating the pattern of wear of crown height with time that makes it possible to evaluate the

pattern using a number of more sensitive criteria, at least when applied to simulated data. When applied to real ageing data the regression approach can be tried first, to see which model fits the data. If a decision cannot be reached then Equations 9 and 12 can be used to check for slope consistency in a way similar to that described in the simulation. Crown heights of the second molar, or their natural logarithms have to be arranged in an ascending or a descending order and divided into groups of more or less equal sizes. Then the runs test and Kruskal-Wallis ANOVA can be used to test intercept consistency.

A particular model may provide the best fit for all the data nevertheless it may not provide the best fit for each age class. This may be the case when b_2/b_1 remains constant for all age groups but b_1 and b_2 change from one age group to another. It should be noted that if the values of b_1 and b_2 are both multiplied by a constant factor, the corresponding values of a_1 and a_2 , or $\ln a_1$ and $\ln a_2$ will change accordingly.

The values of $a_2 - b_2/b_1 \cdot a_1$ and $\ln a_2 - b_2/b_1 \cdot \ln a_1$, on the other hand, will still remain the same. If this is the case Equations 10 and 13 can be used to check the consistency in the amount (linear) or rate (exponential) of decrease of crown heights of any two molars with time provided that a_1 or $\ln a_1$ can be obtained from a different source.

AGEING BY TEETH, KONGONI

Eleven subjective age classes were worked out for kongoni, based on criteria essentially the same as these used to define the wildebeest age classes except for the presence or absence of the intermediate infundibulum which was not a good ageing criterion in kongoni. This infundibulum (exposed when the anterior and posterior cusps are separated) was present in only about 50% of the kongoni skulls. The infundibulum was, therefore, reported 'absent' if it was not present in all the skulls in a particular age class. Crown height of the three molars was measured in the same way as was done in wildebeest and the same equations (5 to 13) were also obtained. The age classes are described below:

Age classes one to five as in wildebeest.

AGE CLASS SIX

Molar one

1. anterior infundibulum slightly hat or U shaped
2. posterior infundibulum y or hat shaped
3. intermediate infundibulum present

Molar two and three as in wildebeest

AGE CLASS SEVEN

Molar one

1. anterior infundibulum U shaped
2. posterior infundibulum y or hat shaped
3. intermediate infundibulum present

Molar two and three as in wildebeest

AGE CLASS EIGHT

Molar one

1. anterior infundibulum U shaped
2. posterior infundibulum y or hat shaped
3. intermediate infundibulum present (sometimes a trace)

Molar two and three as in wildebeest

AGE CLASS NINE

Molar one

1. anterior infundibulum U shaped
2. posterior infundibulum y, hat or U shaped
3. intermediate infundibulum absent

Molar two

1. anterior infundibulum y or hat shaped
2. posterior infundibulum y, hat or U shaped,
3. intermediate infundibulum present or absent

Molar three as in wildebeest

AGE CLASS TEN

Molar one

1. anterior infundibulum shallow U, line or O shaped
2. posterior infundibulum U shaped
3. intermediate infundibulum absent

Molar two and three as in age class nine

Age class eleven as in wildebeest, age class Twelve

Individuals belonging to the first four age classes were assigned age based on horn shape as illustrated by Gosling (1975).

4. RESULTS

ROAD COUNTS

The various habitat types were not equally represented in the sample zone (Table 2). DWG, occupying almost half the area of WRR, was only represented by a 13.9% sampling intensity, while WBG covering only a small portion of the ranch was represented by a 43.6% sampling intensity.

Results of the road counts for the economically important species are presented in Appendix 1 for the sake of comparison with results of the total ground counts (Appendix 2).

The high values of the standard deviations of the series of the four daily counts are evident (Table 3). Comparison of total ground counts and road counts (Appendix 1, 2) indicates that road counts were overestimating population sizes of both Thomson's gazelle and wildebeest.

A visibility bias did not occur in the case of the wildebeest. The high figures as indicated by the road counts for this species can, therefore be assumed to have resulted from the association between wildebeests' distribution and the road system.

Numbers of Thomson's gazelle sighted at intervals of 25 m were progressively decreasing from the centre of the road (Figure 5). The distribution was best described by the equation:

$$N = 1801.6 - 309.8 \ln D$$

(17)

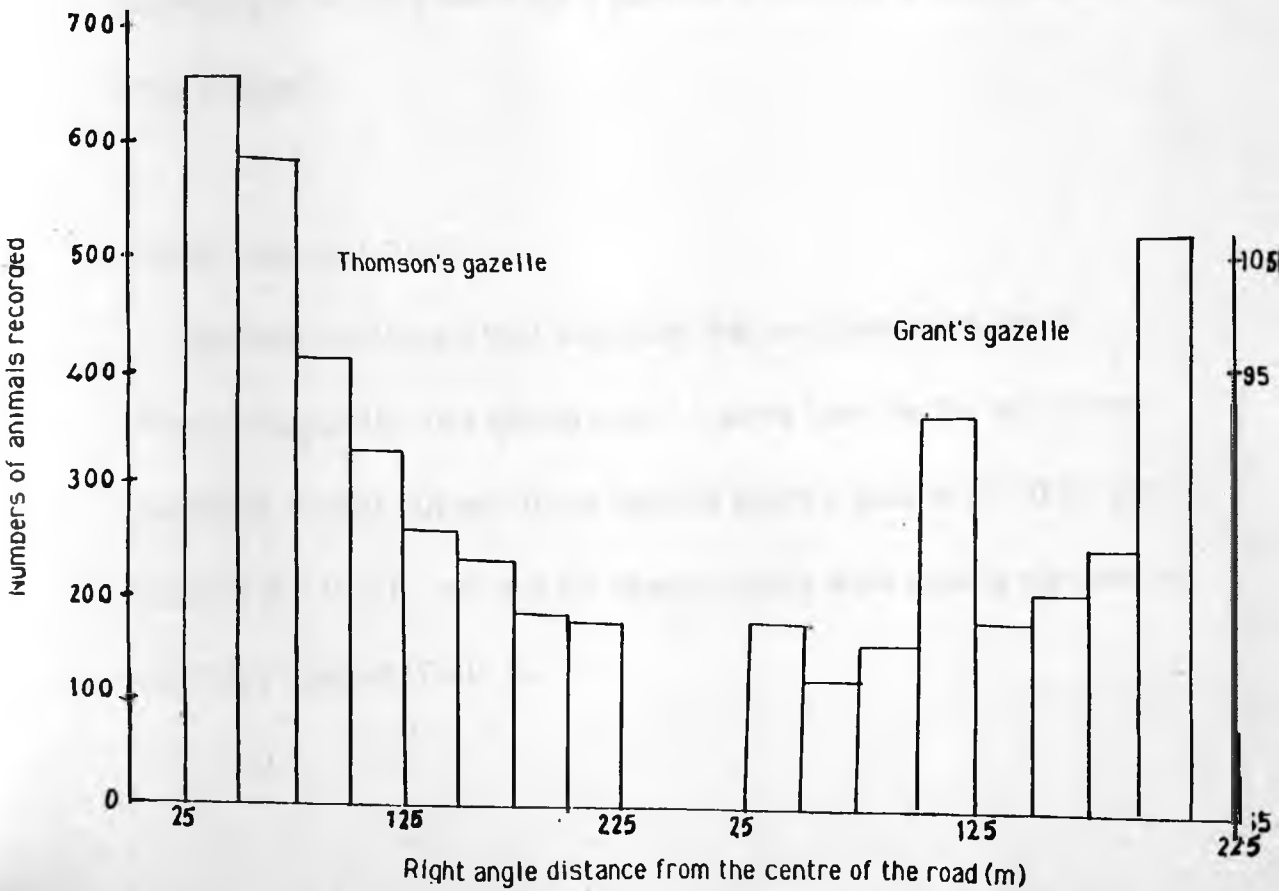
Table 2. Size of the various habitat types in WRR and in the sample zone, and sampling intensities in each habitat type for the road counts carried out at WRR between December 1986 and July 1987.

Habitat type	G	WG	DWG	BG	WBG	W	Total
Area of each habitat type in the sample zone (Km ²)	4.6	10.0	5.5	0.0	2.4	0.5	23.0
Area of each habitat type within WRR (Km ²)	10.0	20.5	39.6	03.6	5.5	1.8	81.0
Sampling intensity (%)	46	48.8	13.9	0.0	43.6	27.8	28.4

Table 3. Mean (\bar{X}) and standard deviation (S.D.) of each series of four daily road counts carried out at WRR used to assign confidence limits to the road counts.

Season	Statistic	T. Gazelle	G. Gazelle	Kongoni	Wildebeest
Middle wet	\bar{X}	606	211	333	574
3-6 Dec. 86	S.D.	69	34	113	214
Late dry	\bar{X}	540	118	365	455
5-10 Mar. 87	S.D.	154	22	139	173
Late wet	\bar{X}	831	262	198	429
23-26 Jun. 87	S.D.	190	85	207	219
Early dry	\bar{X}	735	217	518	1131
27-30 Jul. 87	S.D.	78	68	317	196

Figure 5. Histograms of the numbers of Thomson's and Grant's gazelles recorded at intervals of 25 m on each side of the road, based on the results of the road counts carried out at WRR between December 1986 and July 1987.



$r^2 = 0.98$, $n = 8$, $P < 0.01$. Where

N = the number of animals sighted.

$\ln D$ = the natural logarithm of the right angle sighting distance.

The Anderson and Pospahala method suggested that the distribution of Grant's gazelle was not affected by the road system ($P > 0.05$). When group size (G) of the two gazelle species was regressed on the right angle sighting distance (D), the equations obtained were.

$$G = 10.1 + 0.02D \quad (\text{Thomson's gazelle}) \quad (18)$$

$r^2 = 0.006$, $n = 323$, $P > 0.05$.

$$G = 5.4 + 0.01D \quad (\text{Grant's gazelle}) \quad (19)$$

$r^2 = 0.019$, $n = 126$ and $P > 0.05$.

Equations 18 and 19 suggest that there was no visibility bias in detecting Thomson's and Grant's gazelles within the width (250 m) of the road transect.

TOTAL GROUND COUNTS

The Mann-Whitney U test indicated that wet season counts of Thomson's gazelle were giving higher figures than the the dry season counts ($P < 0.02$), but not in the cases of Grant's gazelle ($P > 0.05$) and kongoni ($P > 0.05$). Wet and dry season counts were equally variable for the three species (Table 4).

Table 4. mean (\bar{X}) and standard deviation (SD) of the Thomson's and Grant's gazelle, and kongoni total ground counts in the wet and dry seasons.

Notation	T. gazelle	G. gazelle	Kongoni
\bar{X} % in wet season	87.01	81.07	82.93
\bar{X} % in dry season	77.06	79.60	85.05
\bar{X} % in both seasons	81.36	80.24	84.14
SD in wet season	13.24	14.31	10.15
SD in dry season	12.42	13.52	12.03
SD in both seasons	13.66	13.80	10.90

The Mann-Whitney U test indicated no significant differences in average group sizes between the wet and dry seasons in each species ($P > 0.05$).

Wilcoxon test indicated that total ground counts produced higher numbers than the total aerial counts of Thomson's and Grant's gazelles, and impala combined ($T = 13.5$, $N = 12$, $P < 0.05$). The ground counts were thus considered more accurate than aerial counts when applied to these species. There was no significant difference in the two counting methods when applied to the four economically important species ($T = 47.5$, $N = 16$, $P > 0.05$), and to the large plains ungulates ($T = 57$, $N = 15$, $P > 0.05$). No significant differences between ground and aerial counts were found when applied to the whole ungulate community of WRR ($T = 160$, $N = 31$, $P > 0.05$).

The most striking feature of Grant's gazelle is the very low recruitment values; the high, positive recruitment value in 1983 and the low, negative value in 1984 seem to be a result of inaccuracy in the counts (Table 5). Percentage recruitment of kongoni was high in the two periods starting at the end of June 1981 and June 1983, and negative in the period starting at the end of June 1984 (Table 6). Percentage recruitment of wildebeest was high in the period starting in 15 March 1982, and very high in the period starting in March 1985 (Table 7).

Table 5. Number of WRR Grant's gazelle harvested and percentage recruitment obtained from the total ground counts and harvest records.

Period (t - t+1)	No.in the middle of year t	corrected No.(Nt)	No.harvested between year t and t+1	Recruitment between year t and t+1	% recruitment (100R/Nt)
JUL 81-	474	591	108	-50	-8.5
JUL 82-	347	433	94	19	4.4
JUL 83-	288	358	22	101	28.2
JUL 84-	351	437	70	-146	-33.4
JUL 85-	177	221	55	7	3.2
JUL 86-	139	173	2	11	6.4
JUL 87-	146	182	-	-	-

Table 6. Number of WRR kongoni harvested and percentage recruitment values obtained from the total ground counts and harvest records.

Period (t - t+1)	No.in the middle of year t	corrected No.(Nt)	No.harvested between year t and t+1	Recruitment between year t and t+1	% recruitment (100R/Nt)
JUL 81-	511	607	154	239	39.3
JUL 82	582	692	170	97	14.0
JUL 83-	521	619	236	289	46.5
JUL 84-	565	671	266	-35	-5.2
JUL 85-	312	370	142	39	10.5
JUL 86-	225	267	59	47	17.6
JUL 87	215	255	-	-	-

Table 7. Number of WRR wildebeest harvested and percentage recruitment values obtained from the total ground counts and harvest records.

Period (between 15th March t and 15th March t+1)	Month of highest count	N_h harvested between month of highest count and March that follows	No in March 15th(N_t)	N_h harvested between March t and t+1	Recruitment between year t and t+1 (R)	%recruitment ($100R/N_t$)
1981	JAN 81	4	260	41	81	31.2
1982	FEB 82	4	300	117	214	71.3
1983	OCT 82	80	397	152	165	41.6
1984	JAN 84	35	410	250	86	21.0
1985	AUG 84	167	246	297	296	120.3
1986	NOV 85	93	245	38	73	29.8
1987	AUG 86	13	280	3	110	39.3
1988	AUG 87	3	387	—	—	—

INCIDENCE OF PREGNANCY IN WILDEBEEBEE

The calculation of CAIP can be obtained from Table 8, which indicates a substantial difference between CAIP and AIP. When CAIP was regressed on AIP, the following linear regression equation was obtained:

$$\text{CAIP} = 4.23 + 1.23\text{AIP} \quad (20)$$

$r^2 = 0.96$ and $n = 5$.

Based on the coefficient of variation CAIP can be easily estimated using the above equation as long as the harvesting strategy doesn't change. The data were too few to statistically evaluate the relationship between CAIP and rainfall but a comparison of the rainfall figures of the first year of any breeding cycle and AIP (Table 8) suggests a possible positive relationship between rainfall and CAIP.

ASIP increased from the age of 17 months, the time wildebeest females first became pregnant (age class 2), until it reached a maximum value in the seventh/eighth age classes, where it remained constant until the age of 10 years, the estimated average age for the last age class (Table 9).

The relationship between foetal weight for foetuses that were more than 500 gm in weight and age was best described by the regression of the cube root of foetus weight on time. The rate of foetal growth before this weight was slower and efforts to fit a regression equation to it were not

Table 8. Corrected annual incidence of pregnancy (CAIP) of the WRR and Mulinge (*) wildebeest for the 1982/83 to 1986/86 breeding cycles. See text for the steps followed in the calculation.

Number of pregnant females killed in each month (n_i)						
Month	Correction Factor	82/83	83/84	84/85	85/86	86/87*
AUG	2.48	0	0	4	5	0
SEP	1.60	0	1	4	10	3
OCT	1.18	0	2	2	13	2
NOV	1.00	7	6	5	15	7
DEC	1.31	8	4	2	19	3
JAN	1.31	0	5	5	4	3
FEB	1.58	3	1	3	6	4
Total ($\sum n_i$)		18	19	25	72	22
No. of females killed ($\sum Ni$)		41	34	95	110	36
AIP ($100 \cdot \sum n_i / \sum Ni$)		43.90	55.89	26.32	65.45	61.11
Corrected No. of pregnant females ($\sum n_i \cdot CF_i$)		22.24	23.35	37.61	98.41	28.36
CAIP ($100 \sum n_i CF_i / \sum Ni$)		54.23	68.67	39.59	89.47	78.79
Rainfall (mm)		473	435	266	728	468

Table 9. Wildebeest age specific incidence of pregnancy (ASIP).

Age classes	No. of pregnant females	No. of females	Corrected No. of pregnant females	ASIP
2, 3 and 4	7	16	8.2	51.3
5 and 6	8	20	12.1	60.5
7 and 8	12	23	17.6	76.5
9 to 12	14	27	19.7	73.1

successful. All foetuses were, however, included in the regressions (Table 10) since one of the objectives was to investigate the effect of the environment on the rate of foetal growth. It was considered that the slight underestimation of the gestation period caused by the inclusion in the regression of foetuses in the early stage of slow growth was of less importance than the increase in sample size.

Analysis of covariance of the regression of the cube root of foetal weight on age (Table 10) indicated that foetal growth rates were not the same in all the years ($P < 0.01$). Rates of foetal growth were low in 1983/84 and 1984/85 breeding cycles, cycles with the lowest rainfall. The rate of foetal growth in 1982/83 was exceptionally high. The coefficient of variation was lowest in 1983/84 and 1984/85 and highest for 1985/86 and 1986/87. The implication is that the coefficient of variation in foetal growth rate is positively correlated to rainfall. The value $-a/b$ gives the average conception date assuming a foetus weight of zero at conception. The mating season was very late in 1982/83.

PREVALENCE OF PREGNANCY IN THOMSON'S AND GRANT'S GAZELLES, AND KONGONI

APP figures of WRR Thomson's gazelle were gradually decreasing between 1982 and 1987 (Table 11). The most distinctive feature of APP

Table 10. Regression equations of the cube root of foetal weight (Y) of WRR and Mulinge (*) wildebeest on coded aged (X), July first was coded as day one. Average conception date is defined as the day when foetal weight is equal to zero.

Statistic	Breeding cycle					Average
	82/83	83/84	84/85	85/86	86/87*	
Intercept (a)	-15.36	-2.80	-5.64	-5.12	-8.63	-4.63
Slope (b)	0.12	0.08	0.09	0.11	0.12	0.09
Coefficient of variation	0.83	0.74	0.77	0.86	0.90	0.73
Sample size (N)	20	21	24	74	23	162
Average conception date	2 Oct.	3 Jul.	31 Jul.	18 Jul.	12 Aug.	7 Jul.

Table 11. Annual prevalence of pregnancy (APP) of WRR and Mullinge (*)

Thomson's and Grant's gazelles, and kongoni.

	No. of pregnant Females harvested	total No. of females harvested	Prevalance of pregnancy (%)
1982			
T. gazelle	10	20	50.0
G. gazelle	11	36	30.6
Kongoni	12	34	35.3
1983			
T. gazelle	18	64	28.1
G. gazelle	7	24	29.2
Kongoni	19	45	42.2
1984			
T. gazelle	5	44	11.4
G. gazelle	0	24	0.0
Kongoni	30	164	18.3
1985			
T. gazelle	71	205	34.6
G. gazelle	17	70	24.3
Kongoni	32	132	24.2
1986			
T. gazelle	7	52	13.5
T. gazelle*	13	51	25.5
G. gazelle*	7	31	22.6
Kongoni	17	72	23.6
Kongoni*	7	30	23.3
1987			
T. gazelle	1	26	3.9
T. gazelle*	8	74	10.8
G. gazelle*	2	9	22.2
Kongoni	2	7	28.6
Kongoni*	14	40	35.0

in WRR Grant's gazelle is the zero value recorded in 1984 and the low APP value in 1985 compared to the ones in 1982 and 1983 (Table 11).

Four periods were selected to reflect the different responses of Thomson's gazelle females, in terms of their pregnancy rate, to the 1984 drought (Table 12). The first (March–October 1984) and third (August–December 1985) periods corresponded with time intervals when prevalence of pregnancy was low, while the periods between November 1984 and May and between June–July 1985 exhibited high pregnancy rate.

Pregnancy in kongoni was first recorded in the fifth age class (Table 13). These animals are two to three years of age (Gosling 1975) implying that the WRR kongoni do not give birth till they are three years of age.

AGEING AND SEXING IN THE FIELD

AIP values of Thomson's and Grant's gazelles, and kongoni were higher in the small young than in the medium and big young (Table 14) probably as the result of calf mortality and the increasing population sizes in these species.

Thomson's and Grant's gazelles, and kongoni were breeding throughout the year (Figure 6) but it is hard to verify whether the periods of high proportions of small young between October and April in Thomson's gazelle, between October and January in Grant's gazelle and between

Table 12. Details of prevalence of pregnancy of WRR Thomson's gazelle for the period extending between March 1984 and December 1985, to show the effect of the 1984 draught on prevalence of pregnancy. The periods were chosen to reflect the different responses of the animals in terms of their pregnancy rate to the drought.

Period	No. of pregnant females killed	Total No. of females killed	Prevalence of pregnancy
March- October 1984	2	31	6.5
November 84- May 85	27	77	35.1
June- July 85	1	44	2.3
August- December 85	46	97	47.4

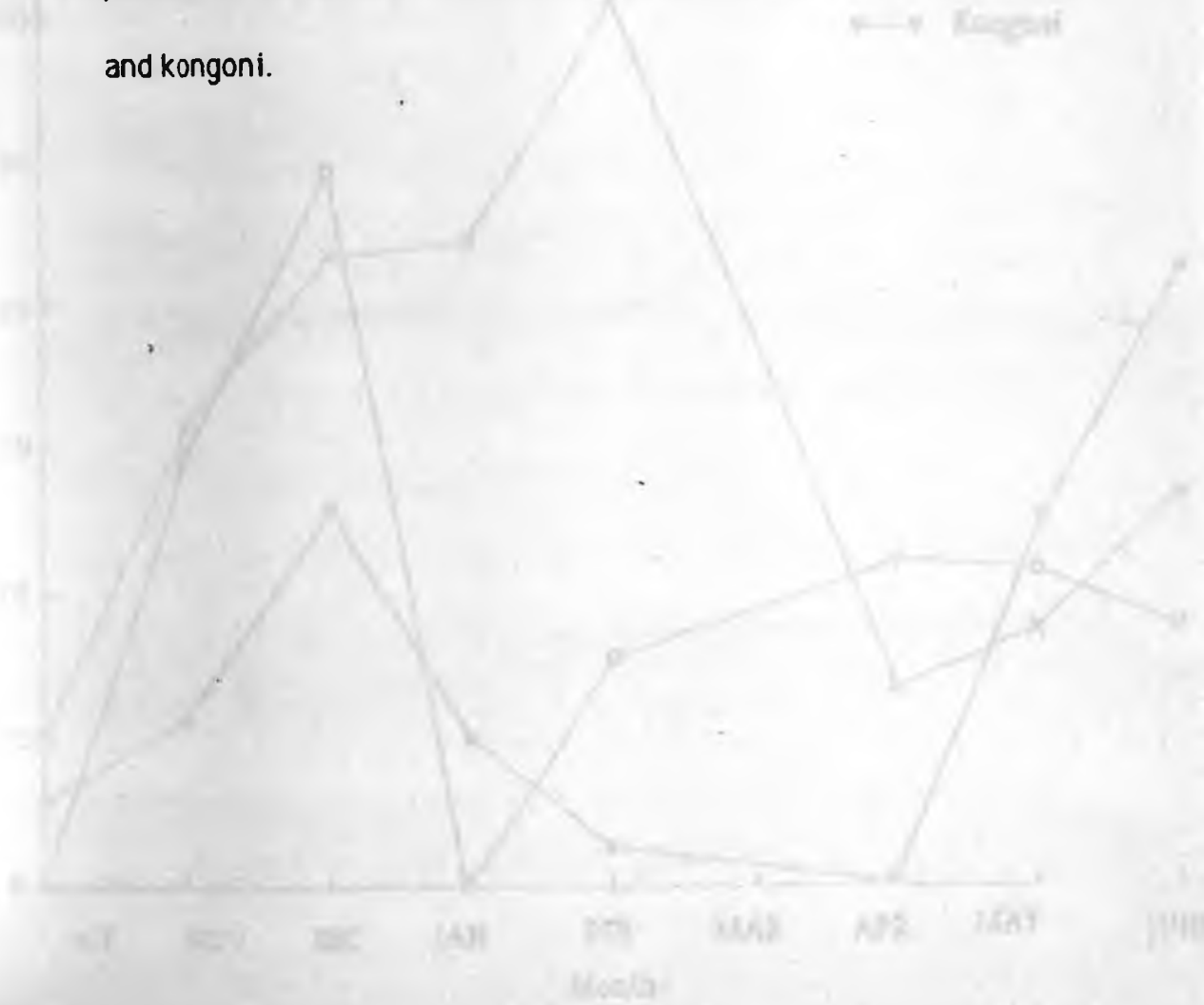
Table 13. Age specific prevalence of pregnancy (ASPP) of WRR kongoni.

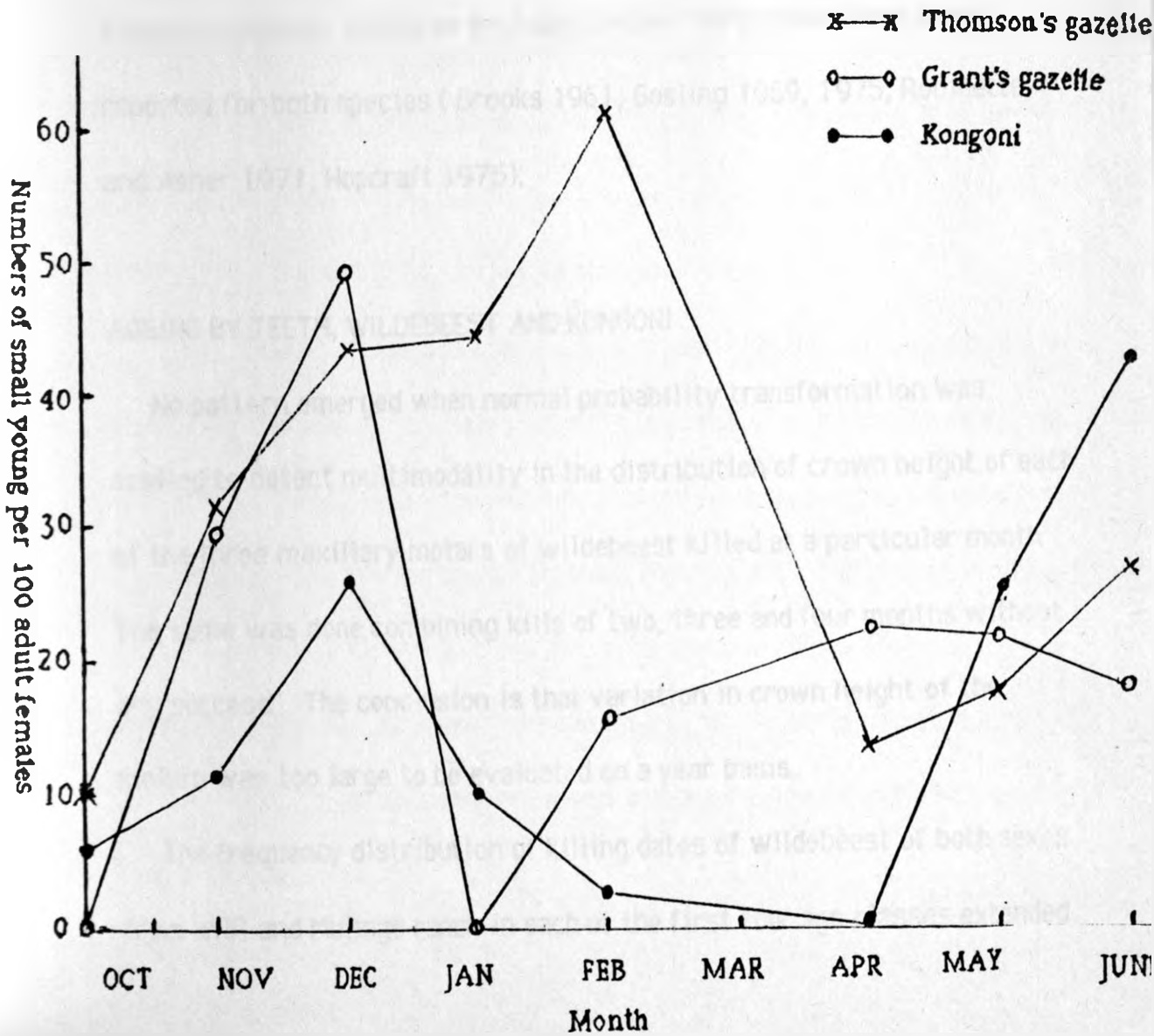
Age class(s)	No. of pregnant females killed	Total No. of females killed	Prevalence of pregnancy
1-4	0	55	0.0
5	2	13	15.4
6	6	18	33.3
7	6	17	35.3
8	9	13	69.2
9	14	43	32.6
10-11	8	20	40.0

Table 14. Results of ageing and sexing in the field carried out between October 1986 and June 1987 for Thomson's and Grant's gazelles and kongoni at WBR. Ranges of age were derived from references cited in text.

	Thomson's gazelle	Grant's gazelle	Kongoni
Range of age (months)			
Small young	0-6	0-6	0-2
Medium young	-	-	3-12
Large young	7-18	7-30	13-24
Total sample size	311	292	400
Numbers per 100 adult females			
Small young	33.1	20.4	16.2
Medium young	-	-	59.4
Large young	80.5	75.4	45.3
Adult males	12.9	9.1	19.7
Number of females as a%			
of the total population	46.6	51.1	42.0
Annual incidence of pregnancy (NP), based on			
Small young	132	61	97
Medium young	-	-	71
Large young	81	36	45

Figure 6. Temporal distribution of the number of small young as a percent of the number of adult females of Thomson's and Grant's gazelles and kongoni.





October and February in kongoni were actual birth peaks. It is easy, however, to see that the high values in Grant's gazelle did not correspond with an actual birth peak. For a birth peak to be indicated the period of high proportion of small young should extend over a time interval longer than the length of that particular age class. The small young class extended for a period of 6 months (Table 14), compared to a period of 3 months over which the period of high proportion of small young extended (Figure 6). The possibilities of birth peaks in Thomson's gazelle and kongoni, however, cannot be excluded because birth peaks have been reported for both species (Brooks 1961, Gosling 1969, 1975, Robinette and Asher 1971, Hopcraft 1975).

AGEING BY TEETH, WILDEBEEST AND KONGONI

No pattern emerged when normal probability transformation was applied to detect multimodality in the distribution of crown height of each of the three maxillary molars of wildebeest killed at a particular month. The same was done combining kills of two, three and four months without any success. The conclusion is that variation in crown height of the molars was too large to be evaluated on a year basis.

The frequency distribution of killing dates of wildebeest of both sexes from WRR and Mulinge ranch in each of the first four age classes extended

for less than a year (Figure 7). The distributions also followed a sequential pattern such that the distribution for animals belonging to a younger age class preceded the one for animals in the older age classes. The frequency distribution of killing dates of the second and third age classes were overlapping, the only difference was the presence and absence of the intermediate infundibulum. Age class three should, therefore, reflect the age at which the intermediate infundibulum appears. No pattern emerged when frequency distributions were plotted for wildebeest belonging to the fifth and older age classes, suggesting that these age classes either extended over a period of more than a year, or that the variation in their eruption time and or change of their pattern of wear, was too great to be evaluated on a year basis, or both.

The first wildebeest age class was assigned specific age by comparing horns of the skulls of harvested animals to those of live animals (Western 1983, Merz 1986). Animals belonging to the next three age classes were then assigned age making use of the fact that the distributions of killing dates of animals belonging to any two adjacent age classes followed a sequential pattern. Each animal belonging to the first four age classes was then aged to the nearest month assuming a median date of birth on the 15th of March (Figure 7).

Crown height of the first maxillary molar of animals belonging to the


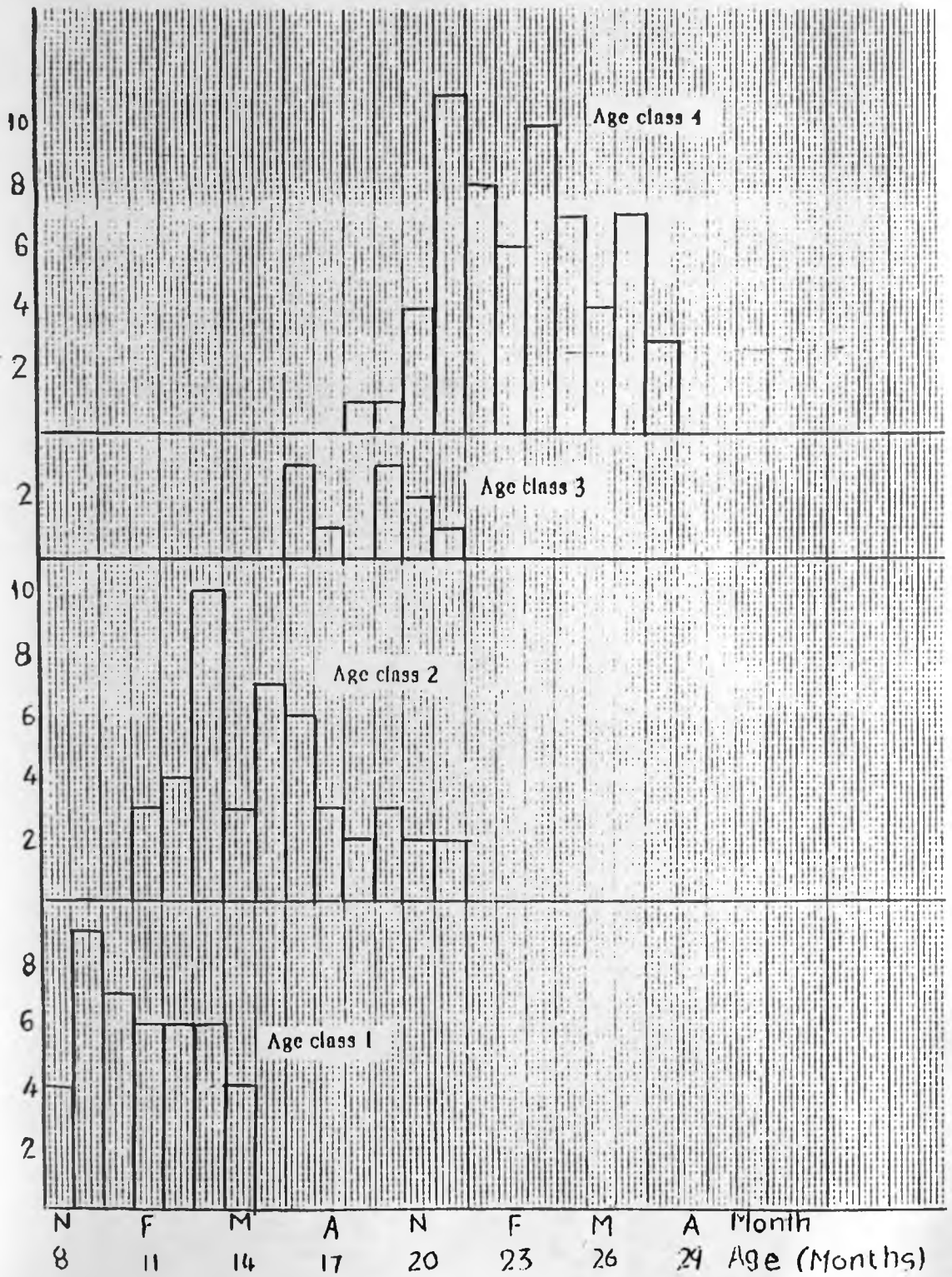


Figure 7. Frequency distribution of killing dates of wildebeest belonging to the first four age classes. Animals were assigned specific age assuming that they were born on March the 15th. Included in the analysis were animals from WRR and Mulinge ranches for the years 1982-1987.



first four age classes was regressed on age, based on killing dates (wildebeest) and horn shape (kongoni), using the linear and exponential models with the two sexes combined. Wildebeest included in the regressions were the ones older than 10 months, while the kongoni skulls included belonged to animals older than 9 months (Table 15). The coefficients of variation were equally low for both models, indicating a large variation in crown heights of animals of the same age, and that any of the two models could equally fit the data.

Average crown heights of the three maxillary molars were progressively decreasing with age class in both wildebeest (Table 16) and kongoni (Table 17). The fact that the decrease in average crown heights was corresponding with the age classes does not indicate that average crown heights were decreasing with age unless the age classes were good ageing criteria. It was, however, seen that the young age classes in wildebeest (Fig. 7) were corresponding with the age of the animals.

Crown heights of the second and third molars were regressed on crown height of the first molar, and crown height of the third molar was regressed on crown height of the second molar using Equations 10 (linear model) and 13 (exponential model) for wildebeest (Table 18) and kongoni (Table 19). Both models were equally fitting the data; the coefficients of variation values were, however, quite high.

Table 15. Summary of statistics of the regression of wildebeest and kongoni crown height of the first maxillary molar (mm) (M_1) on age (months) (t) based on killing dates.

Statistic	Linear model		Exponential model	
	Kongoni	Wildebeest	Kongoni	Wildebeest
Slope	-0.349	-0.385	-0.0096	-0.0079
Intercept	43.16	56.68	3.856	4.047
Sample size	132	135	132	135
Standard error	0.046	0.047	0.001	0.001
Mean age (t)	18.95	18.31	18.95	18.31
Mean crown height (M_1)	36.55	49.64	3.60	3.90
Sum of squares				
(Residual)	592.28	980.00	0.454	0.404
(Total)	853.80	1464.59	0.652	0.604
Coefficient of variation	0.33	0.33	0.33	0.33

Table 16 . Average crown heights (AV., in mm.) and standard deviations (S.D.) of the first (M₁), second (M₂) and third molar (M₃) of the various age classes in wildebeest.

Age class	Molar	AV. (mm)	S.D.	Sample size
2	1	50.36	2.35	56
3	1	49.29	3.63	12
4	1	47.64	2.88	71
5	1	43.07	3.10	58
5	2	60.25	3.21	57
6	1	37.49	4.05	39
6	2	54.84	4.61	41
7	1	32.35	3.81	67
7	2	49.55	4.61	67
7	3	57.95	3.39	66
8	1	29.60	3.05	24
8	2	45.84	2.82	24
8	3	54.96	2.32	24
9	1	24.28	4.09	65
9	2	39.15	4.96	66
9	3	47.81	4.87	64
10	1	17.04	3.88	25
10	2	30.75	6.25	26
10	3	38.87	6.74	25
11	1	13.65	1.61	5
11	2	27.20	2.49	5
11	3	36.38	3.37	4
12	1	6.92	3.13	16
12	2	17.77	4.13	16
12	2	26.78	5.38	15

Table 17. Average crown heights (AV., in mm.) and standard deviations (S.D.) of the first (M₁), second (M₂) and third molar (M₃) of the various age classes in kongoni.

Age class	Molar	AV. (mm)	S.D.	Sample size
2	1	38.01	2.05	42
3	1	37.25	2.12	38
4	1	34.69	1.97	72
5	1	31.85	2.16	53
5	2	44.03	2.10	54
6	1	30.54	1.91	40
6	2	42.49	1.78	38
7	1	27.69	2.47	43
7	2	39.01	2.56	43
7	3	41.79	2.19	37
8	1	24.63	2.70	34
8	2	35.85	2.49	37
8	3	39.36	2.11	37
9	1	19.30	3.25	87
9	2	30.40	4.12	89
9	3	34.27	3.93	85
10	1	12.41	3.31	25
10	2	21.65	3.78	25
10	3	25.55	4.17	24
11	1	6.50	1.77	4
11	2	16.06	2.78	4
11	3	20.38	5.24	4

Table 18 . Regression of wildebeest crown height of the second molar on the first molar (M_2-M_1), the third on the first (M_3-M_1), and the third on the second molar (M_3-M_2) for both the linear and the exponential models.

Statistic	Linear model			Exponential model		
	M_2-M_1	M_3-M_1	M_3-M_2	M_2-M_1	M_3-M_1	M_3-M_2
Slope	1.115	1.065	0.911	0.720	0.557	0.760
Intercept	12.50	22.50	12.39	1.39	2.11	1.09
Sample size	281	210	214	281	212	215
Standard error	0.017	0.035	0.019	0.012	0.017	0.016
\bar{M}_1 (average)	31.42	28.01	43.95	3.40	3.30	3.76
\bar{M}_2 (average)	47.54	52.34	52.44	3.83	3.94	3.95
Sum of squares						
(Residual)	1961.33	2755.66	1378.50	1.18	1.34	0.57
(Total)	30706.3	15328.2	15770.9	16.58	6.76	6.86
Coefficient of variation	0.94	0.82	0.93	0.93	0.83	0.92

Table 19. Regression of kongoni crown height of the second molar on the first molar (M_2-M_1), the third on the first (M_3-M_1), and the third on the second molar (M_3-M_2) for both the linear and the exponential models.

Statistic	Linear model			Exponential model		
	M_2-M_1	M_3-M_1	M_3-M_2	M_2-M_1	M_3-M_1	M_3-M_2
Slope	1.080	0.976	0.914	0.691	0.556	0.828
Intercept	9.31	15.01	6.20	1.38	1.89	0.70
Sample size	282	217	220	282	217	220
Standard error	0.016	0.026	0.015	0.010	0.014	0.014
\bar{M}_1 (average)	24.29	22.39	33.50	3.14	3.05	3.48
\bar{M}_2 (average)	35.54	36.86	36.83	3.54	3.59	3.59
Sum of squares						
(Residual)	950.23	1331.71	566.79	1.00	1.20	0.54
(Total)	17324.7	10237.1	10212.2	18.29	9.76	9.74
Coefficient of variation	0.95	0.87	0.94	0.95	0.87	0.94

No pattern emerged when the new approach, based on intercept consistency, was applied to see which model fits the data.

Equations describing the relationship between crown heights of the three molars (mm) and age of the animal (month) were derived. Equations for wildebeest are given first. The values of a_1 and b_1 are 56.68 and -0.385 (Table 15), respectively in the case of the regression of crown height of the first molar on age using the linear model. The corresponding $\ln a_1$ and b_2 values for the exponential model are 4.047 and -.0079 (Table 15), respectively. The values of $a_2 - b_2/b_1 \cdot a_1$, $a_3 - b_3/b_1 \cdot a_1$, $a_3 - b_3/b_2 \cdot a_2$, b_2/b_1 , b_3/b_1 and b_3/b_2 for the linear model and the corresponding values for the exponential model can be obtained from Table 18. Using the above values, it is possible to derive the following equations that can be used to predict the age of the animals (t) from crown heights of any of the three molars. Equations 21-24 were based on the regression of the first molar on age, the second molar on the first, the third on the first, and the third molar on the second, respectively for the linear model.

$$t = 147.221 - 2.597.M_1 \quad (21)$$

$$t = 176.490 - 2.331.M_2 \quad (22)$$

$$t = 202.266 - 2.440.M_3 \quad (23)$$

$$t = 208.176 - 2.558.M_3 \quad (24)$$

The corresponding equations for the exponential model are given below.

$$t = 512.278 - 126.582.LnM_1 \quad (25)$$

$$t = 759.705 - 176.655.LnM_2 \quad (26)$$

$$t = 994.617 - 228.022.LnM_3 \quad (27)$$

$$t = 1012.890 - 232.580.LnM_3 \quad (28)$$

The equations for kongoni were derived in a similar way as follows.

$$t = 123.694 - 2.866.M_1 \quad (29)$$

$$t = 148.387 - 2.653.M_2 \quad (30)$$

$$t = 167.772 - 2.936.M_3 \quad (31)$$

$$t = 166.393 - 2.902.M_3 \quad (32)$$

$$t = 393.823 - 104.240.LnM_1 \quad (33)$$

$$t = 601.579 - 150.944.LnM_2 \quad (34)$$

$$t = 747.889 - 187.472.LnM_3 \quad (35)$$

$$t = 729.662 - 182.354.LnM_3 \quad (36)$$

Average age (months) of the animals in the various age classes [Table 20 (wildebeest) and Table 21 (kongoni)] was calculated using Equations 21-28 (wildebeest) and Equations 29-36 (kongoni) for both the linear and the exponential models. All the three molars gave similar age to any individual age class based on a particular model. The two models gave similar age values for the various age classes up to the fifth age class. Afterwards, the exponential model resulted in higher age values. The difference in age between the two models also increased with age.

Table 20 . Average age (months) of the different wildebeest age classes, based on the regression of crown heights of the first maxillary molar on age (M_1-t), the second on the first molar (M_2-M_1), the third on the first (M_3-M_1) and the third on the second molar (M_3-M_2) for both the linear (Lin.) and exponential (Exp.) models. Included in the analysis are animals of both sexes from WRR and Mulinge ranch.

Age class	(M_1-t)		(M_2-M_1)		(M_3-M_1)		(M_3-M_2)	
	Lin.	Exp.	Lin.	Exp.	Lin.	Exp.	Lin.	Exp.
2	16.4	16.3						
3	19.2	19.0						
4	23.5	23.3						
5	35.4	36.1	36.0	35.7				
6	49.9	53.7	48.7	52.3	52.6	56.1	51.3	55.6
7	63.3	72.5	61.0	70.2	60.9	68.9	59.9	68.7
8	70.4	83.7	69.6	84.0	68.2	81.0	67.6	81.0
9	84.2	108.9	85.2	111.8	85.6	112.8	85.9	113.5
10	103.1	153.9	104.8	154.5	107.4	160.0	108.7	161.6
11	111.9	182.0	113.1	176.2	113.5	175.1	115.1	177.0
12	129.4	268.3	135.1	251.4	136.9	245.0	139.7	248.3

Table 21 . Average age (months) of the different kongoni age classes, based on the regression of crown heights of the first maxillary molar on age (M_1-t), the second on the first molar (M_2-M_1), the third on the first (M_3-M_1) and the third on the second molar (M_3-M_2) for both the linear (Lin.) and exponential (Exp.) models. Included in the analysis are animals of both sexes from WRR and Mulinge ranch.

Age class	(M_1-t)		(M_2-M_1)		(M_3-M_1)		(M_3-M_2)	
	Lin.	Exp.	Lin.	Exp.	Lin.	Exp.	Lin.	Exp.
2	14.8	14.6						
3	17.0	16.7						
4	24.3	24.1						
5	32.4	33.0	31.6	30.3				
6	36.2	37.4	35.7	35.6	36.5	35.5	36.6	36.7
7	44.3	47.6	44.9	48.5	45.1	48.1	45.1	49.0
8	53.1	59.8	53.3	61.3	52.2	59.4	52.2	59.9
9	68.4	85.3	67.7	86.2	67.1	85.3	66.9	85.2
10	88.1	131.3	90.9	137.4	92.7	140.4	92.3	138.7
11	105.1	198.7	105.8	182.5	107.9	182.7	107.3	180.0

5. DISCUSSION

ROAD COUNTS

The effect of the road on the distribution of Thomson's gazelle continued beyond 250 m, the transect width employed in the counts (Equation 17). I was hoping that the distribution of Thomson's gazelle recorded at intervals of 25 m from the centre of the road was best described by an asymptote equation. Such an equation would show the distance at which the effect of the road on the distribution of Thomson's gazelle came to an end. Equation 17, however, only shows that the effect of the road on the distribution of Thomson's gazelle decreased with increasing distance from the centre of the road. It, however, does not show the distance at which the effect of the road comes to an end, thus it was not possible to correct for the biased estimate of population size resulting from the association between the species and the road.

The approach of detecting visibility bias, based on regressing group size on distance, has the following advantages over the Anderson and Pospahala (1970) approach:

1. it is based on a larger sample size since all the sightings are included in the regression;
2. it is less sensitive to the association between the sampled objects and the sample zone; and

3. it is less affected by inaccuracy in measuring the distance.

It, however, suffers from the following limitations:

1. it fails to correct for visibility bias if detected;
2. it requires that group size is independent of the sample zone; and
3. the assumption of the mathematical model in linear regression which requires that the independent variable (distance) is fixed (Snedecor and Cochran 1967), is usually violated. This may affect the slope value if an association exists between the sampled objects and the sample zone. To solve the problem distance can be fixed at regular intervals and average group size calculated for each interval before regressing the two variables. The conclusion (Equation 18) was not affected when average group size of Thomson's gazelle was calculated for each distance interval of 25 m before regressing the two values.

One advantage of sample counts over total counts is the reduction in time and expenses (Norton-Griffiths 1978). Aerial counts can be excluded on cost basis. They were less accurate than ground counts when applied to the WRR situation. Ideally a random sampling scheme would have been preferable but the practical aspects of such a scheme make its application in WRR almost impossible. This type of sampling is not only time consuming but is also very taxing both on the people as well as the vehicle (Omer 1985).

Various authors investigated different aspects of ground sampling techniques and designs (Hayne 1949, Dasmann and Mossman 1962, Eberhardt 1968, Gates 1969, Hirst 1969, Robinette *et al.* 1974, Anderson *et al.* 1979, Burnham 1979, Seber 1986). Many authors agree that the fixed transect width provides the best design if a reasonably large transect width can be covered and all the animals within that transect can be detected (Norton-Griffiths 1978). The fixed transect method also has got the advantage of a simple sample design. The results, however, indicated that both Thomson's gazelle and wildebeest preferred the road side and all the counts were imprecise (Table 3). Increasing the sampling intensity is expected to reduce searching efficiency because the observer would become more tired. There is also no robust method of relating sampling intensity to precision, though some attempts have been made (Sinclair 1973, Norton-Griffiths 1975 ,1978). To develop such a method the factors that affect the precision of the sample counts must be identified and an equation, or a series of equations must be derived that describe the relationship between these factors, sampling intensity and precision. Until such an equation is developed more frustrations, more expenses and valuable time will be wasted in unsuccessful sample counts.

TOTAL GROUND COUNTS

Counting is carried out to solve specific management problems. A manager must compromise between the time and cost of a count, and its utility. One question a manager must ask how often must the counts be carried out in order to provide answers to the management problems. This will depend on how accurate and how consistent the counts are. Consistency, as used here, refers to the variation in the numbers of animals resulting from repeated counts of the same population if the population remains stationary. A correction factor is needed if the counts prove to be inaccurate. The frequency at which counts are to be carried out is a function of consistency. The more consistent the counts are, the less frequent they need to be carried out. Gerrodette (1987) found that the ability of the regression method to detect changes in population size improved if the rate of population change is high, if counts are carried out more frequently and if the variation in the results produced by the counting method is low. Based on Gerrodette's findings a series of daily or weekly counts could be carried out at the same time once a year and the average of the counts can then be taken. Such a scheme will have the advantage of reducing the variation in the results of the counts, and of making the series of counts evenly spaced in time. Alternatively, counts could be carried out monthly.

Differences between the two seasons which may explain improved

accuracy in the counts of Thomson's gazelle during the wet season include: greener vegetation during the rainy season, providing a greater contrast between the background and the Thomson's gazelle; preferences for hill tops during the rainy season (Stelfox 1985, Sinnary Unpublished), which generally have shorter grass than that in the depressions bear in mind the small size of Thomson's gazelle; and a larger average group size in the rainy season (Sinnary Unpublished).

1984 was a very traumatic year for wildebeest and kongoni due to a very serious drought followed by heavy rains and floods. Breakages in the perimeter fence occurred and analysis of the records indicate that some 250 Kongoni emigrated whilst approximately 200 Wildebeeste immigrated. The drought also had effect on calving rates (Tables 8 and 11) and the ranch management increased the cropping rate due to lack of forage.

The decrease in the population of kongoni since 1984 (Table 6) is attributed to harvesting more animals than were being recruited annually and to the emigration of a large group of kongoni in 1984.

Based on the reproduction rate the high recruitment percentages in kongoni in the first (July 81) and third (July 83) periods (Table 6), and in wildebeest in the second (March 82-March 83) period (Table 7) suggest that the early counts were less accurate than the ones carried out after 1983. The negative recruitment in kongoni (Table 6) in the period starting

at the end of June 1984 was attributed to the migration mentioned above.

Average annual recruitment in kongoni (Table 6) was 14% (calculated from the years 1982, 85 and 86) suggesting that harvesting of kongoni has to be reduced to at least 14% of the population size in order to keep a stable population size. Assuming an annual recruitment of 14%, the doubling time of WRR kongoni population will be five years (Caughley 1977, Caughley and Birch 1971).

The recruitment percentage of 120% in the period starting in August, 1984 (Table 7) reflects the immigration mentioned above. The 32.6% average annual recruitment in wildebeest (calculated from the years 1981, 83, 84, 86 and 87) gives a doubling time of 2.5 years, half the doubling time for kongoni. Various authors reported that calf mortality is the main cause of death in wildebeest, and that high calf mortality is a result of predation and accidental death (Talbot and Talbot 1963, Estes 1966, Watson 1969, 1970). Both factors are of negligible importance in WRR (Sinnary Unpublished). The high birth rate, coupled with the low calf mortality make Wildebeest an excellent ranching animal. To take an example, if the current population of 390 at WRR is not harvested for four years it will increase to 1200. The population can thereafter sustain an average annual offtake of 390 animals (based on the 32.6% annual recruitment). It is also possible that the desired population level can be

achieved while allowing limited harvesting. It should be noted that the above example was given just for demonstration and it does not imply any figure indicative of the carrying capacity.

Stelfox (1985) stated that "Cumulatively, the biomass density of ungulate species on WRR increased by 12% annually (between 1981 and 1983) while withstanding an annual harvest of approximately 40 percent". These data suggest an expansion rate in excess of 50 percent if harvesting had not occurred". Results of this study however, indicated only 32.6% and 14% annual increase in WRR wildebeest and kongoni, respectively, had harvesting not occurred. Stelfox data expressed the increase as a percent of the January biomass densities as indicated by the results of the total ground counts and used the results of the January counts to standardise for the environmental factors which might have affected animal visibility and population size.

This study demonstrated that a total ground count at WRR is 80.2% and 84.1% accurate for Grant's gazelle and kongoni, respectively (Table 4). The counts are expected to have similar levels of accuracy for wildebeest. Results of the road counts in this study also indicated that the total ground counts might have underestimated population size of Thomson's gazelle. The annual increase figures indicated by Stelfox are, therefore, expected to be an overestimate, simply because they were expressed as a

percent of underestimated biomass density figures. Stelfox based his results on the January counts, while my results were based on all the counts in the cases of Thomson's and Grant's gazelles, and kongoni, and on the highest counts in the cases of wildebeest. My approach is therefore, expected to give more precise results of the counts in the cases of Thomson's and Grant's gazelles, and kongoni, as I made use of all the counts carried out in any one year as opposed to Stelfox's approach which made use of only the January counts. Taking the highest count for the year, as I did in the case of wildebeest, will reduce the problem of underestimating the population size, thus getting rid of one of the major problems of the WRR ground counts.

It should be emphasised that a 50% annual offtake can be sustained in a species that gives birth to one calf per year only during the first few years of harvesting. More males can be harvested in the first years, but the age structure will finally stabilise, after which the number of individuals harvested should be equal to the number recruited. Thomson's gazelle can sustain more than 50% annual offtake rate, but 84.3% of the live weight harvested between 1981 and 1983 was contributed by kongoni and wildebeest. In conclusion only Thomson's gazelle and probably Grant's gazelle, among the economically important species at WRR can, in the long run, sustain a more than 50% annual offtake.

INCIDENCE OF PREGNANCY, WILDEBEEST

The low values of coefficient of variation in the rate of foetal growth in cycles with less than average rainfall (Table 8, 10) may result from the females not conceiving in their first estrous cycle as a result of deficiencies in their nutrition. The late conception date and high foetal growth rate in the 1982/83 cycle (Table 10) coincided with an average amount of rainfall (Table 8) and a rainfall distribution pattern (Table 1) that was normal compared to the other cycles investigated. A possible explanation may be that wildebeest reacted to the disturbance caused by harvesting by delaying their mating or by freezing foetal growth. Squibb *et al.* (1986) observed a bimodal distribution of conception dates in the Mountain elk (*Cervus cephalus*), with the two peaks being separated by 30 to 35 days. Conception was suddenly interrupted at the beginning of the bull elk hunting season, and the authors related the disruption to the hunting pressure induced by the hunting season. It was possible that the increased harvesting pressure on the WRR wildebeest delayed the normal conception season in the 1982/83 cycle. Wildebeest harvesting started in January 1981 and, by May (beginning of the breeding activities) 1981 only seven bachelor males had been killed. By May 1982, however, 49 males and 4 females were harvested.

A harvesting strategy in which pregnant and lactating females are

avoided may introduce a number of artificial selective pressures that may increase birth rate by improving the survival rate of females with high pregnancy rate, compared to that of females of low rate. A female with a high pregnancy rate will, on the average, have a higher chance of being found followed by a calf or of being detected as pregnant, compared to a female with a lower average pregnancy rate. The fact that phenotypic variation exists in AIP may lead to the conclusion that there is a possibility of genetic variance on which harvesting selection can work leading to an increased birth rate, however, phenotypic variation in birth rate appears to be related to rainfall (Table 8) and age (Table 9). This suggests that in a year with good rainfall, adult females from the various age classes become pregnant, but in a year with little rainfall, females belonging to young age classes will divert a higher proportion of their energy for body maintenance and growth rather than for reproduction, a case reported in other species in relation to range productivity (Julander *et al.* 1961), and winter severity (Mundinger 1981). The only possibility for harvesting selection to lead to an increased birth rate is if there is genetic variation in birth rate. If such a variation exists, harvesting selection will work on it by eliminating the less reproductive females. This will in turn, reduce the genetic variation in birth rate. By the time the variation is reduced to a minimum, birth rate will reach an asymptote.

This will be the stage beyond which harvesting selection will not be effective.

The success of any selection programme depends on the heritability of the selected trait (Falconer 1985). Reported levels of heritabilities of most reproductive performance traits are generally low (Falconer 1985, Strang and Smith 1979). The low heritabilities may be due to small additive genetic variance due to selection for high reproductive performance in the past, excessive environmental variability, negative correlation between direct genetic and maternal effects or negative genetic correlations between components of the trait (Revelle and Robison 1973).

Controlled selection experiments on the reproductive performance of the wild ungulates are lacking and selection for improved reproductive performance traits in farm animals have generally been unsuccessful (Revelle and Robison 1973, Strang and Smith 1979). Selection for large litter size, on the other hand, has proved more successful in mice despite the low heritability values (Bakker *et al.* 1978). It is hard to predict the outcome of the harvesting selection introduced by the WRR harvesting strategy apart from saying that there is a possibility that the birth rate may be increased as a result. One way of measuring the effect of selection is by documenting the change in the birth rate with time. A

change in the birth rate may also be brought by many other genetic, nutritional and environmental factors (Smith 1962, Falconer 1985). It is however more likely that WRR harvesting strategy is effective in improving the reproductive performance if the trend in the increasing birth rates is the same in all the species harvested.

Two other selective pressures may also be introduced by the WRR harvesting strategy. If a genetic variation exists in the length of the period during which a follower calf (e.g. in Wildebeest) is associated with its mother, then harvesting selection may increase the length of this period. Similarly the hiding period may be shortened if the calf is of a hiding type (e.g. in Thomson's and Grant's gazelle and kongoni). Harvesting selection may be more effective in increasing the length of the following period or reducing the hiding period due to the possible presence of a high genetic variance which is generally the norm with behavioural characters (Falconer 1985).

PREVALENCE OF PREGNANCY IN THOMSON'S AND GRANT'S GAZELLES, AND KONGONI

One assumption, not discussed in AIP of wildebeest, but which holds true for all the species is that the probability of harvesting a female belonging to any foetal weight category or a specific lactation stage, remains

constant throughout and, is not affected by new responses (e.g. members of a specific category learning to avoid being killed, while members of another category do not) which affect that probability in relation to the other foetal weight categories or lactation stages.

After finishing the analysis of APP for WRR Thomson's gazelle it appeared that APP was decreasing (Table 11). Hopcraft (1975) investigated productivity of WRR Thomson's gazelle and his data indicated a 150% AIP. APP for the present study was 50% (Table 11) in 1982, one-third the AIP value obtained by Hopcraft. The 50% APP has to be multiplied by 3 to be equal to the 150% AIP value assuming that AIP in 1982 was similar to the one obtained by Hopcraft. APP values in 1986 and 1987 were 13.46 and 3.85 respectively (Table 11). Applying a correction factor of three will result in an AIP value of 40.38 and 11.55 for 1986 and 1987, respectively. Results of ageing and sexing in the field for these two years indicated a number of 33.1 small young per 100 adult females (Table 14).

The above information can be used to check what number of small young per 100 adult females would result from an AIP value of 150% suggested by Hopcraft's results. It can similarly, be used to check if the number of small young per 100 adult females recorded in 1986 and 1987 (Table 14), as part of the exercise of ageing and sexing in the field, agrees with the

corresponding APP figures obtained from the records for these two years (Table 11).

Equation 4 was used to transform the AIP value of 150%, suggested by Hopcraft into number of small young per 100 adult females, resulting in 37.5 small young per 100 adult females. The number of small young per 100 adult females obtained from the results of ageing and sexing in the field for 1986 and 1987 was 33.1 (Table 14). Applying equation 4 to this number will result in an AIP value of 132%. If however, one accepts the results of ageing and sexing in the field, then there must be an explanation for the apparent decline in APP as indicated by WRR records.

To explain this apparent anomaly it is proposed that old females were becoming more experienced in avoiding being killed, than young ones. Experience, as such, is a function of age. Results of ASIP in wildebeest (Table 9) and ASPP in kongoni (Table 13) suggest that old females have a higher pregnancy rate than young ones as does the literature (Watson 1969, 1970, Munding 1981).

The same trend was not noted in the three other species. This may be due to difference in cohesiveness of the groups formed by each species. WRR female wildebeest live in permanent and cohesive groups. Two or more groups may join together but usually split apart when disturbed. Members of each group generally respond to a disturbance in the same way.

The only time I noted different responses among members of the same group, was during the first two months following the calving season. At that time, lactating females were forming subgroups within the larger groups. When disturbed, the lactating females would be the first to run, usually in a different direction than the rest. I also noticed that the females were generally more wary than during the rest of the year. Long associations among some groups of Grant's gazelle and kongoni were observed and the groups in these two species would usually respond together when disturbed. Only members of the same group of Thomson's gazelle usually responded as individuals, and not as a group.

Mr. Maley, who harvested animals from the end of 1985 on noted that separating an individual or a small group from a wildebeest herd proved quite difficult. The separated animals always tried to rejoin the original group. The reaction of kongoni and Grant's gazelles was intermediate. When an individual or a small group was separated from the main herd, they tried to rejoin, however if they found difficulties in doing so, the separated individuals would form their own group and run in a different direction. Mr. Maley said that Thomson's gazelle represented the other extreme reaction. The tendency to forming groups was not as strong as it was in the other species. Separating an individual or a small group from the main herd has proved relatively easy because members of the group

wouldn't run in the same direction.

Based on Mr. Maley's statement, the probability of harvesting a young female would not be very different from harvesting an old one in species that live in cohesive groups, i.e Grant's gazelle, kongoni and wildebeest. Since these species live in cohesive groups the survival advantage of the experienced animals would be equally shared by all the members of the group, unlike the case for Thomson's gazelle where the survival advantage of the old and more experienced animals is not shared by the other members of the incohesive group. If old animals become more experienced in avoiding being harvested, it is more likely that the probability of harvesting a young individual would be higher than harvesting an old one. In such a case if ASPP is also higher in old females (Table 9, 13), the records would show a declining trend of ASPP through time. This may explain the anomaly in the records of APP of Thomson's gazelle in WRR Thomson's gazelle.

An independent support to the hypothesis that old Thomson's gazelle become more experienced in avoiding being killed is provided by the highly skewed sex ratio in favour of females in WRR Grant's gazelles (Dani 1985). The sex ratio resulted from the WRR harvesting strategy of predominantly killing males. Although all the economically important species were subjected to heavy harvesting pressures, Grant's gazelle was

the only species that exhibited a highly skewed sex ratio in favour of females (Dani 1985). Sexual dimorphism is low in kongoni and wildebeest and high in Thomson's and Grant's gazelles. Since the males of Thomson's and Grant's gazelles are easily distinguished in the field it is expected that the WRR harvesting strategy will result in an equally skewed sex ratio in favour of the females in both species. It is also expected that the sex ratio of kongoni and wildebeest will be less skewed due to the low sexual dimorphism. The sex ratio of Grant's gazelle, kongoni and wildebeest were consistent with this expectation (Dani 1985). The male/female sex ratio in Thomson's gazelle was higher than expected, however, probably because, unlike in the other species, young individuals were not sharing the experience of old members of the incohesive group.

Sinclair and Grimsdell (1982) recommended MPP to be calculated for each month separately; the APP for the year investigated will be the unweighted average for all the months. The procedure will enable assigning a standard deviation to the APP value. It is, however, not suitable to use when there is a large variation in the monthly sample sizes; especially when the majority of the samples are small. This being the case, variations in MPP, resulting from mere stochastic processes, will be incorporated in the analysis leading to an imprecise APP value.

SEASONALITY OF BREEDING, THOMSON'S GAZELLE

The effect of the 1984 drought on the prevalence of pregnancy in Thomson's gazelle (Table 12) raised the question of what factors shape the temporal distribution of reproduction in African ungulates. Discussion of seasonality in Thomson's gazelle requires the differentiation between the terms seasonality and synchrony in birth. A species with a seasonal birth peak is one in which the calving season takes place at the same time(s) every year. It follows that seasonality in birth should also be accompanied by synchronised mating and calving peaks. A synchronised birth peak, on the other hand, is not necessarily one that takes place at the same time(s) every year.

Seasonality of reproduction in Thomson's gazelle has been previously discussed. Brooks (1961) found that peak birth periods showed great local variations among adjacent populations and related the variations to the emergence of fresh grass. Robinette and Asher (1971) found year round breeding with peaks coinciding with the wettest months. Hopcraft (1975), however, found that the peaks were one or two months before the rains. Although the above studies agree that birth takes place throughout the year with apparent peaks, it is doubtful whether these peaks indicate seasonality in breeding because the birth peaks are not clearly related to rainfall.

Analysis of APP in Thomson's gazelle provided some clues as to the possible causes of such peaks and whether they are a result of seasonal or only synchronised breeding. It seems that the first rains after the drought resulted in synchronised mating as a result of the sudden rise in the plane of nutrition in the majority of the females (Table 12) resulting in high values of prevalence of pregnancy between November 1984 and May 1985 after a period of low values (March–October 1984). Another indication of the suggested synchronised breeding was the low values of prevalence of pregnancy in the period extending between June to July 1985, probably because the females started giving birth, and the high values recorded between August to December 1985 as a result of another synchronised mating. It seems not a coincidence that the above sequence of events was related to the 1984 drought. The evidence for the drought effect was only circumstantial however, but it is more likely to be true as no similar pattern could be observed in prevalence of pregnancy of the species during any other period. The low pregnancy rates reported for Grant's gazelle, kongoni (Table 11) and wildebeest (Table 8) in 1984 could also be related to the drought. It is also possible to predict the sequence of events following a drought if droughts affect prevalence of pregnancy in the species. The sequence is:

1. the pregnancy rate decreases during the drought;

2. the rate increases at the end of the drought as a result of synchronised mating, brought about by the rise in the plane of nutrition after the first rains, this will later result in a birth peak;
3. the pregnancy rate drops by the time the females start giving birth and increases again as a result of another synchronised mating, later resulting in another birth peak;
4. the birth peaks continue to exist but they progressively become less and less sharp as a result of variation in the intervals between births among different females, and as a result of females reaching maturity and being serviced at times outside the synchronised mating periods;
5. the birth peaks of the same population will not take place at the same time every year, and the peaks may be shifted by another drought; and
6. the sharpness of the peaks will be directly related to the severity and duration of the drought.

It should be noted that such birth peaks may not lead to seasonal breeding. The only way they can do so is if the average time interval between two birth peaks is 12 or 24 months, resulting in one peak; 6 or 18 months, resulting in 2 peaks or 8; or 16 months, resulting in 3 peaks; or 9 months, resulting in 4 peaks. The peaks will not be stable in time as they will be shifted by the onset of another drought. This suggests that many of the birth peaks observed in species that breed throughout the

year but exhibit birth peaks may not result from seasonal breeding, but rather from the effect of a previous drought.

The temporal distribution of reproduction of African ungulates varies widely, both between different species within the same area and in the same species between different areas (Leuthold and Leuthold 1975, Jarman 1976). Various authors tried to explain the reasons for the variation in the patterns of reproduction among African ungulates. Brooks (1961) found a local correlation between time of birth and availability of fresh fodder in adjacent populations of Thomson's gazelle. Estes (1966, 1976) attributed the synchronised calving season in wildebeest to predation pressure. Leuthold and Leuthold (1975) could relate seasonality in breeding to the feeding habits of the 10 species they studied. Freyhell (1985, 1987) attributed seasonality in reproduction of the white-eared kob (*Kobus kob leucotis*) to resource limitation.

The factors that shape the temporal reproduction patterns of the African ungulates are poorly understood. In the temperate zone the temporal distribution of reproduction is explained by the sharp seasonal differences between winter and summer. The frequent occurrence of droughts in East Africa may indicate that proximate factors assume a higher role in shaping the breeding patterns of the different ungulates. Droughts affect the plane of nutrition by reducing both the quality and

quantity of the food. It is, therefore, expected that frequent occurrence of drought in East Africa does not only affect rates of reproduction of the ungulates, but also shapes the temporal distribution of the reproductive activities of these animals.

GRANT'S GAZELLE, A DECLINING POPULATION

The Grant's gazelle of WRR have been decreasing since 1981 for reasons that still remain unclear. Stelfox (1985) noted that the WRR Grant's gazelles were decreasing while the other populations affected by harvesting were increasing. He attributed the decrease to jackal predation on calves. WRR initiated a jackal control programme in 1981, which ended in 1985. The numbers of the Grant's gazelles nevertheless continued to decrease.

Dani (1985) noted 1/25 and 1/3.8 male/female and calf/female ratios, respectively in WRR Grant's gazelle. These values were lower than the figures Dani (1985) obtained from the other species. Though his results on pregnancy were not quantitative, the author stated that the proportion of pregnant females from WRR records was low for Grant's gazelle in comparison to that of the other harvested species at WRR. Dani (1985) attributed the decline in the numbers of Grant's gazelle to the highly skewed sex ratio in favour of females. In 1986 WRR stopped harvesting

Grant's gazelle and I observed that the sex ratio started to revert to normal early in 1987.

The problem of the Grant's gazelle may not be completely explained by either jackal predation or the skewed sex ratio alone. If jackals were responsible for the decline it is expected that the numbers of Grant's gazelle should have decreased further after the jackal control programme came to an end. This was not the case however, as my results indicated signs of recovery in 1986 and 1987 (Tables 5,14). If the skewed sex ratio was responsible, low pregnancy rates would be indicated, however, this study suggests that the skewed sex ratio was only partly responsible for the decrease in the pregnancy rate (Table 11).

Recruitment (R) was defined earlier as the number of newborns in the population minus the number of individuals that died between time t and time $t-1$. Average annual recruitment in the species between 1981 and 1987 was less than 1% (Table 5). The total number of individuals harvested in the same period was 437, resulting in an average annual harvesting rate of 14.7%. It is clear that the decline in the numbers of Grant's gazelle has not resulted from high harvesting rates. The low recruitment was also not a result of low pregnancy rate (Table 11). It is logical, therefore, to assume that the low recruitment value resulted from an unknown mortality factor affecting the individuals after birth. Such an

effect could be due to predation, chronic disease, or due to the disruption of the social structure as a result of harvesting. If the effect was due to the disruption of the social structure as a result of harvesting, it is expected that the effect would have been observed in the pregnancy rate rather than in high mortality rate. The possibility of a chronic disease could not be excluded as Buar (1983) reported high lung condemnation rate in the two gazelle species and Stelfox (1985) reported higher levels of carcass condemnation in WRR grant's gazelle. The problem needs an immediate investigation of the possible factors that had lead to the situation.

AIP of Grant's gazelle, based on the big young, was 36% (Table 14).

This value corresponded with the period extending between April 1984 and January 1987. AIP, based on the small young, was 61% (Table 14). This value corresponded with the period extending between April 1986 and June 1987. The indication is that birth rate started to increase in 1986 and 1987 after the period of low recruitment.

The problem of decreased productivity in Grant's gazelle may lead to the question of how a skewed sex ratio can be maintained, without affecting the reproduction of the species. The most striking aspect of reproduction in Grant's gazelles was the zero APP value in 1984, a drought year (Table 11). Harvesting of female Grant's gazelle, however, started in

May, a time where the drought started to take serious proportions. The first pregnancy recorded after the drought was in February 1985 suggesting an end to the effect of the drought. An APP value of zero in 1984 suggests a relationship between APP and rainfall. It is, therefore, expected that the APP value in 1985 would have been higher than that in 1982 (a year with a lower rainfall) had it not been due to the effect of the skewed sex ratio. The APP for Grant's gazelle was 24.29 in 1985 (Table 11). This value resulted from a sex ratio of 1:25 males/females (Dani 1985), compared to the APP value of 30.56 realised in 1982, under a more or less, normal sex ratio. Assuming that the effect of the skewed sex ratio was not there in 1985, one would expect an APP value of 40%. This means that about $61\% = 100 \times 24.29/40$ of the females in 1985 were serviced under a sex ratio of 1 male to 25 females. A sex ratio of 1 male to 15 females = $[25 \times 61]/100$, may be the right one to service all the females, assuming that these males have access to all females. To allow for this and to be on the safe side, a sex ratio of 1 male to 10-12 females is recommended. To ensure that the right sex ratio is maintained, it can be checked in the field at intervals of three to six months, an interval that provides an adequate monitoring of the ratio.

IMPLICATIONS FOR MANAGEMENT

The results of incidence of pregnancy in wildebeest (Table 8), prevalence of pregnancy in Thomson's and Grant's gazelles and kongoni (Table 11) and ageing and sexing (Table 14, Figure 6) in the field have a number of points related to the practical harvesting aspects of these species. Wildebeest females are best harvested between December and January if the aim is to reduce the number of pregnant and lactating females killed, because at such a time the calf has reached a minimum age of 6 months, where it has practically become independent of its mother, and killing the mother will not greatly affect its chances of survival. This is also a time when pregnancy can easily be detected. Yet another advantage is the fact that such a harvesting regime may introduce artificial selective pressures that may increase the birth rate.

When to harvest males is also of relevance to management. Bachelor wildebeest males are best harvested between May and August, because this is the time when the yearling and nondominant males form bachelor herds after they have been driven from the female groups by the dominant males before the beginning of the mating season. I noticed that during the other months bachelor males joined the female groups without being harassed by the dominant males, but between May and August the bachelors were forced to leave the female herds. It is important, however, not to harvest either females or breeding males (accompanying the females)

during this period because this may disturb the mating season. Otherwise males can be harvested during any other period, but females must not be harvested during the calving season if they have to be harvested during times other than the ones suggested above, because of the possible disturbing effects.

The birth peaks observed in Thomson's gazelle and kongoni (Figure 6) suggest that harvesting may be adjusted in relation to these peaks. This requires monitoring in the field the ratio of small young to the adult females. These young can be distinguished because they lack horns. Horns in male Thomson's gazelle show up for the first time at about four to six months. Their emergence in females is late and may not take place until an age of seven months (Hopcraft 1975). By an age of four months, most calves give up on suckling. After the ratio of young below six months of age to adult females reaches a peak and starts declining, these young would have actually passed the critical period of suckling. Harvesting the females at such a time may not affect the survival of their calves.

Another advantage is that the majority of the females will be in their late stages of pregnancy, which enables the harvester to detect pregnancy. A similar argument can be employed to show that kongoni females can best be harvested one or two months before the number of medium young as a percentage of the adult females starts to peak. Males can be harvested

during the other periods of the year.

Unlike the others, APP in kongoni was not affected much by the drought (Table 11). The effect of the drought, though small, seems to have lasted longer however. This indicates that females may best be harvested when a drought has taken serious proportions. The harvesting may also be continued for two years or so after the end of the drought. This is a time when APP is still low enough to reduce the chances of harvesting lactating and pregnant females. Female harvesting can be completely stopped after APP has recovered, for a period of at least two years or so, to allow for population rebuilding.

The fact that AIP sharply drops during droughts in wildebeest (Table 8) and the two gazelle species (Table 11) suggests that the level of female harvesting in these species can be increased during the drought. This is a time when the risk of harvesting a lactating or a pregnant female is minimum. Harvesting the females should be stopped immediately after the drought is over to reduce the risks of harvesting pregnant and lactating females and to allow the populations to rebuild. The level of male harvesting can be increased during years of average or more than average rainfall accordingly.

AGEING BY TEETH, WILDEBEEST AND KONGONI

The entire practice of ageing WRR wildebeest has been achieved without having a single animal of known age. On the other hand, ageing based on killing dates provided the basis for the practice of calibrating crown heights of the three molars with age. It is, therefore, important to devote some time to discuss the assumptions underlining the procedure.

The distribution of killing dates of the first four age classes (figure 7) is ideally expected to follow a normal frequency distribution pattern. For such a pattern to emerge a number of assumptions have to be fulfilled first including.

1. The probability of including an animal in the harvest is independent of the animal's age, sex, physiological and dominance status.
2. The proportion as well as the number of animals belonging to any age or sex class remain constant throughout. This assumption can only be true under the following two conditions:
 - a. the live wildebeest population had achieved a stable age and sex structure before the harvesting started; and
 - b. harvesting is carried out in such a way that the instantaneous harvesting mortality (r_p) is equal to the fecundity-survival rate of increase (r_s) (Caughley 1977).
3. The rate of tag loss is zero or else, remains constant for all the age and

sex classes throughout.

For a normal distribution to emerge from the plotting of killing dates (Figure 7), harvesting should be random as far as age and sex classes are concerned. Harvesting in WRR started in November 1980 with a policy of excluding females. Females were not included until it was difficult to find males (1983). Again, it is the Ranch's policy not to harvest pregnant and lactating females. Territorial males were also not included till it was difficult to find bachelor groups, after which harvesting has been random for adult males. Harvesting has been selective with respect to the age in the sense that apparently young animals have been excluded.

The male directed harvesting strategy is expected to have created a gap in the age structure of this group before 1983, such that the male segment of the population consisted predominantly of young and old individuals, with males of intermediate age missing due to the harvesting of bachelor males.

A harvesting strategy that increases adult mortality relative to mortality of younger individuals (as has been the case for WRR animals) changes the age structure in favour of the young segment of the population.

The tagging system was introduced by the end of 1982 and by that time far more males were harvested than females. When the tagging system was introduced the proportion of young in the male segment has, therefore,

increased while it remained largely unaffected in the female segment of the population and the proportion of young males exceeded that of young females in any age class among the harvested animals as a result.

An age class dominated by young individuals will have a higher average age as well as a higher average crown height for any one molar than an age class dominated by old animals. The distribution of killing dates as well as the distribution of average crown heights for any age class of the WRR males is expected as a result ^{to} be more skewed towards young individuals compared to that in females; and is also expected to be more skewed towards young individuals in both sexes due to the effect of mortality. The small sample sizes in the case of the distribution of killing dates did not allow for significance test to be carried out. The distribution of crown heights were in agreement with this expectation, but the differences between average crown heights of males and females belonging to the same age class were not significant (except in one age class), probably as a result of the high variation in crown height of animals of the same age. The practical importance is that differences in crown height between males and females of the same age class may not be real differences between the two sexes, but rather due to differences in mortality. This should also be the case in two different populations with different age specific schedules of survival. The higher the differential

mortality between the sexes (or populations) and the longer the period over which the age classes extend, the larger will be the difference in crown heights between the two sexes (or populations). Subjective age classes should, therefore, be designed to extend over as a short period as possible.

The tagging system at WRR has seen periods of inconsistency or of improper tagging. To be on the safe side all skulls belonging to such periods were eliminated from the analysis. They were used only in the calculation of average crown heights of the various age classes and in the regression of crown height of the molars on each other.

Variance of average age of any particular age class is a compound one consisting of two variances viz:

1. variance due to the birth date;
2. variance due to variation in the schedules of eruption time and wear pattern. The two variances are additive (Caughley 1965).

A number of reasons might have made the new approach insensitive in distinguishing the model that best fits the data. The high variation in crown heights of animals of the same age might have made the two models provide a close fit to the data. The new approach was based on the assumption that 100% of the variation in crown height of any of the two regressed molars is explained by the regression of that molar on age. The

variation in crown height of any of the two regressed molars is not completely explained by the age of the animal however. Part of the variation is explained by the regression of that molar on the other irrespective of age. Another part is attributed to a normally distributed, random error, with a mean value of zero. The random error is not a problem as it can be overcome by increasing the sample size. The major problem seems to be related to the proportion of variation in crown height of any one molar that is explained by its regression on an other molar.

The close fit to the regression of crown height of the first molar on age (Table 15) provided by the linear and exponential models might have been a result of the small range in the age of the animals included in the analysis. It could also be a result of the high variation in crown heights of animals of the same age. Klein *et al.* (1981) tested the fit of the linear and exponential models to crown heights of the first two molars and the fourth premolar from the lower jaw of the American elk (*Cervus canadensis*). The range of age of the animals included in the regression of the first molar was larger than that in the case of my samples. Klein *et al.* (1981), however, invoked the same explanation that the low range in the age of their animals might have been responsible for the equally high coefficients of variation (they used the regression coefficient instead) for both models. The possibility of the regression technique not being

sensitive enough in detecting the differences between the two models, however, could not be excluded.

The fact that the coefficients of variation were higher in the cases of the regression of the second on the first molar, and the third on the second, than in the case of the regression of the third on the first molar (Tables 18, 19), suggests that individual animals were using either the anterior or posterior portion of the jaw more often than the other for mastication. If individuals prefer to use one portion of the jaw more often than the other, the coefficient of variation resulting from the regression of two adjacent molars will be lower than that resulting from the regression of two molars separated from each other by another tooth. In order to reduce the variation in crown height as an ageing criterion with the minimum efforts, it is suggested that measurements be taken from the second molar from both the right and left sides of the jaw. If it becomes evident, during the course of data collection, that the variation due to animals using one side more than the other is negligible, the measurements can be taken from only one side. The ultimate decision is, however, a compromise between time available, the level of precision required and the range of the age of the animals included in the analysis.

Ecological longevity in wildebeest and kongoni have been reported to be 20 and 19 years (Spinage 1986). Klein and Cruz-Urbe (1984) reported

ecological longevity of 18 years for both wildebeest and Cape hartebeest. Based on crown height of the third molar, the exponential model gives an age of 52.5 and 36.5 years, respectively for wildebeest (Equations 27, 28) and kongoni (Equations 35, 36) with a 5 mm third molar crown height. It is not uncommon, however, to see skulls of both species with crown heights of their third molar almost completely worn out. The linear model, on the other hand, results in an age of 17 and 13.9 years for wildebeest (Equation 23, 24) and kongoni (Equation 31, 32), respectively for a third molar with zero crown height. Klein and Cruz-Uribe (1984) argued that potential ecological longevity in ungulates is usually determined by the age at which crown height of the third molar is worn to zero. If this is true the results are clearly in favour of the linear model. The exponential model was, therefore, rejected in favour of the linear model. If it is true that the linear model provides a better fit, then it will be logical to assume that the inability of the new approach to evaluate the fit of the two models was a result of the fact that a higher proportion of the variation in crown height of any molar was explained by its regression on crown height of another molar rather than by the age of the animal.

Crown height as an ageing criterion has received much attention in the last decade and a number of models have been proposed to describe the

pattern of its decrease with age. The first attempts were made by Spinage (1971, 1973). Spinage's model is described by the equation below:

$$Y = Y_0 \left[1 - \left(\frac{T}{N} \right)^{\frac{1}{2}} \right], \text{ where:}$$

Y = crown height of a tooth,

Y_0 = initial (unworn) crown height,

T = age of the animal at crown height of Y , and

N = the age at which Y becomes zero.

Spinage's (1971, 1973) model states that crown height is reduced by a certain percentage of the initial crown height at a specific age. The age is taken as a percentage of the age at which crown height becomes zero. The percent decrease of crown height is a function of the exponent $1/2$. According to the model, crown height starts to decrease immediately after birth. Molars, however, in ungulates do not erupt at birth and not all molars erupt at the same age but rather in a sequential pattern. Spinage's (1971, 1973) model, therefore, predicts that crown height of each molar starts to decrease even before a particular molar erupts. The exponent, $1/2$ also does not have a biological significance.

Klein *et al.* (1981) proposed a linear model for predicting age of ungulates, but later on the authors shifted to a curvilinear model (Klein 1982, Klein and Cruz-Urbe 1983, Klein and Cruz-Urbe 1984). The Klein's

models do not suffer from the limitations of Spingale's (1971, 1973) model, but they assume that crown height of a permanent tooth becomes zero at age Y_{pe1} (the potential ecological longevity). In wildebeest this age will be 12.3, 14.7, and 17.1 years, based on the first, second and the third molars, respectively (Equations 21 to 24). The fact that ecological longevity is underestimated by 28% when based on the first molar is a major problem of these models. The use of Y_{pe1} in the models results in overestimating the rate of decrease of crown heights of the first and the second molars resulting in different molars in the same animal giving different age estimations. Klein and Cruz-Urbi (1984) argued that the problem resulting from the three molars being worn to zero at different ages is not a serious one when the molars are used to construct mortality profiles, a practice commonly done by archaeologists. Ecologists, however, use ageing data for completely different purposes. The data are usually used in the analysis of population dynamics, (e.g. constructing life tables), or to construct models that investigate the effect of specific incidences on the population, (e.g. harvesting). Most of these models assume that age is accurately estimated. Caughley (1967) argued that when a population with a stationary age distribution is sampled and the percentage error in ageing is the same for all age classes, the following errors in the construction of life tables would normally result:

1. age-specific life expectancies are overestimated;
2. maximum sampled longevity is overestimated;
3. the differences between mortality rates over different age intervals are decreased; and
4. the distribution of age frequencies is smoothed.

If an error can result in the four points which were mentioned above, a bias introduced by the incorporation of the potential ecological longevity would necessarily lead to more serious effects.

Correcting for the bias introduced by potential ecological longevity does not completely solve the problem however. A model that best describes the pattern of decrease of crown height with age should be found first. That both the linear and exponential models provide a similar fit to the ageing data does not necessarily mean that the real pattern of the decrease of crown height can be described by either model as old animals are usually underrepresented in ageing samples. This problem is inevitable as it results from differential mortality which eventually biases the sample in favour of young animals. The use of a weighted regression model may offer a solution to the problem.

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Appendix 1. Results of the road counts carried out at WRR between December 1986 and July 1987 for the economically important species.

Date	T. Gazelle	G. Gazelle	Kongoni	Wildebeest
3.12.86	638	152	423	323
4.12.86	704	234	274	781
5.12.86	546	232	178	791
6.12.86	535	226	458	402
8.1.87	409	184	367	185
6.2.87	563	191	331	755
5.3.87	613	91	542	376
6.3.87	274	148	171	634
7.3.87	647	128	439	600
10.3.87	625	104	309	208
16.4.87	1341	200	277	315
3.5.87	440	228	7	378
23.6.87	514	235	64	170
24.6.87	1007	174	547	437
25.6.87	942	236	23	770
26.6.87	861	402	158	337
27.7.87	852	272	821	1304
28.7.87	690	120	14	1126
29.7.87	645	187	483	814
30.7.87	754	287	752	1281

Appendix 2. The number of individuals of economically important species recorded during the total ground counts.

Month	<u>Numbers</u>			
	T. gazelle	G. gazelle	kongoni	Wildebeest
NOV 86	355	119	242	249
DEC 86	302	160	208	227
JAN 87	368	159	220	219
FEB 87	331	151	239	211
APR 87	339	112	220	364
MAY 87	293	109	165	237
JUN 87	316	176	185	364
JUL 87	337	162	226	247
AUG 87	294	163	203	390
SEP 87	239	141	238	314

APPENDIX 3. LIST OF FREQUENTLY USED ABBREVIATIONS

AIP	Annual Incidence of Pregnancy
APP	Annual Prevalance of Pregnancy
ASIP	Age-Specific Incidence of Pregnancy
ASPP	Age-Specific Prevalance of Pregnancy
CAIP	Corrected Annual Incidence of Pregnancy
CF _i	Correction factor of MPP
MPP	Monthly Prevalance of Pregnancy
MPP _{Nov.}	November's MPP Value
WRR	Wildlife Ranching and Research Ltd.