

RESOURCE LIMITATION AND POPULATION ECOLOGY OF
WHITE-EARED KOB

by

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ABSTRACT

In this study I examine the effect of seasonal resource limitation on the behavior and population dynamics of white-eared kob, Kobus kob leucotis, in the Boma region of the southern Sudan. This population, numbering over 800,000, migrates seasonally between savannah grasslands in areas with low rainfall and ephemerally swamped grasslands in areas with high rainfall. The aims of the study were: (1) to examine whether kob migration tracks ephemeral distributions of food or water resources, (2) to test the hypothesis that the Boma kob population is limited by food availability, (3) to determine if calf production is cued to seasonal peaks in food abundance, and (4) to evaluate the effect of breeding synchrony on lekking behavior and male competition.

Seasonal climatic changes produced pronounced changes in the distribution and abundance of both green forage and water supplies. Dry season migration primarily tracked limited supplies of water. Within the dry season range, kob aggregated at high densities (over 1,000 per km²) in low-lying meadows that supported grass re-growth when little green grass was available elsewhere in the ecosystem. However, southerly movements in the wet season were not explainable by the resource hypothesis, since both food and water were widely distributed during the wet season. I suggest that kob may move southward in order to avoid surface flooding during the wet season.

Kob mortality during the dry seasons of 1982 and 1983 was considerably higher than estimated mortality during the wet season. Unusual rainfall during the dry season of 1982 provided a "natural experiment" to test the food limitation hypothesis. Adult mortality was significantly lower during the dry season of 1982 than during the more typical dry season of 1983. Calf mortality did not vary significantly between years. Adult mortality rates were related to dry season duration. Dry season mortality was related to sub-maintenance food intake and declining fat reserves. The age structure of the kob population in 1983 suggests that large-scale mortality (ca. 40%) occurred in the 1980 drought that immediately preceded this study. These findings support the food limitation hypothesis.

Kob exhibited a 4 month period of calf production during the late wet season, when food availability was highest. As a consequence, females continued lactation through the dry season period of food scarcity. I suggest that kob reproductive phenology may result from an obligatory delay during which females restore their fat reserves prior to calving or selection pressures imposed by predation during the vulnerable post-partum period.

Synchronous breeding in the Boma kob was related to increased rates of aggression between males and increased color dimorphism, in comparison to the asynchronous breeding Uganda

kob, Kobus kob thomasi. Male aggression served not only to establish dominance relations between males on leks, but also disrupted the mating activities of neighboring males. Young adult males suffered higher age-specific mortality than females, possibly resulting from injuries incurred during strenuous fighting on leks.

In order to analyze the age structure of the kob population, I devised a new method for estimating age-specific mortality rates that is free of the restrictive assumptions that underlie most conventional techniques. The proposed method has somewhat greater sampling variation, but is considerably more robust, than two current methods. Moreover, the proposed method permits calculation of age-specific mortality at frequent intervals during periods of population fluctuation and, under some circumstances, population numerical trends may be directly determined from age structure.

TABLE OF CONTENTS

ABSTRACT	ii
LIST OF TABLES	vi
LIST OF FIGURES	vii
ACKNOWLEDGEMENTS	ix
CHAPTER 1. GENERAL INTRODUCTION	1
CHAPTER 2. SEASONAL MIGRATION IN RELATION TO RESOURCES	8
Introduction	8
Methods	10
Aerial surveys	10
Ground Observations	13
The study area	17
Physical features and vegetation types	17
Climatic seasonality	20
Results	24
Aerial survey results	24
Seasonal changes in green biomass	24
Seasonal changes in water availability	27
White-eared kob population numbers	29
Seasonal migration of white-eared kob	29
Dry season ground observations	35
Kob distribution patterns	35
Factors affecting forage abundance	45
Feeding selection for plant parts	49
Food availability relative to kob requirements	53
Discussion	55
Seasonal changes in resource distribution	55
Seasonal kob migration	56
Benefits of migration	59
CHAPTER 3. FOOD LIMITATION AND KOB MORTALITY PATTERNS	61
Introduction	61
Methods	62
Population density	62
Carcass density	63
Sex and age distribution	65
Tooth cementum lines	66
Post-mortem examination	67
Results	68
Age distribution in the live population	68
Age distribution at death	68
Age-specific mortality	72
Sex ratio	72
Seasonal changes in body condition	76
Seasonal changes in mortality rates	79
Dry season mortality in relation to food intake	82
Cumulative dry season mortality	85
Discussion	89
Causes of mortality during the dry season	89
Predation	89
Disease	92
Age structure of the kob population	93
Evidence for food limitation	96

CHAPTER 4. KOB REPRODUCTIVE PHENOLOGY	100
Introduction	100
Methods	101
Results	103
Discussion	111
CHAPTER 5. BREEDING SYNCHRONY AND MALE AGGRESSION	114
Introduction	114
Methods	119
Sexual dimorphism	119
Lek observations	119
Results	121
Sexual dimorphism	121
Temporal change in mating and agonistic behavior	121
Spatial distribution of females and agonistic encounters	124
Functions of fighting behavior	128
Consequences of fighting	131
Discussion	133
CHAPTER 6. AGE-SPECIFIC MORTALITY: AN ALTERNATIVE APPROACH	137
Introduction	137
The model	138
Methods	140
Calculation of age-specific mortality	141
Sampling distributions	144
Effects of an unstable age distribution	146
Results	147
Discussion	151
Advantages of the proposed method	151
Comparisons between methods	154
CHAPTER 7. GENERAL DISCUSSION	158
Food limitation	158
Seasonal migration	160
Breeding phenology	162
Breeding synchrony and male aggression	163
Age-specific mortality patterns	164
General conclusions	165
LITERATURE CITED	168
APPENDIX 1. PLANT SPECIES COLLECTED	183

LIST OF TABLES

Table 2.1 Akobo monthly climatic normals.	21
Table 2.2 Kob population estimates 1980-1983.	30
Table 2.3 Dry season grass biomass estimates.	39
Table 2.4 Nutritional analyses of meadow vs. tall grasses.	41
Table 2.5 Feeding selection for leaf vs. stem tissue.	52
Table 3.1 Dry season weekly mortality estimates.	80
Table 3.2 Mortality in relation to food intake	84
Table 5.1 Changes in lek behavior over the dry season.	123
Table 5.2 Female movements following disruption.	132
Table 6.1 Data used to calculate q_x using method C	143
Table 6.2 Skewness and kurtosis of sampling distributions obtained using 3 alternative methods	149

LIST OF FIGURES

Figure 1.1 Map of the southeast Sudan.	4
Figure 1.2 Lines of investigation.	7
Figure 2.1 Calibration of photometer readings.	14
Figure 2.2 Map of the study area.	15
Figure 2.3 Map of woody vegetation cover.	19
Figure 2.4 Mean monthly rainfall totals.	22
Figure 2.5 North-south gradient in seasonal green biomass abundance.	25
Figure 2.6 Seasonal distribution of green biomass.	26
Figure 2.7 Seasonal distribution of water supplies.	28
Figure 2.8 Seasonal distribution of kob.	31
Figure 2.9 Kob distribution in relation to nearest water. .	33
Figure 2.10 Kob dry season concentrations.	36
Figure 2.11 Population densities in woodland vs. meadow habitats.	37
Figure 2.12 Kob diurnal movements onto meadows.	38
Figure 2.13 Dry season meadow grass growth.	42
Figure 2.14 Dry season leaf and stem tissue growth.	43
Figure 2.15 Kob aggregation around meadows.	46
Figure 2.16 Kob abandonment of meadows.	47
Figure 2.17 Dry season grass growth in relation to soil moisture.	48
Figure 2.18 Soil moisture decline over the dry season.	50
Figure 2.19 Feeding concentration near water.	51
Figure 3.1 Age structure of the live population.	69
Figure 3.2 Age structure of found carcass sample.	70
Figure 3.3 Age frequencies of carcasses by sex.	71
Figure 3.4 Age-specific mortality curve.	73
Figure 3.5 Carcass frequencies in relation to distance from observers.	75
Figure 3.6 Dry season decline in fat reserves.	77
Figure 3.7 Dry season adult mortality rates (Ajwara).	81
Figure 3.8 Dry season calf mortality rates (Ajwara).	83
Figure 3.9 Adult mortality as a function of dry season duration.	86
Figure 3.10 Graphical explanation of the body condition/mortality hypothesis.	88
Figure 3.11 Cumulative mortality during a drought in Nairobi National Park.	90
Figure 3.12 Kob population estimates 1979-1983.	95
Figure 4.1 Frequencies of births by month.	104
Figure 4.2 Female reproductive condition January to May. ..	105
Figure 4.3 Dry season body condition of lactating vs. non-lactating females.	107
Figure 4.4 Activity patterns of males vs. females.	108
Figure 4.5 Seasonal changes in calf/female ratio.	109
Figure 5.1 Sexual selection in relation to breeding synchrony.	116
Figure 5.2 Hypothetical cost-benefit relations of male fighting intensity.	118
Figure 5.3 Kob live weights at age.	122

Figure 5.4 Changes in agonistic behavior rates over the breeding season.	125
Figure 5.5 Female spatial distribution on leks.	126
Figure 5.6 Female group sizes with single males.	127
Figure 5.7 Spatial distribution of fights between males. ..	129
Figure 6.1 African buffalo age-specific mortality curves ..	142
Figure 6.2 Sampling variation resulting from the use of 3 alternative methods	148
Figure 6.3 Age-specific mortality estimated from an unstable age distribution	150
Figure 6.4 Sampling variation as a function of denominator value	156

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CHAPTER 1. GENERAL INTRODUCTION

Assumptions of food resource limitation underlie many fundamental hypotheses in large-mammal ecology. Limited resources are commonly presumed to constrain foraging adaptations, habitat suitability, and social behavior of individuals (Geist 1974; Jarman 1974; Owen-Smith 1982). Resources may determine population densities through density-dependent effects on recruitment, mortality, or dispersal (Bobek 1977; Sinclair 1977; McCullough 1979; Fowler 1981). Finally, resource scarcity may structure communities through niche partitioning or facilitation (Vesey-Fitzgerald 1960; Lamprey 1963; Bell 1971; Jarman and Sinclair 1979).

Direct evidence of food limitation has been documented for roe deer (Bobek 1977), African buffalo (Sinclair 1977), kangaroo (Bayliss 1985), and wildebeest (Sinclair et al. 1985) populations. Also, there is considerable circumstantial evidence that large-mammal populations are limited by food availability. Klein (1968) documented the rapid increase and catastrophic die-off of reindeer introduced onto St. Matthew Island, which Klein concluded was caused by the overgrazing of available vegetation. Caughley (1970) reviewed evidence for similar ungulate eruptions, which Caughley and Lawton (1981) later explained using a theoretical model based on trophic interactions between herbivores and vegetation. Coe et al. (1976) demonstrated that large-herbivore biomass in African game reserves was positively correlated with annual rainfall and,

presumably, vegetation abundance. Sinclair (1977) found a similar positive correlation between African buffalo population density and annual rainfall. Leader-Williams and Ricketts (1980) and Clarke and Henderson (1981) found demographic evidence suggesting food limitation in reindeer and chamois.

In addition, numerous long-term studies indicate that many large-mammal populations exhibit density-dependent responses in fecundity and age at first reproduction (Woodgerd 1964; Gross 1969; Geist 1971; Fowler and Smith 1973; Gambell 1975; Lett et al. 1981; McCullough 1979; Fowler 1981; Clutton-Brock et al. 1982), juvenile survival (Grubb 1974; Lett et al. 1981; McCullough 1979; Clutton-Brock et al. 1982; Houston 1982), and adult survival (Grubb 1974; Sinclair 1977; Sinclair et al. 1985). Many of these authors speculated that food availability was ultimately responsible for the density-dependent response.

However, there is also empirical evidence that some large-herbivore populations are limited by predators or disease. Gasaway et al. (1983), Mech and Karns (1977), and Messier and Crete (1985) suggested that juvenile survival in moose and white-tailed deer was related to wolf population density and that predators could maintain prey populations at low levels for which food was not limiting. Smuts (1978) suggested that lion predation limited wildebeest population numbers below the carrying capacity set by vegetation abundance. Caughley et al. (1980) argued that dingo predation may "control" some kangaroo and emu populations in Australia.

Berry (1981) argued that combined effects of disease and

predation limited wildebeest population numbers in a Botswana game reserve. Christian et al. (1960) suggested that density-dependent stress disease caused the catastrophic mortality of a herd of introduced Sika deer. Finally, results from Serengeti suggest that an introduced disease, rinderpest, limited buffalo and wildebeest populations at low numbers prior to eradication of the disease in the early 1960's (Sinclair 1977; Sinclair and Norton-Griffiths 1979).

Thus, while there is evidence that at least some natural populations of large herbivores are limited by food availability, this is by no means universally true. In this study, I investigate whether a large migratory population of an African antelope, the white-eared kob (Kobus kob leucotis, Lichtenstein and Peters, 1854), is limited by food abundance and examine the effects of food limitation on kob movement patterns, breeding phenology, and mating system. The central theme of my study is that food resource limitation determines many of the most important life history characteristics of herbivores.

The white-eared kob population under study numbers about 830,000 in the Boma National Park region of the southern Sudan (Fig. 1.1). The Boma ecosystem is composed of broad expanses of tropical savannah grasslands punctuated by a patchy cover of woody vegetation. Like most African savannahs, the Boma grasslands are subject to seasonal extremes in rainfall; mean monthly rainfall ranges from less than 20mm to over 150mm. This extreme variation in monthly rainfall causes reduced food abundance during the dry season, from January to April, and at

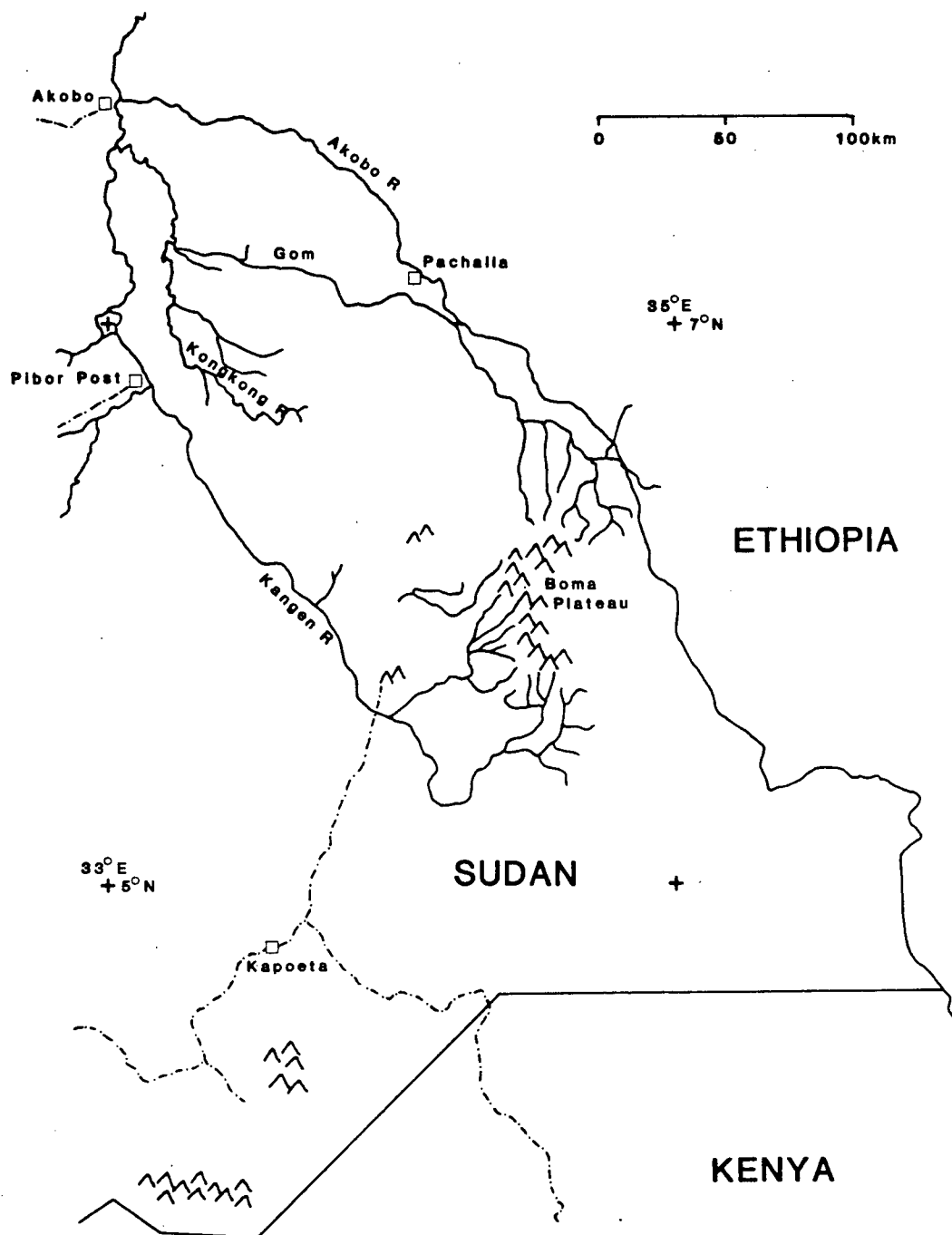


Figure 1.1 Map of the S.E. Sudan. Watercourses and international boundaries indicated by solid lines, roads indicated by broken lines, and townships indicated by boxes.

this time food may be limiting for the kob.

In Chapter 2, I describe seasonal climatic changes in the Boma ecosystem and consequent effects on the distribution and abundance of green grass and water supplies. Having shown that resource distribution changes dramatically throughout the year, I test whether kob migratory movements are responses to temporal changes in the distribution of scarce supplies of water (Western 1975) or green forage (Pennycuick 1975). I examine movement patterns at three different scales: 1) annual migration of the entire kob population between wet and dry season ranges 200 km apart, 2) dry season movement patterns between different habitat types, and 3) foraging movements of individuals within specific dry season habitats.

In Chapter 3, I investigate the effect of dry season food scarcity on kob demographic patterns, particularly mortality. I test the hypothesis that dry season food abundance determines kob population numbers through nutrition-related mortality. In addition, I examine the impact of large-scale mortality that occurred at the outset of the study by evaluating the current age structure of the population. Finally, I suggest an empirical model of kob population mortality as a function of dry season duration.

I examine the phenology of calf production in Chapter 4. I use these data to test the hypothesis (Sadleir 1969; Sinclair 1983a) that production of young in mammals should be synchronized to periods of peak food abundance. If food abundance is limiting during the dry season, this hypothesis

predicts that kob should produce young during the wet season.

In Chapter 5, I investigate the effect of breeding synchrony (resulting presumably from adaptation to seasonal changes in food abundance) on the mating system of the white-eared kob. The Boma population has a lek system (Bradbury 1981; Bradbury and Gibson 1983), with a presumably high degree of polygyny. I test Emlen and Oring's (1977) hypothesis that moderate breeding synchrony should increase the degree of polygyny and competition between males for females, by comparing published data on the conspecific Uganda kob (Kobus kob thomasi) to original data for the white-eared kob.

In order to evaluate the age structure of the kob population, I derived a new method for estimating age-specific survival. This method is described and compared to two conventional methods in Chapter 6.

As shown in Fig. 1.2, the lines of investigation in this study derive from a unifying assumption of periodic food limitation for the white-eared kob population. In Chapter 7, I summarize my conclusions, and consider the merits and drawbacks of this approach.

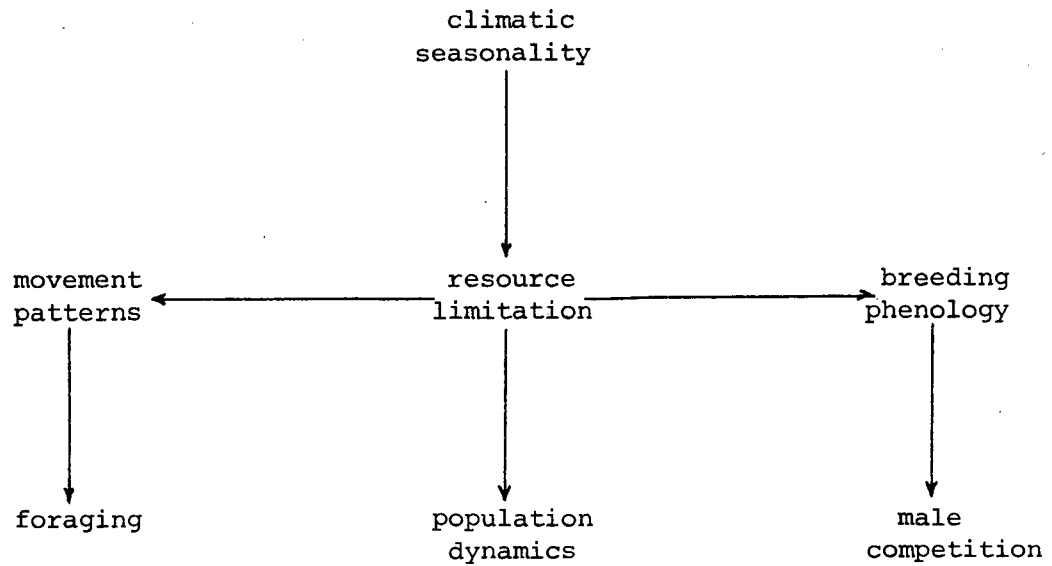


Figure 1.2 Lines of investigation employed in this study.

CHAPTER 2. SEASONAL MIGRATION IN RELATION TO RESOURCES

Introduction

Long distance movements are characteristic of many large herbivores in African savannah ecosystems. Although some populations exhibit nomadic movements apparently unrelated to season (Delaney and Happold 1979), most large herbivore migrations follow seasonal changes in resource distribution and abundance (Sinclair 1983b), as do migrations of species drawn from a wide variety of other taxa (Dingle 1980).

African savannah ecosystems exhibit pronounced seasonal changes in grassland productivity due to periodic variation in rainfall (Phillipson 1975; Sinclair 1975; Strugnell and Pigott 1978; McNaughton 1979). As well, many grasses decline in nutritional quality as they flower and mature, and this process is usually a response to rainfall seasonality (Plowes 1957; Laredo and Minson 1973; Reid et al. 1973; Egan 1977). Early in the growing season, grasses produce new leaves with high protein content and high digestibility. At later growth stages, many perennial grasses cease vegetative production and translocate most of the soluble constituents back into the roots and stem bases, leaving highly lignified, poorly digestible, low protein tissues above ground. As a result, grazing animals in savannah grasslands are faced with seasonally variable food quality and absolute abundance: in the wet season food is abundant, widely distributed, and nutritious; in the dry season food is scarce,

unevenly distributed, and of relatively poor quality.

The most detailed studies of large-herbivore migration in Africa are on the Serengeti wildebeest population (Pennycuik 1975; Maddock 1979). These studies suggest that migration tracks seasonal changes in the distribution and abundance of high quality forage. Wildebeest move into low-rainfall (400mm per year) short grass plains during the wet season, when these areas support substantial production of nutritious grasses. During the dry season, wildebeest migrate northwards into high rainfall (1000mm per year) tall grass areas that produce limited quantities of nutritious regrowth as the result of infrequent dry season rainstorms.

However, Western (1975) pointed out that in many African savannah ecosystems, water supplies become restricted during the dry season, due to the evaporation of water-filled depressions. As a consequence, species that are unable to meet their metabolic water requirements solely from their forage (i.e. most grazers) are obliged to concentrate around permanent water supplies during the dry season. In contrast, many browsers can obtain sufficient water from their forage to meet body requirements and, as a consequence, do not exhibit dry season movements to watering points. Thus, the availability of water constrains the dry season foraging options of grazers.

In this chapter, I examine whether the seasonal migration of white-eared kob tracks shifting distributions of food, water, or both. If kob migration is an adaptation for exploiting seasonally restricted resources, I predict the following:

1. Resources should be unevenly distributed throughout the ecosystem.
2. Resource abundance should follow predictable seasonal trends.
3. Kob distribution should be correlated with resource distribution.
4. Kob should remain in locations only as long as those locations have greater abundance of resources than surrounding areas.

In this chapter, I first describe seasonal climatic characteristics of the Boma ecosystem. Then, I examine seasonal changes in the distribution of food, water, and the kob population, as determined from aerial surveys. Finally, I test the proposed predictions against findings from both aerial surveys and ground observations in the dry seasons of 1982 and 1983.

Methods

Aerial surveys

The distribution and abundance of large mammal populations, forage, water resources, and habitat characteristics of the entire study area were measured by systematic aerial surveys. A full description of the aerial survey procedures employed is given in Norton-Griffiths (1978).

Aerial surveys of the whole study area were conducted in

early April 1980, October 1980, and July 1982. In addition, a survey of a smaller portion of the study area was performed in May 1982. Aerial survey teams consisted of a pilot, a front seat observer, and two rear seat observers. The pilot was responsible for correct orientation of transect lines, maintenance of constant flying height, and for signalling the start and finish of transect lines. At 1 minute intervals, the front seat observer recorded photometer and radar altimeter readings, observations of water sources, and estimates of woody vegetation cover and woody species composition. The rear seat observers counted all animals observed within a strip of fixed width on both sides of the aircraft. Transect width was delineated by 2 fibreglass rods attached to either wing strut. When rear seat observers encountered groups of more than 25 individuals, they took color photographs of the entire group and, time permitting, also made a visual count of group numbers. All rear seat observations were recorded immediately on a tape recorder as well as the time interval of the observation.

Transect width was calibrated at the end of each survey by flying at known height perpendicular to an airstrip marked off in 20m intervals by white sand bags. As the plane passed over the markers, the rear seat observers counted the number of bags seen inside the rods. Several passes, at a wide range of heights, were taken. A regression line was drawn through the resultant strip width estimates at given heights; this regression was used to calculate transect width during the actual survey from height above ground data.

Transect width varied between 150 and 300m for the three surveys. Transects were spaced at regular 10km intervals over the study area, with an east-west orientation. The first 2 surveys were flown at a height of 91m above ground, the final 2 surveys at 76m above ground. Flight speed varied between 150 and 200km per hour. During the first 2 surveys, flight position was determined using a Global Navigation System. During the final 2 surveys, flight lines were oriented to known landmarks, such as prominent rocky outcrops.

White-eared kob population estimates for each survey were calculated as the observed total for all transects divided by the ratio of the sample area to the total area. Confidence limits for individual surveys were calculated according to Jolly's method 2 for unequal sampling units (Jolly 1969). The white-eared kob population estimate for the entire study period was calculated from the weighted population estimates and variances of the four surveys (Norton-Griffiths 1978). Seasonal distribution patterns were obtained by summing animal counts for 10km segments along each transect line, then dividing this count by the area observed to arrive at the density per km².

Green biomass was estimated from digital photometer readings. The photometer consists of two probes with filters allowing passage of light at 800nm (infra red) and 675nm (red) wavelengths respectively. Red light is absorbed by chlorophyll in green vegetation, while it is reflected by non-green matter. Infrared light is reflected by both green and non-green vegetation. Thus, the ratio between these reflectance values is

correlated with the abundance of green biomass (Tucker et al. 1973; McNaughton 1979). Photometer readings were calibrated against measurements of the dry weight of green matter obtained in 0.25m² clip plots (Fig. 2.1). The resulting regression line was used to estimate green biomass from digital photometer readings obtained during aerial surveys.

Ground Observations

At five study sites (Fig. 2.2), I measured grass biomass and kob population density along 5km transects throughout the dry season (January 1 to April 30). I measured grass biomass within 0.25m² clip plots taken at 0.5km intervals along transects. Subsequent to clipping, grass samples were sorted into green leaf, green stem, and brown fractions, weighed on a triple-beam balance, dried in the sun for 8 hrs, and re-weighed. Preliminary observations confirmed little weight change following 8 hrs of sun drying.

Kob population density was estimated by counting all kob encountered within a strip 100m either side of a moving vehicle. Strip width was measured using a range-finder at the beginning of each transect; thereafter observers estimated the 100m transect strip width. Animal totals were subsequently summed for 0.5km transect intervals. In order to reduce the effect of diurnal movements on observed distribution patterns, I performed all transects in the early morning. At approximately monthly intervals during the dry season, I made similar measurements of kob population density along a 25km transect that bisected the

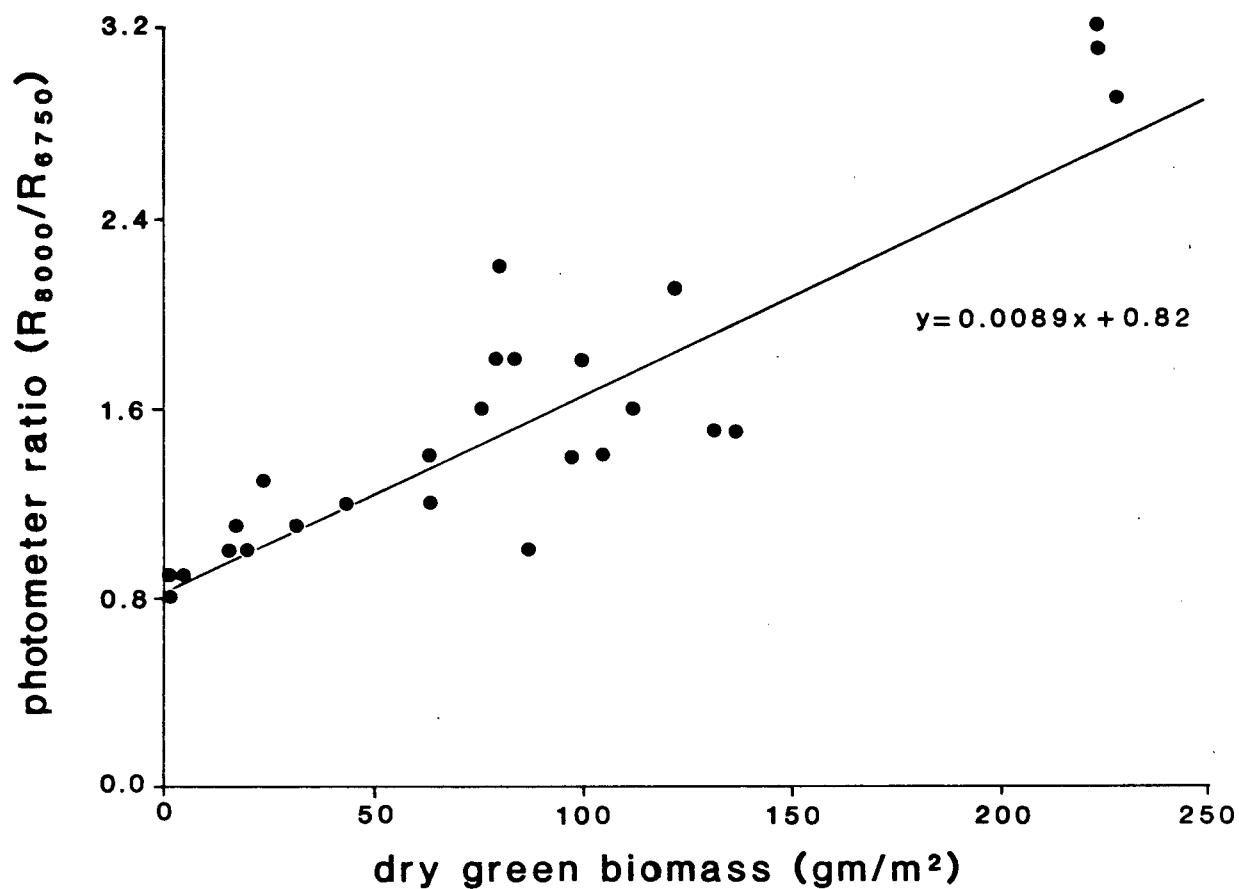


Figure 2.1 Calibration of photometer readings. The ratio of reflectance values recorded by the 800nm and 675nm probes was positively related to green grass dry weight ($r^2=0.812$; $p<0.05$).

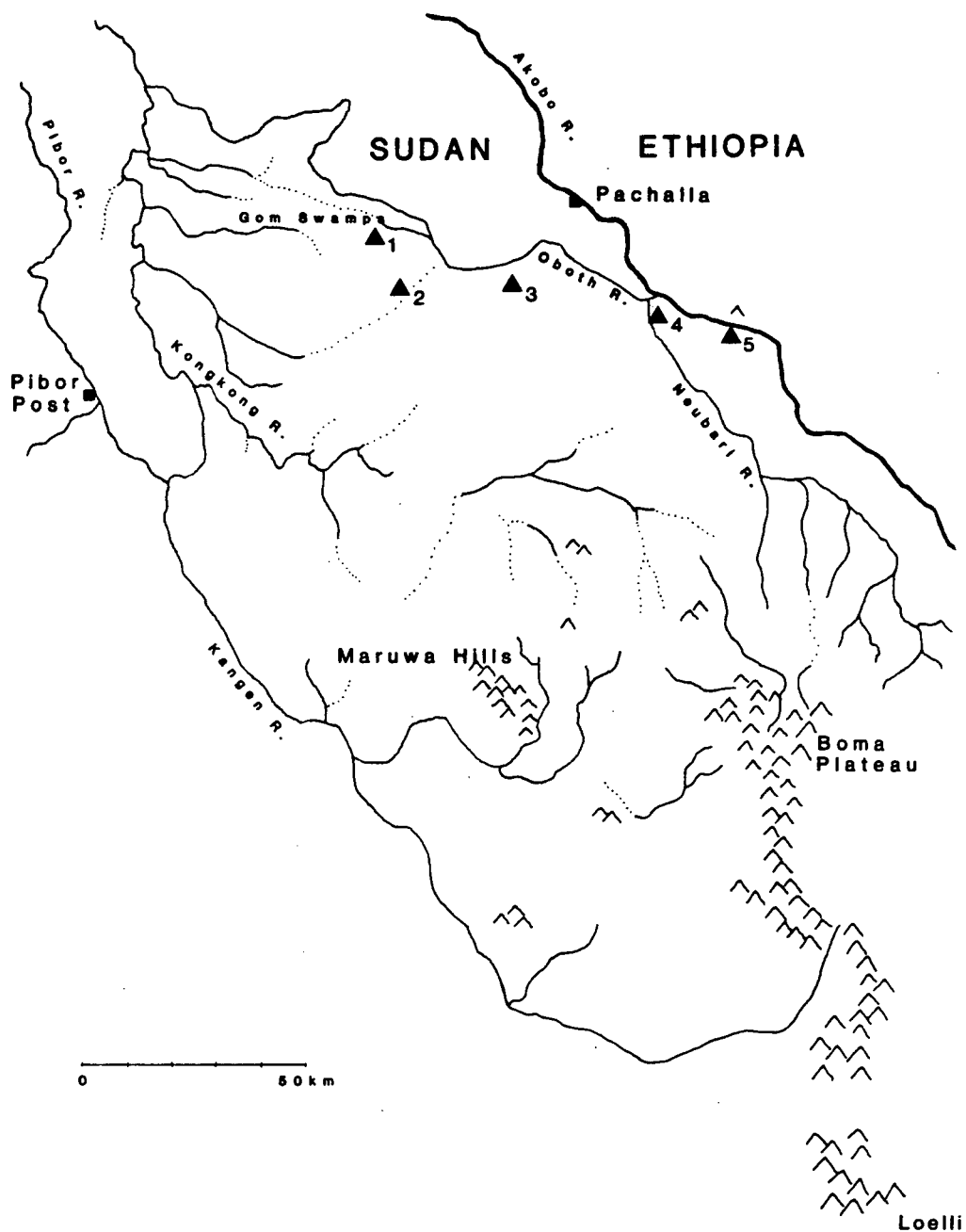


figure 2.2 Map of the study area. Study sites are indicated by triangles (1=Gom swamps; 2=Wangchira; 3=Ajwara; 4=Neubari; 5=Ungwala).

kob dry season range.

Diurnal changes in kob distribution pattern were recorded using two methods. First, at the Ajwara study site I made total counts of kob present throughout the day on a 0.5km² grassy meadow on selected dates over the course of the dry season. Second, at the Gom Swamp study site I repeated a 4km transect at intervals throughout the day.

Grass growth over the course of the dry season was determined from 0.25m² clip plots taken inside exclosures constructed in both swampy meadows and wooded grassland areas. Grass growth rates were calculated from regressions of green biomass over time.

Soil moisture content throughout the dry season was recorded for 7 meadow and 1 wooded grassland exclosures at the Ajwara study site. Soil samples (300-500gm) were obtained at a depth of 10cm below the surface, weighed, sun-dried for 2 days, and re-weighed. The difference between wet and dry weight indicated relative water content.

Kob feeding rates were calculated from the difference between green biomass measurements inside and outside exclosures. Since at all study sites no other grazing ungulates were observed, I assume that all grass biomass removed was taken by kob. In order to determine whether kob were feeding on particular plant parts, I measured the length of leaves and stems inside and outside exclosures after kob had been feeding for several weeks.

The nutritional quality of stoloniferous grasses was

estimated by analysis of: (1) crude protein content, (2) in vitro digestibility, and (3) detergent fiber content (Johnson et al. 1964; Van Soest 1963a, b; Van Soest and Marcus 1964). All chemical analyses were performed by the Wildlife Habitat Laboratory, Washington State University, Pullman, WA.

Plant species identifications were made by the East African Herbarium, Nairobi, Kenya.

The study area

Physical features and vegetation types

Physical features of the Boma region are depicted in Fig. 2.2. The study area, covering some 28,000 km², is bordered by the Boma escarpment in the south-east, the Kangen/Pibor River system in the west, and the Akobo River to the north-east. The entire region is in a watershed that ultimately empties into the Nile River via the Sobat River. Terrain is flat over most of the area, except in the vicinity of the central Maruwa Hills and around the Boma escarpment. Most of the plains are characterized by chernozems, or black-cotton soils, which are nutrient rich, have a high clay content, and range in consistency from being highly adhesive in the rains to rock-hard and cracked in the dry season. These soils seal quickly after being wetted, and, as a result, subsequent rainfall puddles on the surface. The soils at the base of the Boma escarpment are red-colored, volcanic loam, and are considered nutrient rich

(Willimott 1956). Red-colored sandy soils are also present near basalt monoliths and small hills that are scattered in the southern and eastern parts of the study area. Termitaria are present over most of the region, and are particularly abundant in the north.

Much of the study area has some degree of woody vegetation cover, being particularly dense (>25% cover) in the north-east and around the Boma escarpment (Fig. 2.3). Intermediate woody cover (10-25%) occurs along the margins of the Kong-kong River, in the far south, and in patches of the north-eastern woodlands. Light cover (< 10%) characterizes much of the rest of the area, except for expanses of open grassland in the north and south central parts of the study area.

Most of the areas of dense woody cover are composed of a community of deciduous, broadleaf trees, dominated by Combretum fragrans. The Kong-kong River area is characterized by low-growing thicket species, dominated by Ziziphus mauritiana and Balanites aegyptiaca. The lightly wooded grasslands in the north are composed of scattered Balanites aegyptiaca, Acacia seyal, and Acacia sieberiana. The southern lightly wooded grasslands are dominated by extensive stands of Acacia zanzibarica. The far southern bushed grasslands are characterized by scattered patches of low-growing Acacia mellifera, Acacia polycantha, and an unidentified Combretum species.

Virtually the entire Boma region supports substantial grass cover, excluding areas of gallery forest and thin strips of

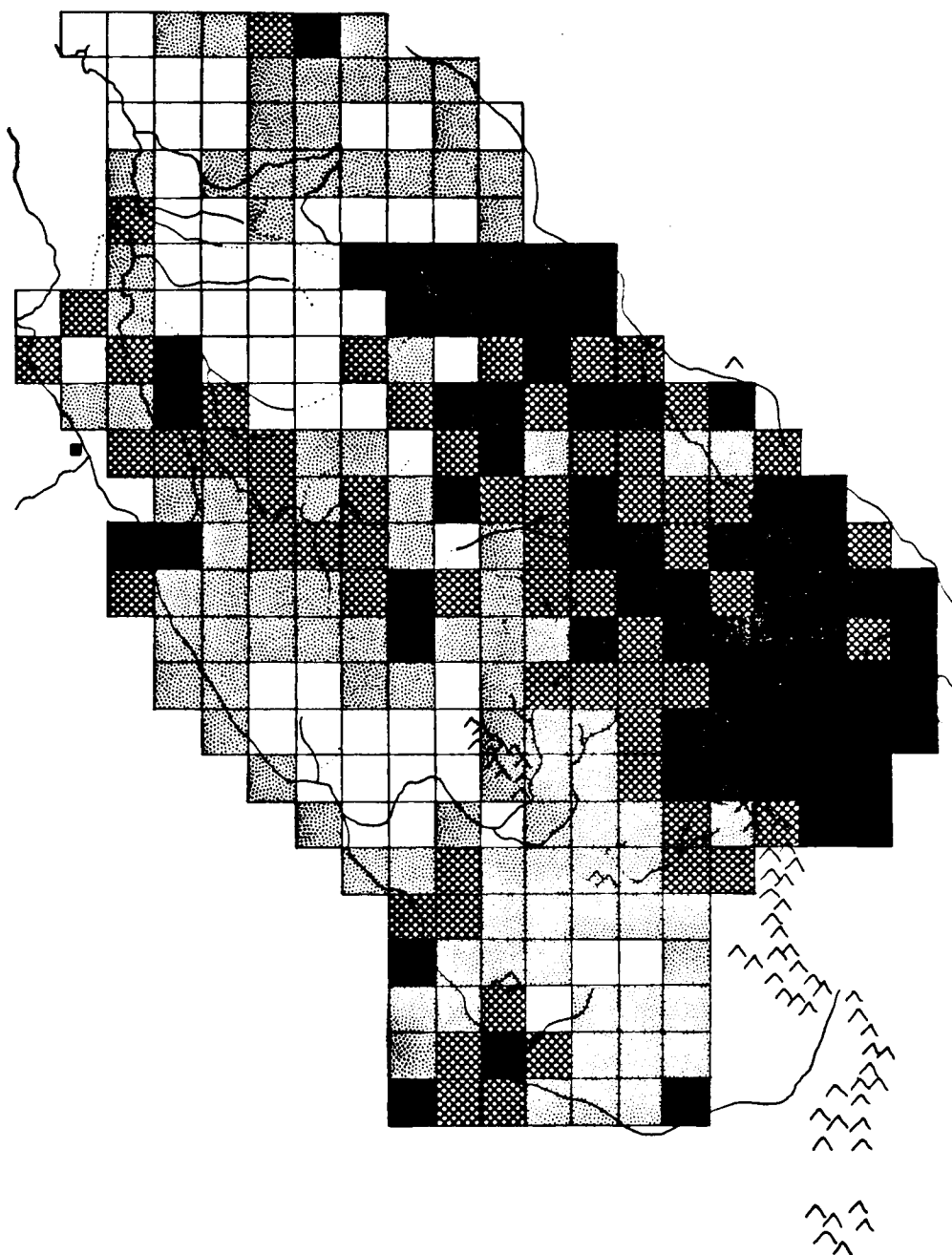


Figure 2.3 Map of woody vegetation cover, as estimated during aerial surveys (shaded=25% cover; hatched=10-25%; stippled=1-10%; open 1%). Each grid square is 10 x 10 km.

riparian woodland along the margins of the Akobo River. Even the extensive Combretum woodlands support substantial grass growth. The predominant grass species over much of the region is Hypparhenia rufa, which grows to heights of 2-3m each year. In the far south and in sandier areas, a wide variety of grasses are common: Heteropogon contortus, Setaria incrassata, Sporobolus ioclados, and Panicum ioclados. A stoloniferous grass species, tentatively identified as Echinochloa pyramidalis, characterizes the flood plain margins of major watercourses. Due to surface flooding, it was not feasible to visit study sites during the wet season, and the absence of reproductive structures during the dry season field study period permitted only tentative identifications of grass species. A full list of all identified vegetation samples is given in Appendix 1.

Climatic seasonality

Mean monthly records of temperature, relative humidity, wind direction, and evaporation piche from the nearby Akobo township are given in Table 2.1. Mean daily maximum temperatures range between 38.9°C in March to 30.8°C in August. Mean daily minimum temperatures range between 23.2°C in April and 19.9°C in December. Relative humidity is highest during the rainy season, from May to November, but is considerable throughout the year. Seasonal changes in evaporation rate follow seasonal temperature variation.

Seasonal changes in rainfall are illustrated in Fig. 2.4.

Table 2.1 Monthly climatic normals for Akobo township (see Fig. 1.1).

Data are mean values for 27 years of records between 1941 and 1970

(from the Meteorological Department, Government of the Sudan).

month	max temp	min temp	relative humidity		wind direction	evaporation piche
			6:00	12:00		
Jan.	36.6	20.0	47%	27%	NE	9.7
Feb.	37.9	21.6	41	24	NE	11.2
Mar.	38.9	23.1	49	27	SE	10.4
Apr.	37.5	23.2	62	35	SE	8.2
May	34.9	22.2	74	47	SE	5.7
Jun.	32.6	21.5	82	55	SE	4.1
Jul.	30.9	21.5	87	62	SE	2.9
Aug.	30.8	21.1	88	65	SE	2.6
Sep.	32.0	22.7	86	59	SE	2.9
Oct.	33.5	21.8	82	54	SE	3.5
Nov.	34.6	21.2	75	46	SE	4.7
Dec.	35.4	19.9	59	34	NE	7.1

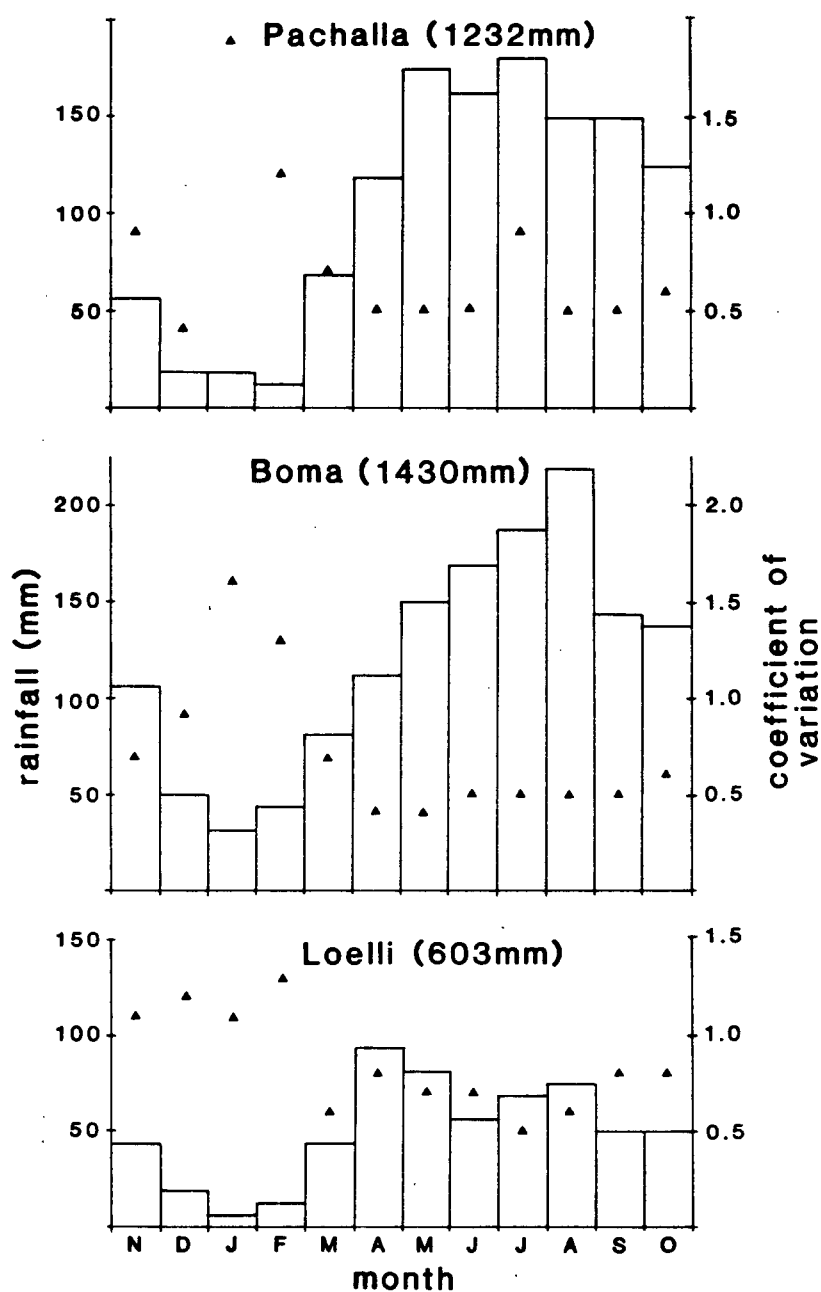


Figure 2.4 Mean monthly rainfall totals for Pachalla, Boma Plateau, and Loelli (see Fig. 2.2) indicated by histograms. Triangles indicate coefficient of variation (S/mean) for monthly rainfall totals.

At all sites, rainfall is highest between April and November, inclusive. Between year variation in rainfall (measured as the coefficient of variation) is highest during the dry season, indicating that rainfall is most unpredictable at this time of year.

Seasonal rainfall patterns in the southern Sudan are closely related to movements of the Inter-Tropical Convergence Zone (ITCZ) (Griffiths 1972). The ITCZ is the interface between south-easterly and north-easterly winds in the tropics. This zone moves north during the northern hemisphere summer, and south of the equator during the northern hemisphere winter. After the ITCZ passes through the southern Sudan each March or early April, prevailing winds shift from a northerly to a southerly direction (Table 2.1). These winds bring in moisture-laden air from the Atlantic coast. During the dry season, sporadic rainfall results from thunderstorms that arise from the Ethiopian Highlands. However, during most of the dry season hot, dry winds are typical.

Mean annual rainfall totals for the Pachalla and Loelli sites (Fig. 2.4) suggest a gradient from high rainfall in the north (1232 mm per year) to low rainfall in the south (603 mm per year). This trend is consistent with published rainfall isohyet maps for the entire southern Sudan (Griffiths 1972). Rainfall on the Boma escarpment is unusually heavy because of its high elevation.

Results

Aerial survey results

Seasonal changes in green biomass

There was considerable seasonal and spatial variation in green biomass over the study area (Fig. 2.5). In the early wet season (July), the northern half of the region supported biomasses in excess of 300 gm/m², while southern areas supported less than 300 gm/m². In the late wet season, the northern region supported more than 200 gm/m² while southern areas supported less than 200 gm/m². In both the early and late wet seasons, green biomass increased from south to north (early wet: ANOVA, $F=42.8$, $p<0.05$; late wet: ANOVA, $F=60.5$, $p<0.05$). In the dry season, green biomass abundance was low in all areas (ANOVA, $F=2.0$, n.s.), but was greatest along the margins of the Kong-kong, Kangen, and Oboth watercourses and on the Boma escarpment (Fig. 2.6). Less than 5% of the study area had dry season green biomasses in excess of 50 gm/m², mostly around the Boma escarpment. In all seasons, the spatial distribution of green biomass was patchy, possibly indicating that rainfall was unevenly distributed.

These results suggest that annual grass production rates were highest in the north and on the Boma escarpment, and lowest in the southern areas. This trend is consistent with the north-

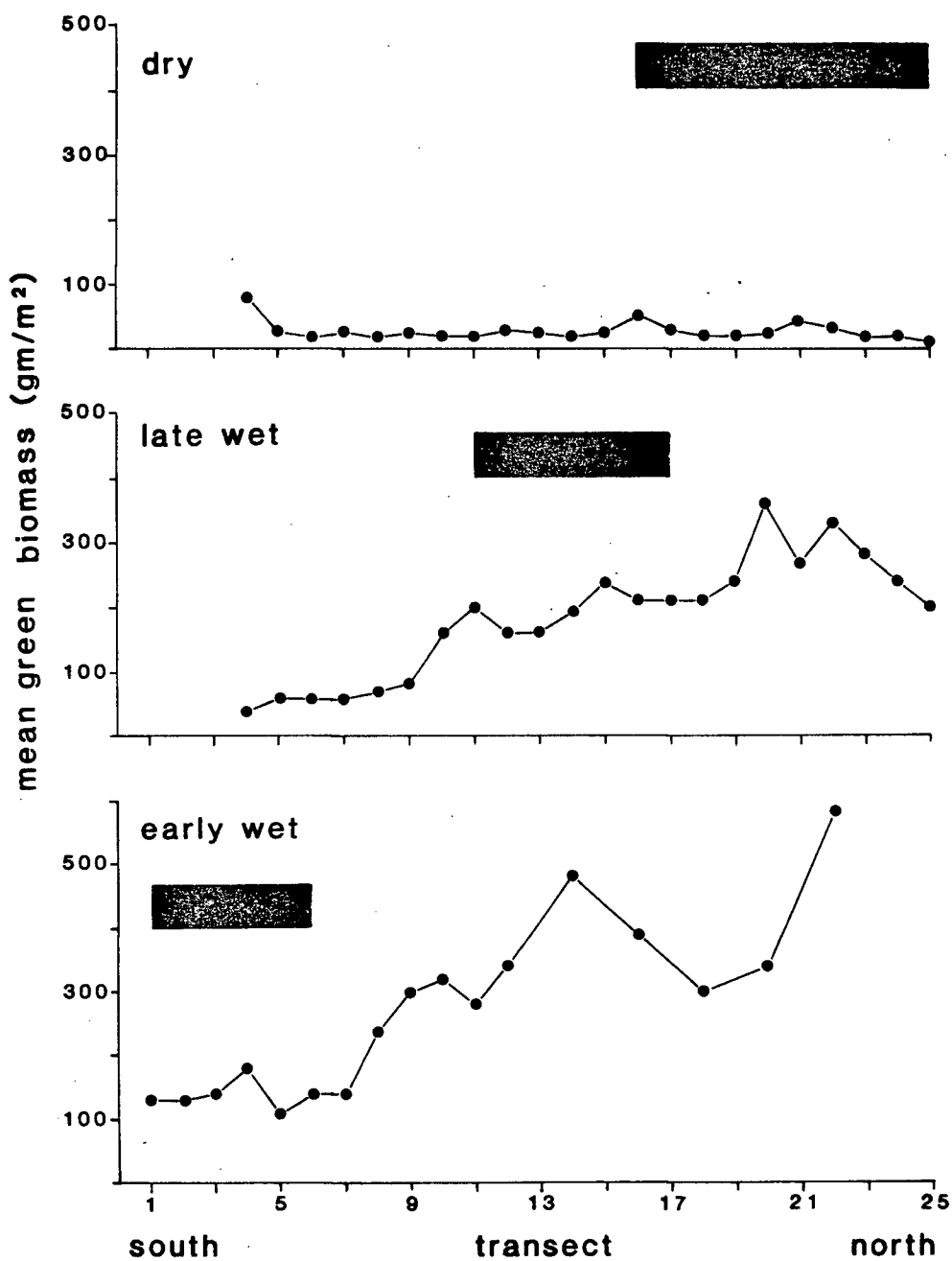


Figure 2.5 North-south gradient in seasonal green biomass abundance, estimated from digital photometer readings during aerial surveys. Shaded bars indicate transects in which kob were observed during specific aerial surveys (dry: April 1980; late wet: October 1980; early wet: July 1982).

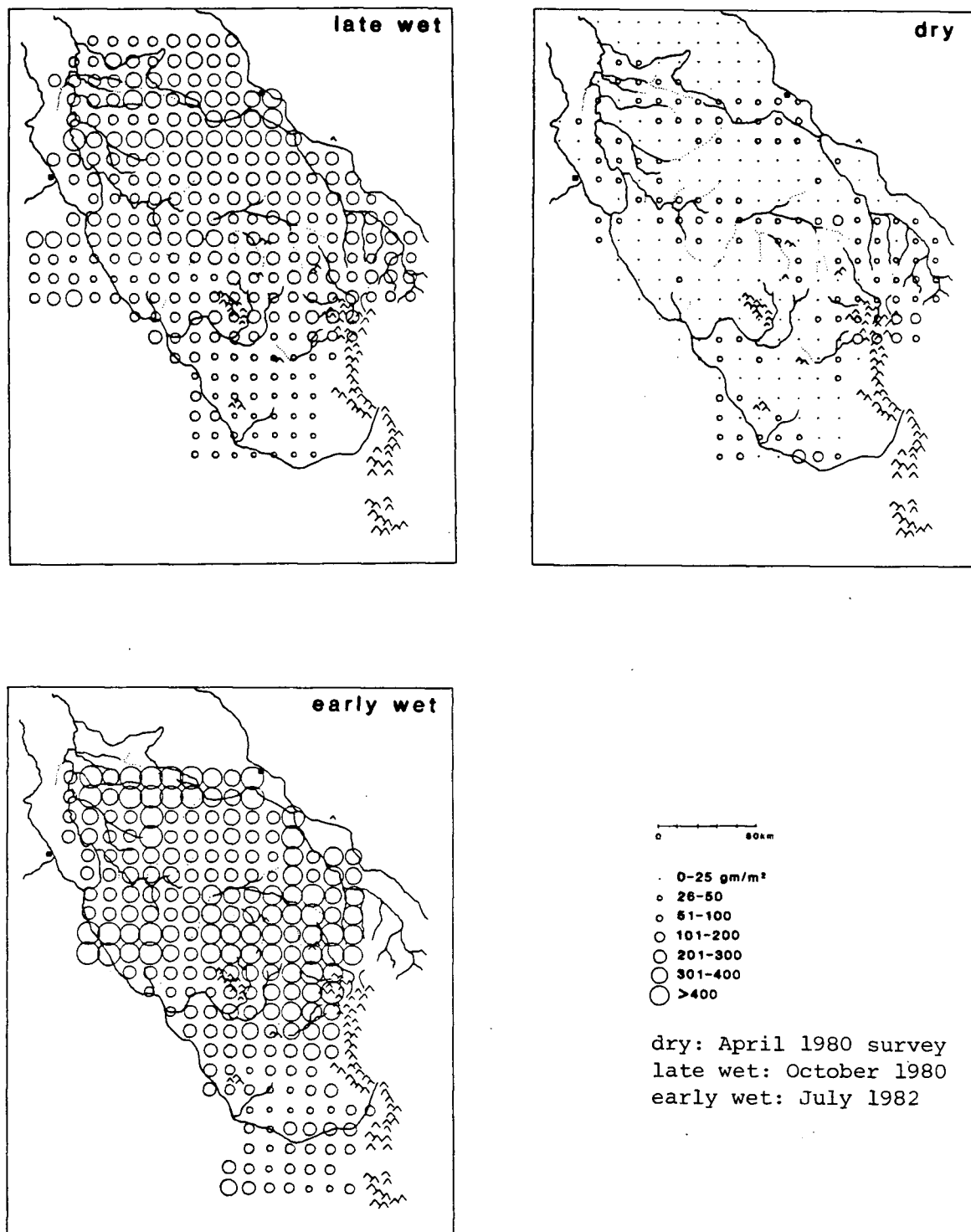


Figure 2.6 Seasonal distribution of green biomass, estimated from digital photometer readings during aerial surveys.

south rainfall gradient described earlier. In the dry season, green biomass values were generally low across the ecosystem, but were somewhat greater along the margins of northern watercourses and at higher elevations.

Seasonal changes in water availability

The seasonal distribution of water supplies is shown in Fig. 2.7. During the rains, water supplies were widely distributed throughout the region. The north-central plains were inundated; standing water covered several thousand km². Swamping did not occur south of the Maruwa Hills, near the Boma escarpment, or in the Combretum woodlands to the east of the plains, but during the rains there were large numbers of full watercourses and waterholes scattered throughout these areas. By the late wet season, most of the ephemeral swamped grasslands in the north dried out and water was chiefly restricted to watercourses and waterholes. The south was less well supplied than the north, possibly as a result of lower rainfall. In the dry season, water was mainly restricted to the northern watercourses: the Oboth, Neubari, and Akobo Rivers. The largest remaining swamps, called the Gom Swamps, are part of the Oboth drainage system. Some waterholes remained in the Combretum woodlands and around the Boma escarpment.

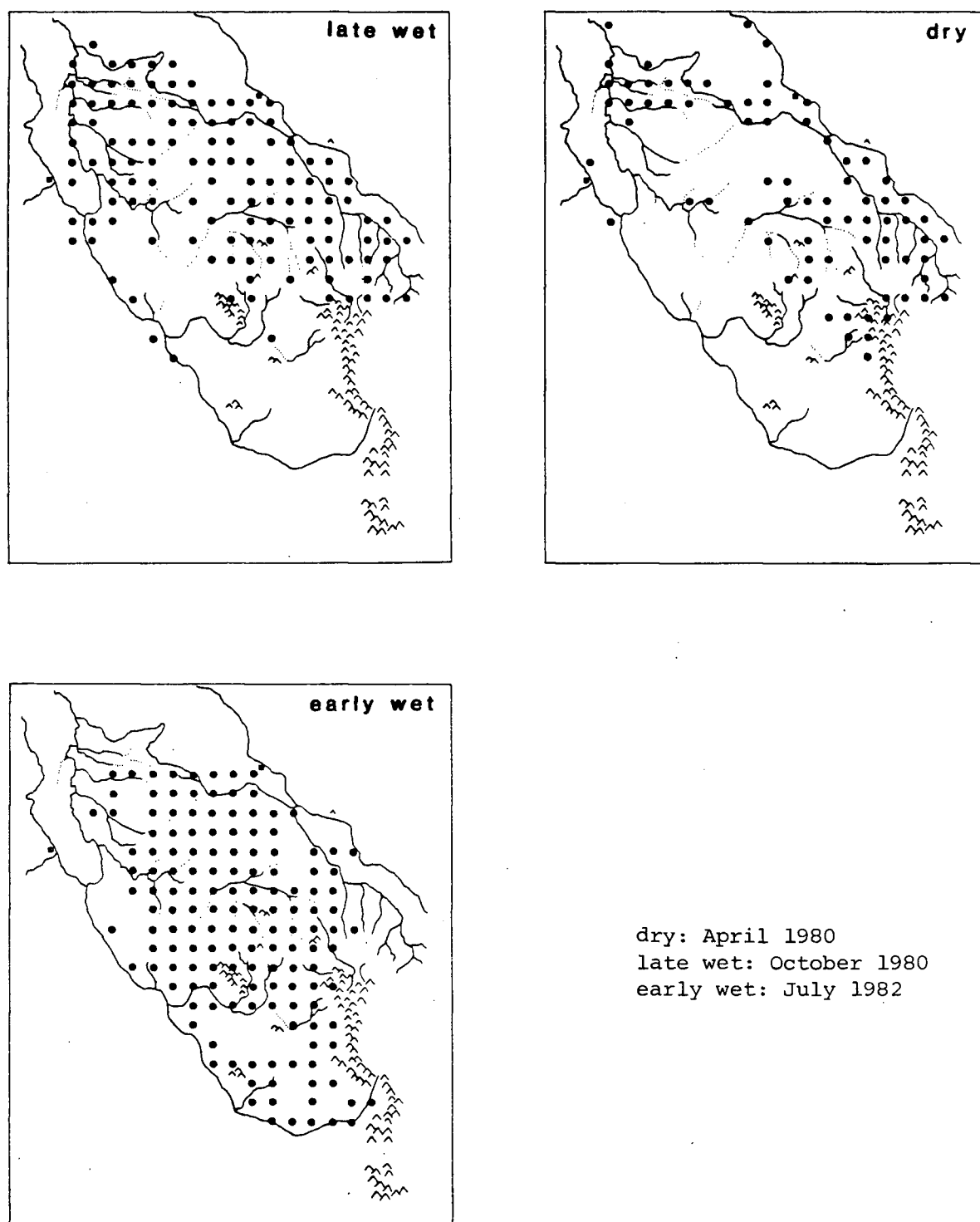


Figure 2.7 Seasonal distribution of water supplies, estimated during aerial surveys. Solid dots indicate standing water observed at least once per 10km in a given transect. Boundaries of the study area as indicated in Fig. 2.6.

White-eared kob population numbers

During 1980-82, the Boma kob population numbered approximately 830,000, making it the second largest migratory ungulate population in Africa, after the Serengeti wildebeest (Sinclair and Norton-Griffiths 1982). There was no significant change in kob population numbers over the course of the study (Table 2.2; t-tests for all pairs of census totals, n.s.).

Seasonal migration of white-eared kob

The seasonal distribution pattern of white-eared kob is shown in Fig. 2.8. During the rains, kob were concentrated in large herds south of the Kangen River, in lightly wooded grasslands where rainfall is low. By October, kob moved northwards along the Kangen River, crossing the river at several points. Large numbers of kob proceeded as far north as Pibor Post before crossing the Kangen River. Aerial reconnaissance flights and field observations indicated that kob moved into the dry season range by early January. The dry season range, adjoining the Neubari/Oboth River system, was maintained until the onset of rains. The southward migration was sporadic; the herds often remained stationary for a number of days and even reversed direction on occasion. By May, migratory kob herds were in the vicinity of the Maruwa Hills and the Boma escarpment. The wet season range was reached by early July. The dry season and wet season ranges were 150 to 200km apart.

The Oboth River system was the only watercourse that showed

Table 2.2 Boma white-eared kob population estimates from aerial censuses (1980-1982). The mean population estimate for the entire period was calculated from the weighted estimates of individual censuses (Norton-Griffiths 1978).

survey date	population estimate	95% confidence interval
April 1980	888,880	$\pm 70 \%$
October 1980	651,020	$\pm 93 \%$
May 1982	869,553	$\pm 47 \%$
July 1982	964,932	$\pm 104 \%$
mean	831,081	$\pm 31\%$

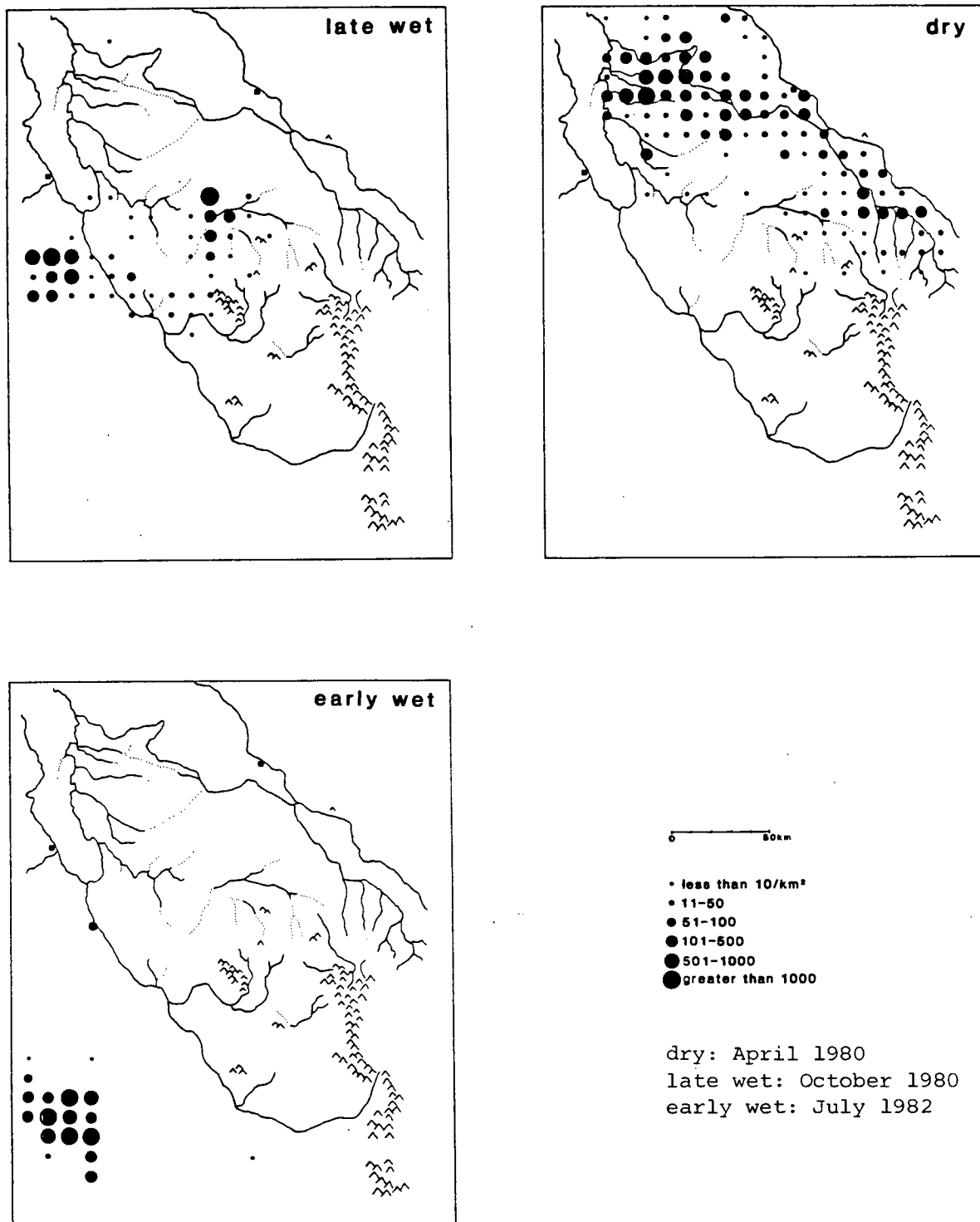


Figure 2.8 Seasonal distribution of white-eared kob. Size of the solid dots indicates kob density per km².

continued flow during the dry season, although limited supplies of water were available in woodland waterholes during part of the dry season. Aerial surveys suggest that the dry season range was better endowed with water than surrounding areas. Fig. 2.9 depicts the relative frequency distribution of kob in relation to distance to the nearest water supplies. Kob were concentrated closer to water supplies than expected if distribution was random (Kolmogorov-Smirnov test, $D=0.49$, $p<0.05$). This histogram indicates that few kob (<5%) were located farther than 20km from the nearest known water supplies, and most kob (75%) were within 10km. During the wet season, no locations in the study area were further than 20km from the nearest water supplies.

If kob migration tracks the seasonal availability of food, then one would expect a positive correlation between kob population density and green biomass. As shown in Fig. 2.5, kob vacated high biomass northern areas and concentrated in the south during the early wet season (July). By the late wet season (October), kob began to move north into the high biomass swamped grasslands. By the late dry season (April), northern areas occupied by the kob did not differ significantly from southern areas in terms of green biomass.

Aerial survey results showed no significant correlation between kob population density and green biomass during the dry season ($r^2=0.01$, n.s.). Since kob are restricted in their choice of habitats by the accessibility of water supplies, I examined the same data, excluding all ecosystem locations

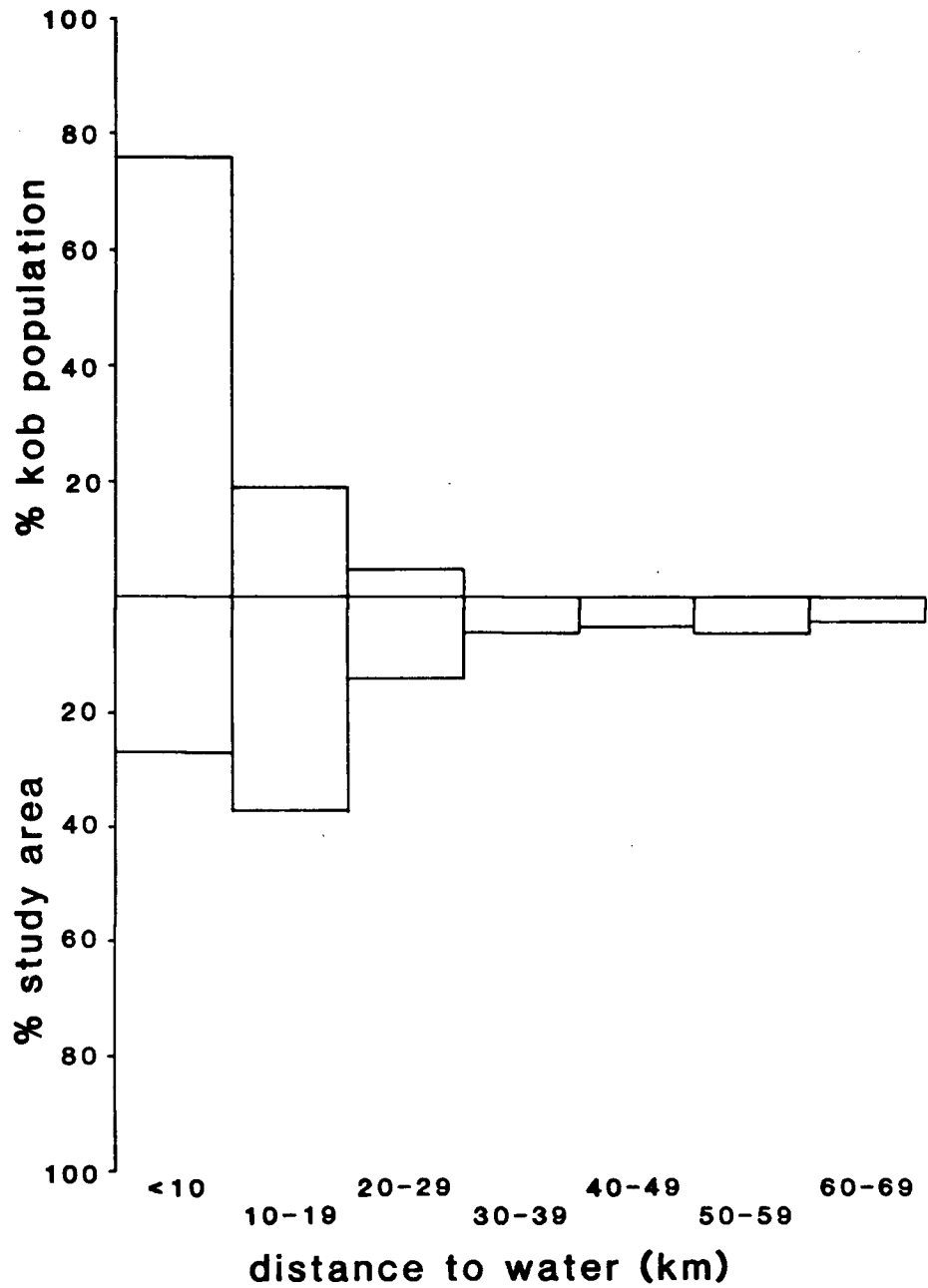


Figure 2.9 Kob distribution in relation to the nearest water supplies during the dry season (April) aerial survey.

further than 20km from water. Results indicate there was still no correlation ($r^2=0.01$, n.s.). However, forage distribution patterns observed in the late dry season may not reflect forage distribution patterns available at the time kob actually migrated into the dry season range, since kob quickly reduce grass biomass to low levels. A clearer test might be to consider the abundance of green biomass in all regions at the end of the wet season, before kob had an opportunity to graze it down. After doing this, I found a substantially higher correlation between kob population density during the dry season and the amount of green biomass that was available in the late wet season, prior to migration into the dry season range ($r^2=0.187$; $p<0.05$).

Thus, while there was weak evidence that kob migration tracked forage abundance during the transition from wet to dry seasons, there was no indication that migration tracked shifting distributions of green biomass at other times of the year. There was more substantial evidence that the dry season distribution of kob was correlated with the availability of nearby water supplies.

Dry season ground observations

Kob distribution patterns

Habitats in the kob dry season range may be lumped into three main types: 1) wooded grassland with a scattered woody cover of Acacia sieberiana, Combretum fragrans, Balanites aegyptiaca, and Ziziphus mauritiana, and an understory of Hyparrhenia rufa grass; 2) tall H.rufa open grasslands; and 3) swampy meadows with dense low growing stoloniferous grass, Echinochloa pyramidalis, interspersed with occasional patches of taller clump-forming grasses. Data from 25km transects show that kob were unevenly distributed across the dry season range, and were concentrated around the swampy meadows (Fig. 2.10). Much lower population densities were found in areas of tall open grassland or in the wooded grasslands that surround the swampy meadows (Fig. 2.11).

Although substantial numbers remained in swampy meadows throughout the day, most kob moved off into surrounding woodlands during the hottest part of the day (Fig. 2.12). This diurnal movement pattern became more pronounced, as the dry season progressed. Large numbers of kob continued to feed on swampy meadows throughout the night.

Clip plot measurements (Table 2.3) show that there was nine times as much green biomass in swampy meadows than in surrounding wooded grasslands (t-test, $t=3.66$, $p<0.05$) even though total biomass was similar (t-test, $t=0.10$, n.s.). The

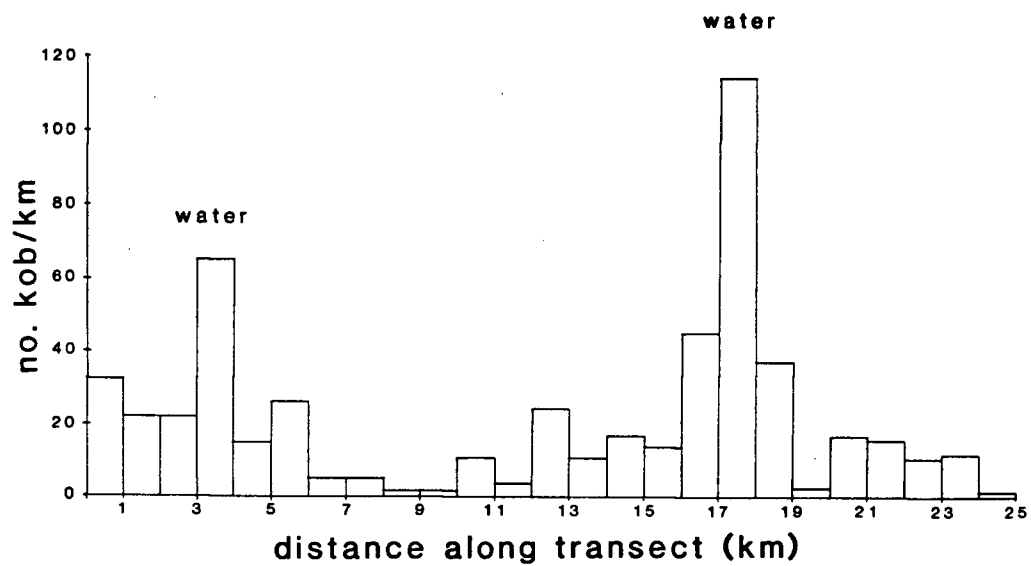


Figure 2.10 Kob dry season aggregation near swampy meadows, as indicated by mean numbers seen per km during 25km transects from January to April, 1983 (n=3).

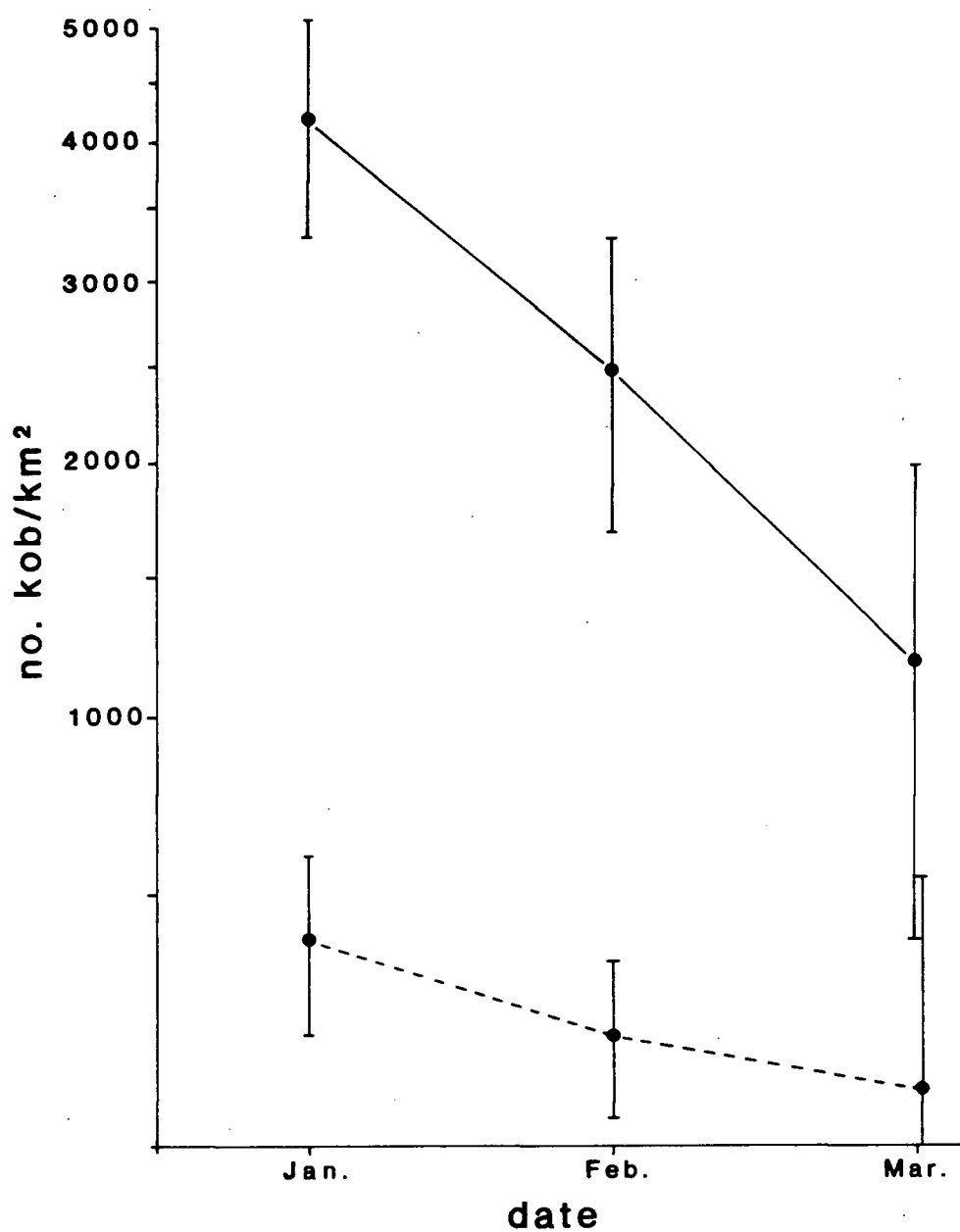


Figure 2.11 Kob population densities in wooded grassland (broken line) vs. swampy meadow (solid line) habitats at the Ajwara study site during the 1983 dry season (vertical bars=95% confidence limits).

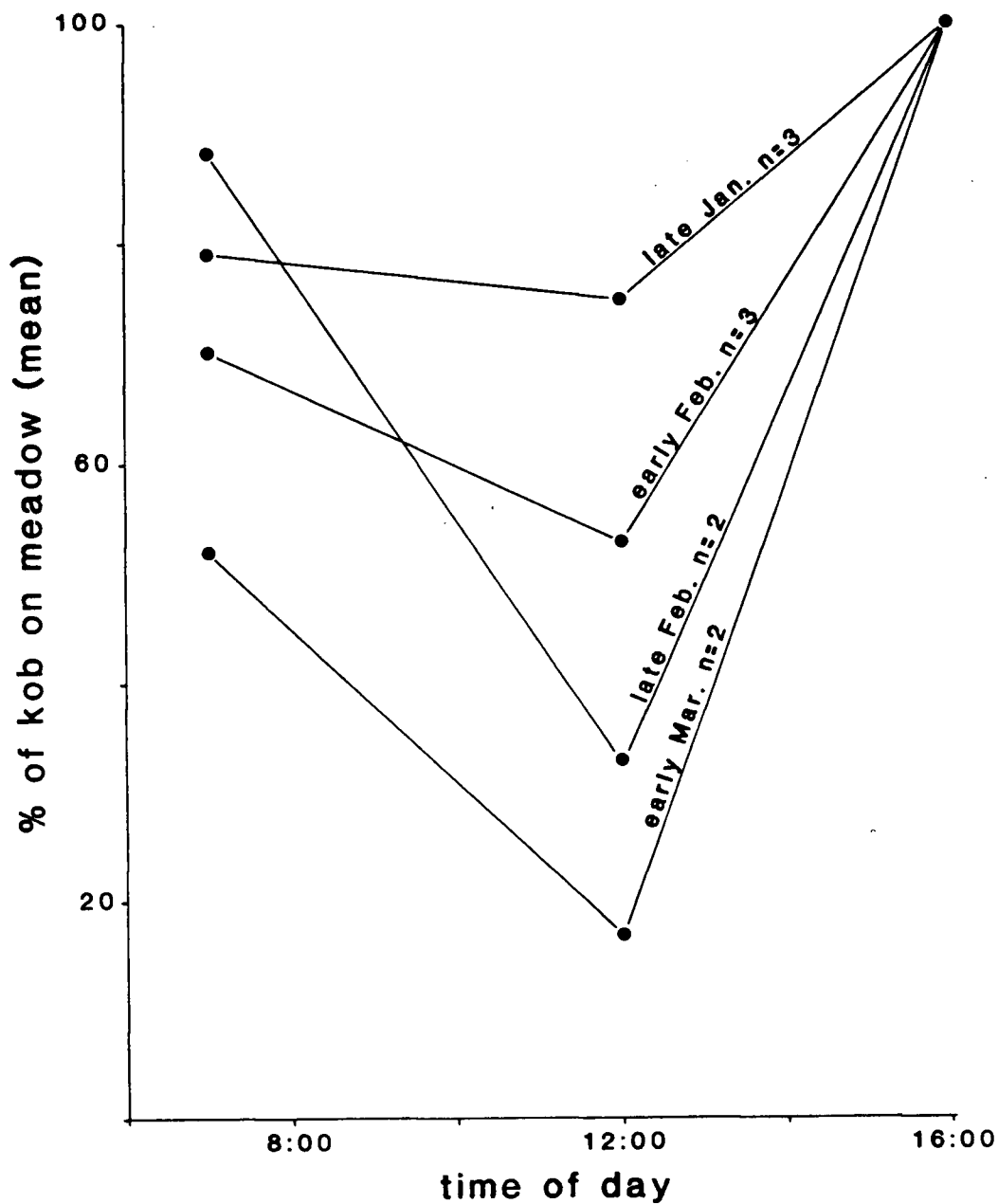


Figure 2.12 Kob diurnal movements onto meadows. Maximum kob numbers were present in the early morning and late afternoon. Note the increasing tendency to abandon meadows at mid-day as the dry season progressed from January to March.

Table 2.3 Dry season grass standing crops in meadows vs. wooded grasslands at the Ajwara study site in 1983. Meadows had more green biomass than wooded grasslands (t-test; $t=3.66$; $p<0.05$), but no other significant differences were observed.

<u>MEADOWS</u>					
mean dry wt. (gm/0.25m ²)					
location	date	brown	green	total	sample size
Neubari	2-3-83	7.7	9.1	16.0	7
Neubari	23-3-83	1.0	2.3	3.3	2
Gom	14-3-83	5.9	7.9	13.8	5
Gom	1-4-83	1.7	4.9	6.6	5
Wangchira	13-2-83	1.8	3.7	5.5	11
Wangchira	21-3-83	9.5	17.3	26.8	8
Ungwala	24-3-83	42.1	7.5	49.6	6
Ajwara	16-1-83 to 14-4-83	7.5	15.8	23.3	18
mean		9.7	8.5	18.2	8 dates
SE		4.5	1.8	5.0	

<u>WOODED GRASSLANDS</u>					
Neubari	2-3-83	29.7	0.4	30.1	7
Neubari	23-3-83	24.3	0.1	24.4	6
Gom	14-3-83	14.1	0.8	14.9	6
Gom	1-4-83	0.3	1.1	1.4	6
Wangchira	13-2-83	1.1	0.9	2.0	11
Ungwala	24-3-83	6.2	1.1	7.3	5
Ajwara	16-1-83	38.4	2.1	40.5	17
mean		16.3	0.9	17.2	7 dates
SE		5.2	0.2	5.2	

stoloniferous grasses remained green throughout the dry season long after taller grasses had flowered and senesced. Since green grasses are generally more protein rich than senescent grasses (Wilson 1976), kob that fed in the meadows should have obtained forage higher in protein than those that fed in surrounding wooded grasslands. Small ruminants require food with higher protein content than larger ruminants, since they need to process food at a faster rate to compensate for their smaller gut capacity (Owen-Smith 1982; Demment and Van Soest 1985). Following Owen-Smith's (1982) calculations, I estimate that kob require forage with a minimum 9% crude protein content. Stoloniferous grass samples collected from meadows contained on average 17% crude protein, well above the minimum requirements for kob (Table 2.4). In contrast, senescent Hyparrhenia grass in surrounding wooded areas was probably too low in protein to be utilized by kob, since other studies in nearby grasslands report crude protein values of 2% in mature Hyparrhenia grass (Jonglei Investigation Team, unpublished). Since kob rarely fed on tall Hyparrhenia grass, I conclude that dry season grazing was largely confined to meadows because only these areas offered forage of sufficient quality.

Moreover, results from exclosure plots indicate that stoloniferous grasses continued to produce new green growth throughout the dry season (Fig. 2.13; ANOVA, $F=178.7$, $p<0.01$), when tall grasses were no longer productive. This growth was manifested in elongation of stem and leaf tissue (Fig. 2.14; stems: ANOVA, $F=50.8$, $p<0.05$; leaves: ANOVA, $F=106.8$, $p<0.05$).

Table 2.4 Nutritional analyses of above-ground tissues from stoloniferous vs. Hyparrhenia grasses. No differences were observed between stoloniferous grass fractions except in crude protein content (ANOVA; $p < 0.05$). Statistical comparisons were not possible between Hyparrhenia and stoloniferous grasses because variances were not stated in Mefit-Babtie report (1983). CP=crude protein; IVDDM= in vitro digestible dry matter; NDF=neutral-detergent soluble fraction; ADF=acid-detergent soluble fraction; LIG=lignin content; AIA= acid insoluble ash.

grass type	part	n	CP	IVDDM	NDF	ADF	LIG	AIA
stoloniferous	green leaf	19	21.7	39.3	66.8	30.1	8.8	4.8
stoloniferous	green stem	17	16.1	45.7	62.8	30.9	12.1	4.7
stoloniferous	brown	10	18.2	43.3	64.8	32.5	9.2	4.4
<u>Hyparrhenia</u> ^{1.} <u>rufa</u>	total plant	n.a.	1.7	n.a.	n.a.	n.a.	n.a.	n.a.

1. From: Mefit-Babtie, 1983 (April). Development Studies in the Jonglei Canal Area. Range Ecology Survey, Livestock Investigations, and Water Supply. A report to the Jonglei Executive Organ, Government of the Sudan, Vol. 1-10.

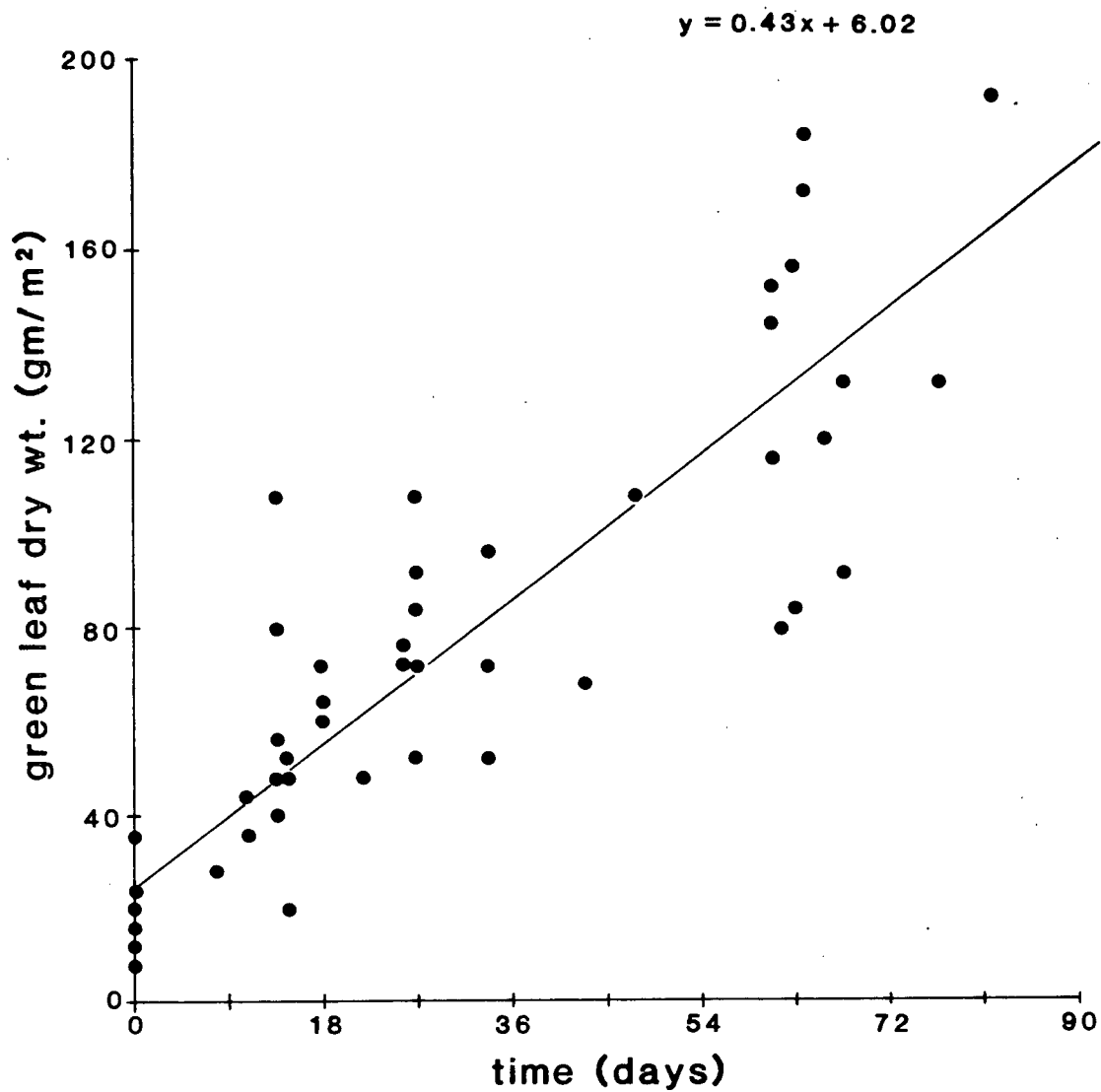


Figure 2.13 Dry season meadow grass growth, Ajwara study site. Values determined by 0.25m^2 clip-plots from exclosures erected in mid-January, 1983 ($r^2=0.78$; $p<0.05$).

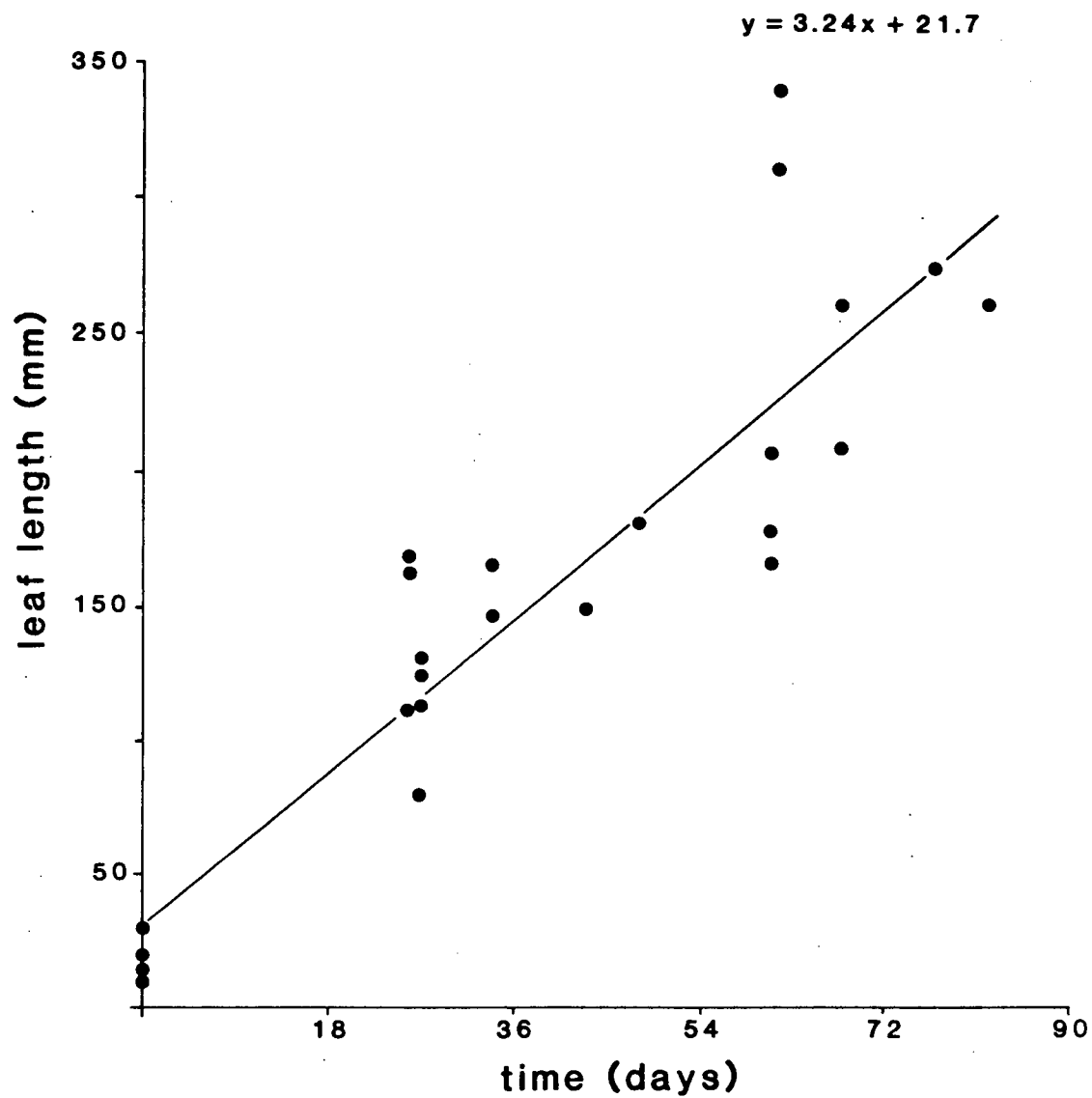


Figure 2.14a Dry season leaf growth, Ajwara study site ($r^2=0.82$; $p<0.05$).

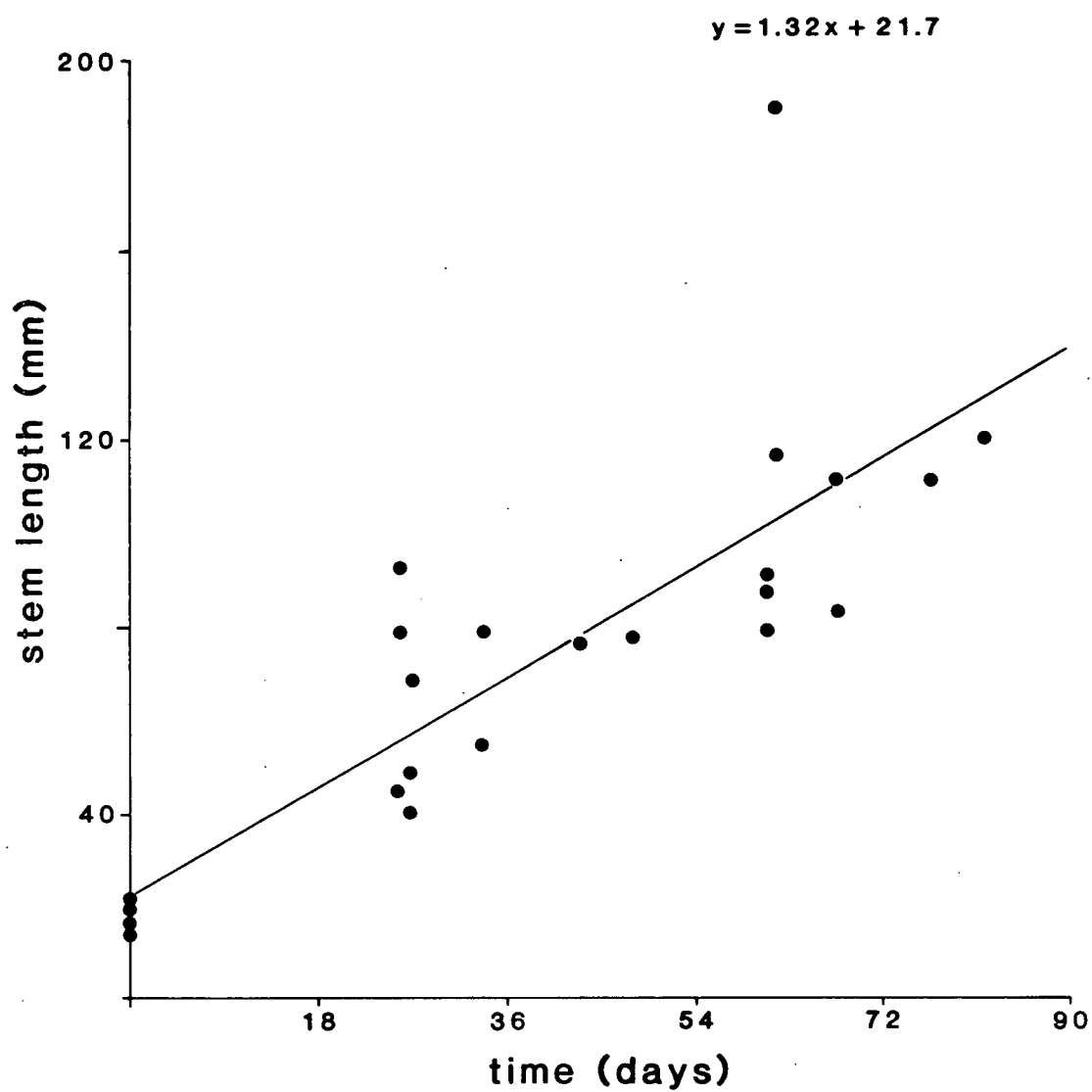


Figure 2.14b Dry season stem growth, Ajwara study site ($r^2=0.68$; $p<0.05$).

These results suggest that kob concentrate at high densities during the dry season in feeding refugia (swampy meadows) that continue to produce high protein food when other grasslands have little green growth.

In 1983 there was essentially no dry season rainfall in the kob dry season range. By contrast, in 1982 approximately 70mm of rain fell in late February, in the middle of the dry season. While this rainfall was insufficient to form new waterholes, substantial amounts of green regrowth appeared in the tall Hyparrhenia open grasslands and in the wooded grasslands. A comparison between 1982 and 1983 transect distributions suggest that kob dispersed away from the swampy meadows in response to the widespread occurrence of this unusual flush of green growth (Fig. 2.15).

Circumstantial observations from several of these dry season refugia also illustrate the importance of nearby water supplies. While the meadows continued to produce substantial regrowth, kob abandoned these areas as soon as nearby waterholes dried up (Fig. 2.16). Thus, high quality food alone was insufficient to meet kob dry season habitat requirements; they also needed nearby supplies of water.

Factors affecting forage abundance

Dry season grass growth rates in swampy meadows depended on residual soil moisture (Fig. 2.17; ANOVA, $F=16.0$, $p<0.05$). Totally saturated soils were approximately 40% water by weight. Tall Hyparrhenia wooded grasslands surrounding swampy meadows

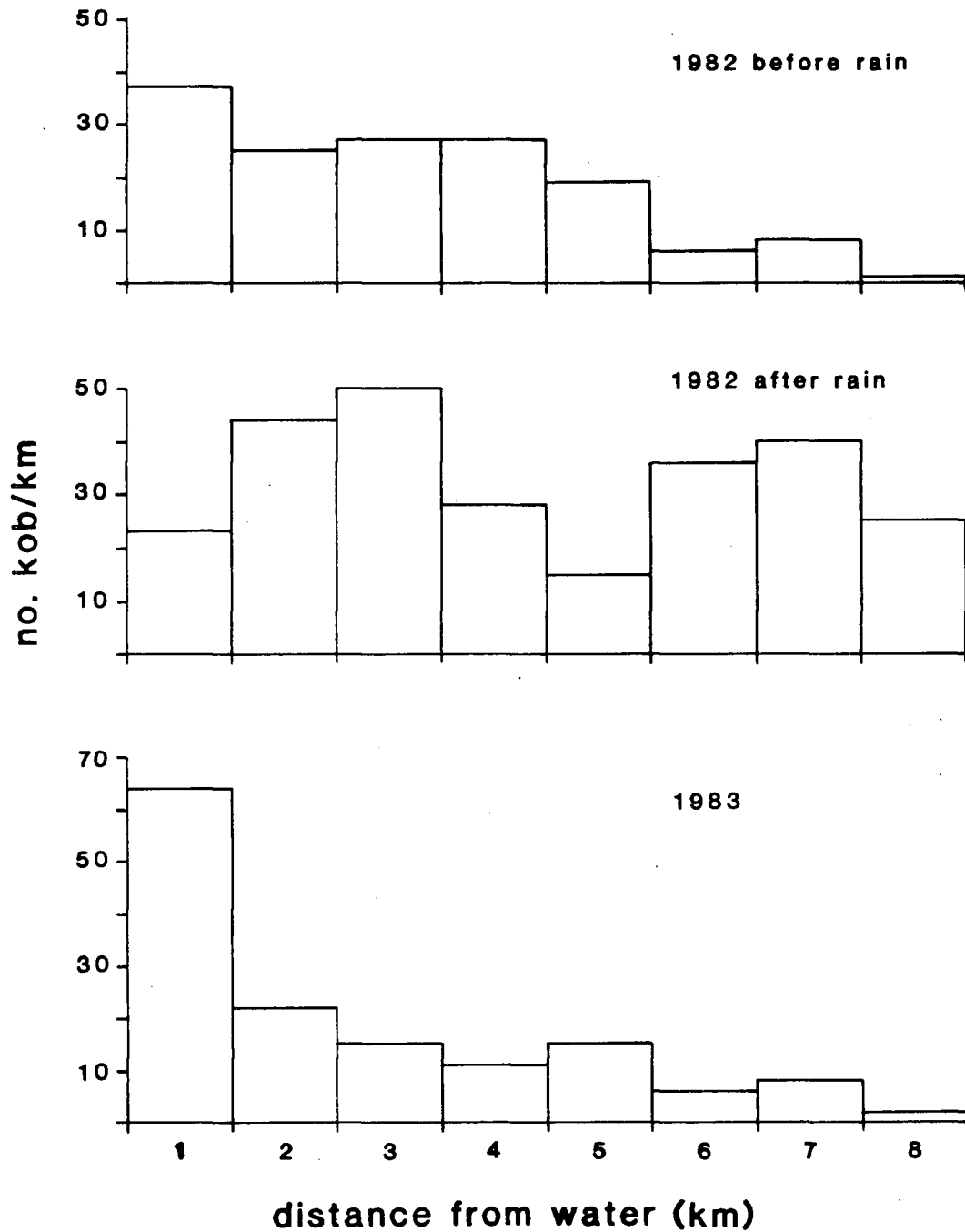


Figure 2.15 Kob aggregation near meadows, as affected by dry season rainfall. Data from 25km transects show that kob dispersed away from meadows following 70mm of rainfall in the 1982 dry season. In 1983, kob remained concentrated near meadows throughout the dry season.

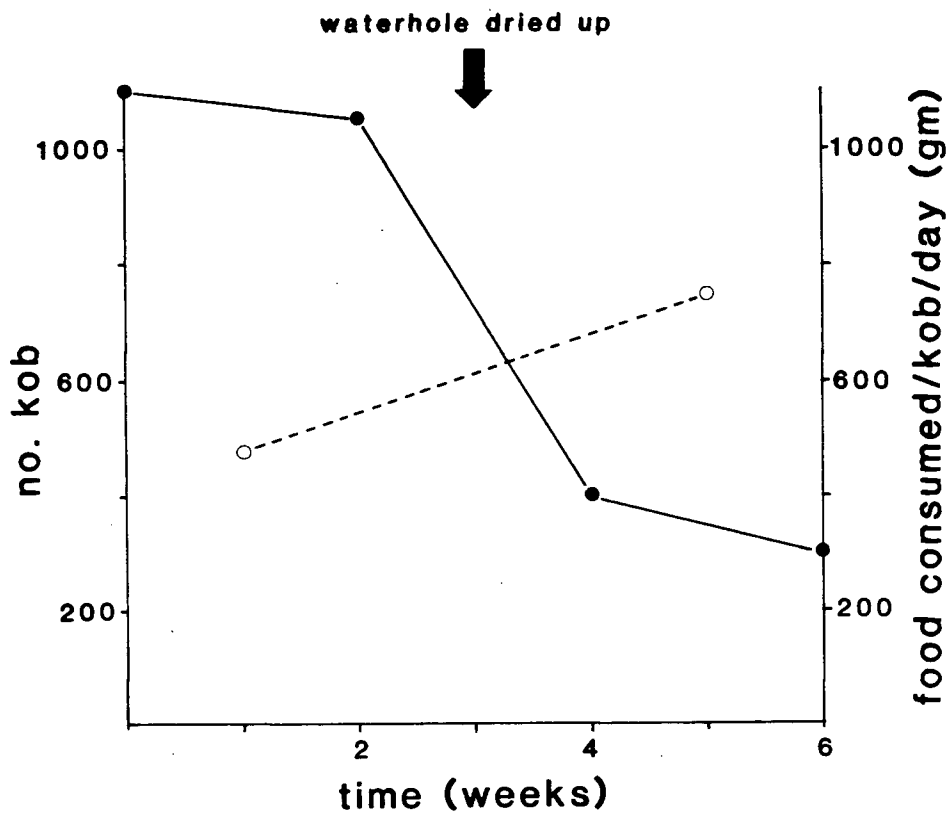


Figure 2.16 Kob abandonment of meadows following disappearance of water supplies. The mean number of kob present on meadow declined following evaporation of the central water hole (solid line), despite the fact that food intake over the same period was increasing (broken line).

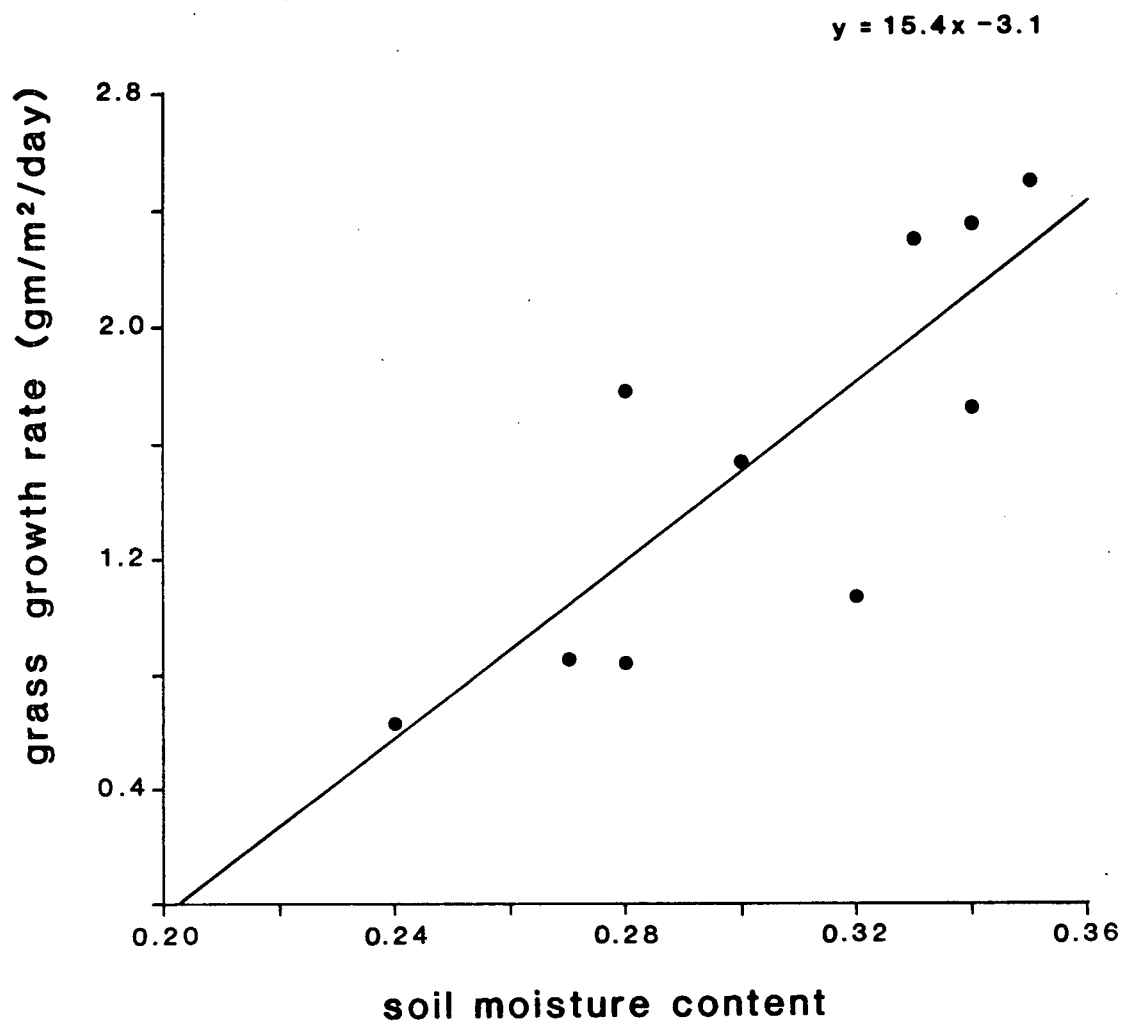


Figure 2.17 Dry season stoloniferous grass growth rate as a function of soil moisture content, Ajwara study site ($r^2=0.86$; $p<0.05$).

had soil moisture values of less than 18% during the dry season and none of the exclosures in the wooded grasslands produced dry season grass re-growth. Soil moisture declined even in the meadows over the course of the dry season (Fig. 2.18; ANOVA, $F=17.2$, $p<0.05$).

Kob maintained a uniformly short sward (stems < 25mm) in the swampy meadow areas: new regrowth was immediately utilized as forage. This explains why the dry season grass biomass in meadows was little different from the unproductive surrounding wooded grasslands.

While new regrowth occurred over the entire meadow, kob concentrated their feeding close to the margins of drying waterholes (Fig. 2.19; males: $\chi^2=212.7$, $p<0.01$; females: $\chi^2=788.2$, $p<0.05$). Since grass growth was related to soil moisture content, kob probably concentrated in those areas in order to exploit faster growing grasses, although I have no data to test this directly. Females showed a greater tendency to concentrate close to the water margin than did males ($\chi^2=39.2$, $p<0.05$).

Feeding selection for plant parts

Comparisons between grass structure inside and outside exclosures suggest that at times kob selected for certain parts of the grass plants (Table 2.5). When feeding on young tall grasses (1-2m), kob selected green leaves but fed little on stems. However, kob fed on both stems and leaves of stoloniferous grasses. There was a small difference in protein

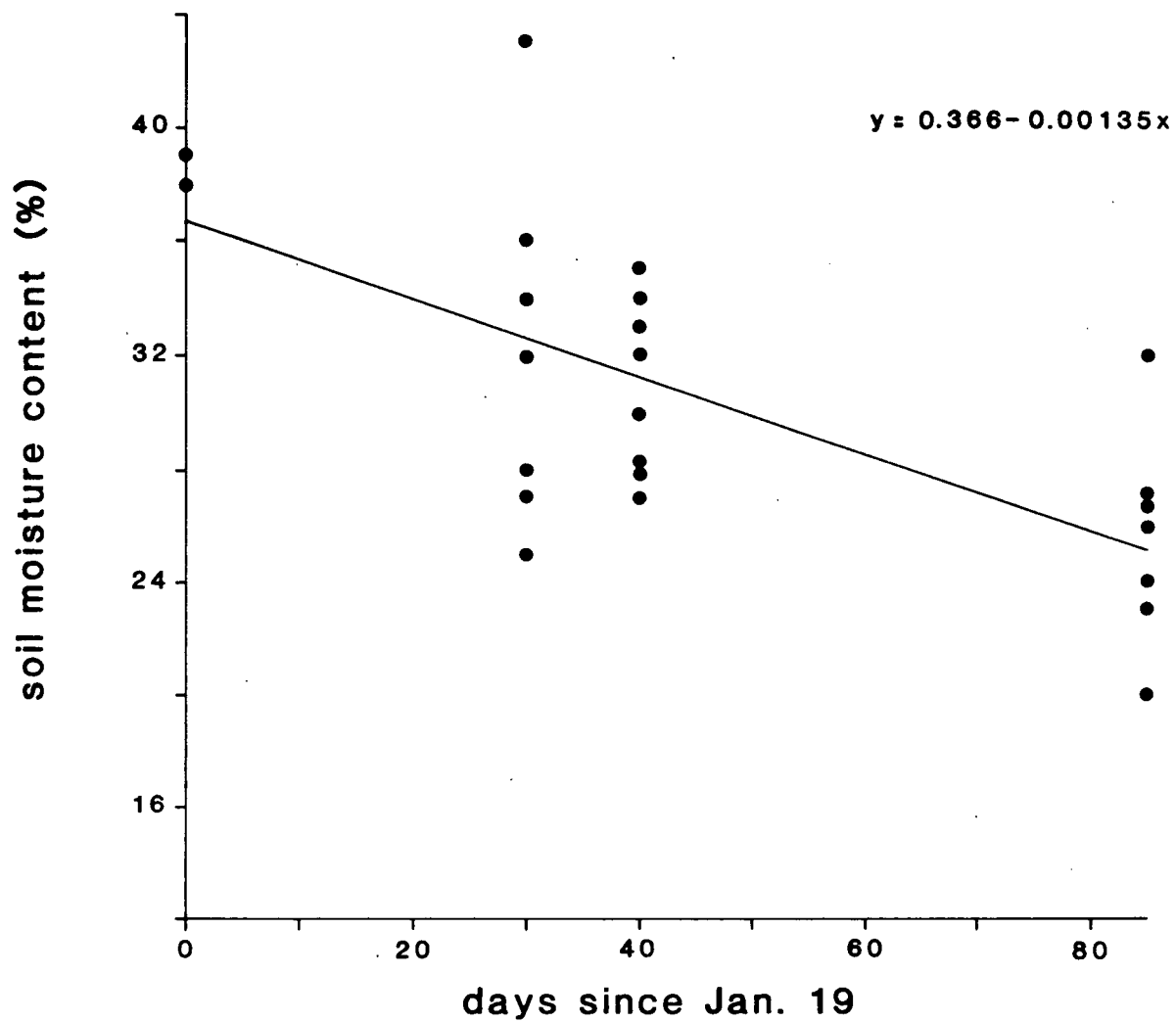


Figure 2.18 Soil moisture decline over the dry season in meadows at the Ajwara study site ($r^2=0.44$; $p<0.05$).

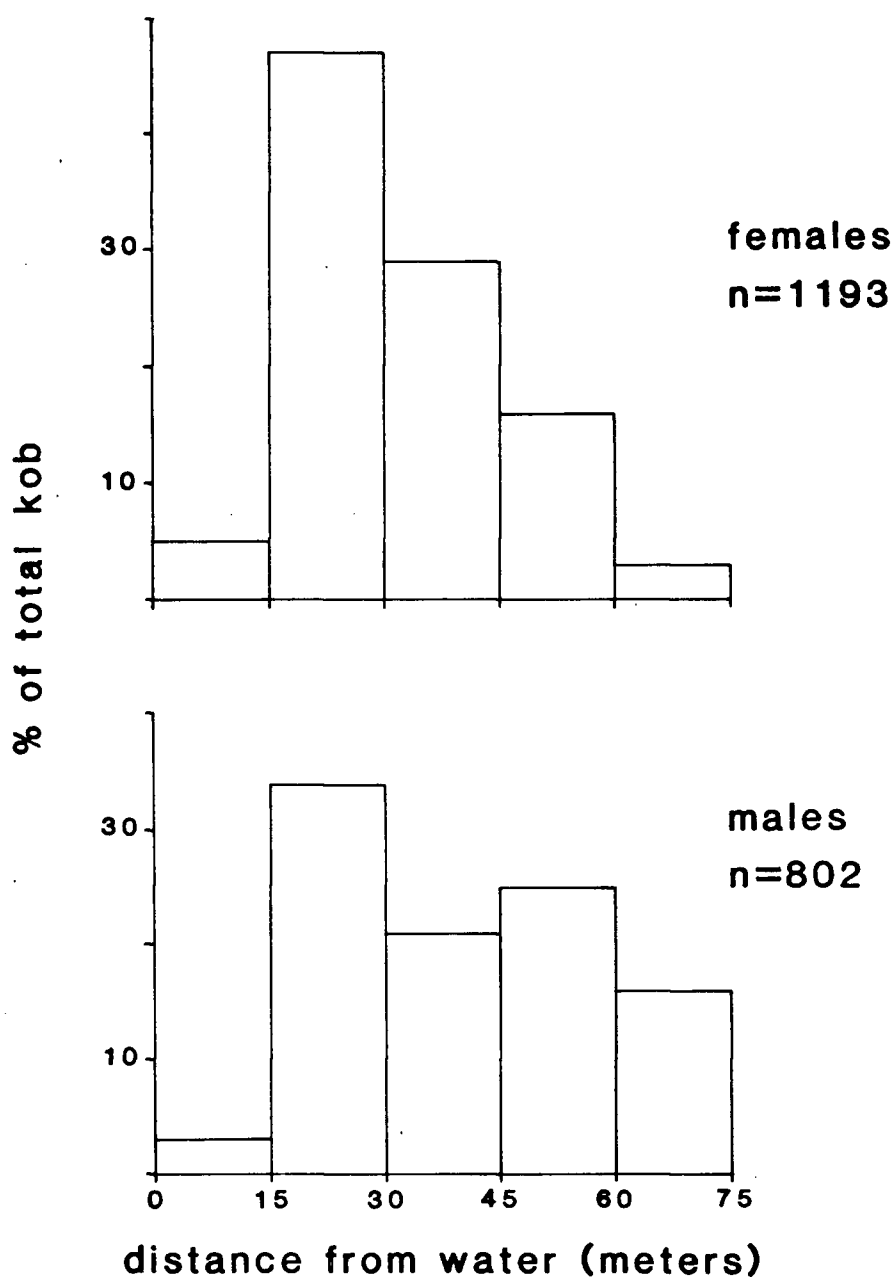


Figure 2.19 Kob feeding concentration near drying waterholes, Ajwara study site. Although both sexes concentrated in the region 15-30m from the water's edge, this tendency was most pronounced in females ($\chi^2=39.2$; $p<0.05$).

Table 2.5 Kob dry season feeding selection for leaf vs. stem tissue. There was no significant difference in tall grass stem lengths inside and outside exclosures, while there were significant differences in the lengths of tall grass leaves, short grass stems, and short grass leaves (t-tests; $p < 0.05$).

plant part	mean stem or leaf length		t
	inside	outside	
tall grasses stems	961 $\pm$ 235	874 $\pm$ 180	1.3 , n.s.
tall grasses leaves	175 $\pm$ 20	31 $\pm$ 4	30.4 , *
short grasses stems	137 $\pm$ 14	22 $\pm$ 4	20.3 , *
short grasses leaves	290 $\pm$ 23	36 $\pm$ 6	27.5 , *

content between stoloniferous grass stems and leaves (Table 2.4). However, Owen-Smith (1982) has documented elsewhere a substantial difference in protein content and digestibility between leaves and stems of tall grasses. Thus, kob apparently selected leaves when feeding on tall, presumably highly lignified grasses while they showed no such selection when feeding on stoloniferous grasses.

Food availability relative to kob requirements

There is little information available on food requirements of free-ranging African ungulates, so I estimated kob food requirements from data on domestic sheep, which are similar to kob in size and feeding habits. The maintenance energy requirements of rams and non-lactating ewes is $536 \text{ kJ/W}^{0.75}$ (NRC 1975). During lactation, energy requirements increase to $1335 \text{ kJ/W}^{0.75}$. The energy content of stoloniferous grass during the dry season was 16.53 kJ/gm ($n=21$; $SE=0.042$) and the dry matter digestibility was 42.3% ($n=14$; $SE=2.1$). Thus, the digestible energy available in forage was 6.94 kJ/gm ($=16.53 \text{ kJ/gm} \times 0.42$). The ratio of energy required over digestible energy available provides an estimate of minimum forage requirements (Demment and Van Soest 1985). On this basis, males should require 1.56 and non-lactating females 1.23 kg of forage per day. A large proportion of kob females continued lactating throughout the dry season (Chapter 4). These females would require 3.08 kg/day to meet their energy needs.

Kob daily food intake during the 1983 dry season averaged

0.93 kg/individual ($n=5$; $SE=0.20$). This rate of food intake was significantly less than requirements of males ($t=-3.15$; $p<0.05$) and lactating females ($t=-10.80$; $p<0.05$), but not of non-lactating females ($t=-1.49$; n.s.). Thus, even though kob selected the best feeding locations available in the dry season range, they were still unable to meet their daily forage requirements.

A series of simple calculations indicates that food availability during the wet season probably exceeded kob requirements. The green biomass available in the early wet season range was approximately 0.13kg/m^2 . Since kob were distributed over an area of 1500km^2 for no more than 90 days, the food available per individual per day was at least 2.7kg, or almost twice the daily kob requirement. This is a conservative estimate, since it ignores grassland productivity during the wet season and the possibility of kob foraging in adjoining areas. Similar calculations in the late wet season indicate that food availability was at least $4.2\text{kg/individual/day}$. While other factors, such as sward structure (Bell 1971), might constrain actual forage availability, these calculations demonstrate that, in theory, there was sufficient green biomass available during the wet season to meet kob energetic needs.

Discussion

Seasonal changes in resource distribution

It has been often assumed that the tropics are less seasonal than temperate regions (Dobzhansky 1950). This is untrue, particularly in tropical savannahs. While annual temperature variation is often minor, most tropical savannahs have marked seasonal variation in rainfall. In Africa, rainfall seasonality is linked to trans-equatorial movements of the Inter-Tropical Convergence Zone (ITCZ). Resultant shifts in wind patterns produce increased rainfall in the wake of the ITCZ.

As a result of highly seasonal rainfall, resources essential to the white-eared kob population varied considerably in distribution and abundance. In this study, both green forage and water supplies became increasingly restricted during the dry season. During the wet season, abundant supplies of both forage and water were available throughout the Boma region.

There was a north-south gradient in annual rainfall and peak green biomass in the Boma ecosystem. During the wet season, green biomass was highest in the north and lowest in the south. During the dry season, swampy meadows that produced continued grass re-growth occurred along the major northern watercourses, as well as permanent water supplies. Little green grass or water was available elsewhere during the dry season.

These results are consistent with the first two predictions

outlined at the beginning of this chapter. Both food and water were unevenly distributed throughout the ecosystem, as a result of an increasing rainfall gradient from south to north. Resource abundance exhibited pronounced variation throughout the year because of seasonal climatic changes.

Seasonal kob migration

The Boma white-eared kob population migrated each year from southern wooded grasslands in the wet season to the northern Neubari/Oboth River system in the dry season. Comparisons between observations from this study and anecdotal observations by early European visitors to the Boma region suggest that the migratory phenology has changed little since the 1940's (Cave and Cruikshank 1940; Lyeth 1947; Weeks 1947; Anderson 1949; Zaphiro 1949). As well, all observers commented on the extraordinary numbers of kob in the migratory herds, suggesting that kob have been abundant in the region for at least forty years. Finally, these historical records of kob migration were all from southern areas, but in widely separated locations. This suggests that the wet season range may vary in location from year to year. Since kob concentrate in the dry season along one specific river system, one would expect the dry season range to vary comparatively little in location from year to year.

During the dry season, permanent water supplies were chiefly restricted to the Neubari/Oboth River system. Kob concentrated in locations adjoining this watercourse,

particularly in the Gom Swamps. Dry season movement towards permanent water supplies was consistent with Western's (1975) hypothesis that most grazers must migrate seasonally in order to obtain sufficient water supplies. Laboratory trials indicate that the conspecific Uganda kob requires water on a daily basis (Schoen 1971).

However, within their dry season range, kob concentrated at high densities (over 1,000/km²) in feeding refugia that produced nutritious regrowth throughout the dry season when surrounding grasslands showed little green biomass. Many of these swampy meadows were old meander channels of the Oboth River that have been subsequently cut off from the main flow. These low-lying depressions remained flooded longer than surrounding tall Hyparrhenia grasslands. As a consequence, the soil in the meadows retained moisture longer than surrounding soils. This residual soil moisture supported substantial regrowth of stoloniferous grasses high in protein throughout the dry season. Thus, migration to ephemerally swamped grasslands during the dry season ensured the availability of both nutritious forage and water when these resources were scarce elsewhere in the ecosystem. These findings are consistent with my third prediction, that kob distribution should be correlated with resource abundance.

During the wet season, however, kob migrated south into low rainfall areas that supported lower biomasses of green forage than in the north. This is inconsistent with the hypothesis that migration facilitates the exploitation of shifting

distributions of important resources. Why don't kob simply remain in the northern grasslands on a year-round basis? I suggest that kob can not do so because much of the north becomes flooded during the wet season. Kob exhibited signs of restlessness following extensive rains, even during the dry season, as was seen in February 1982. Following 70mm of rainfall, kob aggregated into larger groups and began moving in columns southwards, vacating areas that several days previously had supported upwards of 1000 individuals per km². When these temporary rains ceased, kob returned in large numbers to the swampy meadows in the north. By contrast, in February and March of 1983, northern areas received no rain, while 50mm of rain fell around the Boma plateau, producing luxuriant grass regrowth. Kob showed no signs of migratory restlessness until the north received heavy rains in the middle of April. Thus, kob may utilise the onset of rains in their location as the proximate cue to begin the migration south. These observations are consistent with the hypothesis that kob vacate northern areas in order to avoid waterlogged soils and surface flooding.

The fourth prediction outlined at the beginning of this chapter is that kob should remain in a given location only as long as food and water resources are more abundant than in surrounding areas. Dry season observations were consistent with this prediction, since kob dispersed away from swampy meadows either when nearby water supplies dried up or when dry season rainfall produced new green re-growth (with presumably high protein content) in surrounding Hyparrhenia grasslands.

In conclusion, kob movements from the wet season to dry season ranges apparently tracked increasingly scarce supplies of both food and water. However, wet season movements were inconsistent with the resource exploitation hypothesis, since kob moved into grasslands with lower green biomass and less abundant water supplies than the areas they had left. It seems likely that another factor, such as avoidance of surface flooding, explains this southward migration.

Benefits of migration

Numerous studies suggest grazers can improve their nutritional intake by selective feeding. Studies on domestic stock suggest that the rate of food intake is related to the protein content of forage, due to effects on forage digestibility, rumen retention time, and possibly appetite suppression (Laredo and Minson 1973; Reid et al. 1973; Egan 1977). This is particularly important in savannah grasslands because tropical grasses generally have lower digestibilities than temperate grasses (Minson and McLeod 1970; Reid et al. 1973). Grazers have minimum forage protein requirements below which they begin to lose weight, because they are forced to metabolize their own body reserves to compensate for nutritional insufficiency (Chalmers 1961; Bredon and Wilson 1963).

Pastoralists living in the Boma region also migrate with their cattle herds between wet season ranges west of the Pibor River to the Kong-kong River and Gom Swamps during the dry

season. Similar pastoralist migrations were once common in much of the Sahel region of Africa (Sinclair and Fryxell 1985). Thus, traditional methods of animal husbandry, presumably designed to maximize secondary production, apparently mimic evolved behaviors in natural herbivore populations. These findings suggest that migration is a particularly successful strategy for coping with resource scarcity in highly seasonal environments.

CHAPTER 3. FOOD LIMITATION AND KOB MORTALITY PATTERNS

Introduction

Numerous studies suggest that food availability limits many ungulate populations (Klein 1968; Caughley 1970; Bobek 1977; Sinclair 1977; McCullough 1979; Leader-Williams and Ricketts 1980; Fowler 1981; Clutton-Brock et al. 1982). Many of these studies illustrate changes in recruitment or survival rates as a function of population size (e.g. McCullough 1979; Fowler 1981; Clutton-Brock et al. 1982). However, comparatively few ungulate population studies have actually documented that resources are limiting or measured the effect on consumer populations (Bobek 1977; Sinclair 1977; Bayliss 1985; Sinclair et al. 1985). Thus, while ungulate populations do exhibit density dependent responses, there is little evidence that food limitation is responsible.

An alternative view is that herbivore populations can not be limited by food abundance because only a small fraction of potentially edible food is ever consumed (Hairston et al. 1960; Slobodkin et al. 1967; Van Valen 1973). Moreover, at least some large-mammal populations may be maintained below the vegetation limited carrying capacity by predation (Mech and Karns 1977; Smuts 1978; Caughley et al. 1980; Gasaway et al. 1983), or disease (Christian et al. 1960; Sinclair and Norton-Giffiths 1979; Berry 1981).

If white-eared kob are limited by food availability, I

predict the following:

1. Survival and/or recruitment rates should decline during years of limiting food abundance and during seasonal periods of food scarcity.
2. There should be a direct correspondence between body condition indices and survival rates.
3. Survival in specific locations should be positively correlated with food availability.

In this chapter I examine these predictions. First, I consider trends in population numbers and age structure of the population in relation to a large-scale drought that occurred in 1980, immediately preceding this study. Second, I report on field observations of mortality and recruitment of yearlings for 1982 and 1983. Third, I relate dry season mortality rates to rates of food intake and indices of body condition. Finally, I compare my findings against the predictions of the food limitation hypothesis.

Methods

Population density

I recorded population density and carcass numbers at four study sites, from February to April, 1982 and at five study sites from January to April, 1983 (Fig. 2.2). Population numbers were estimated in two ways: at the Ajwara study site I counted total numbers of kob present at various times throughout

the day on a 0.5km² grassy meadow; at all other study sites I estimated population density from 5 km transects that bisected each study site. Two observers stood in the back of a moving vehicle, counted animals seen within a 100m strip either side of the vehicle, and recorded all observations at 0.1km intervals into a tape-recorder. The driver maintained a straight course and called out 0.1km intervals to the observers.

Strip width was estimated during transects, following calibration with a range-finder at the outset of each transect. Observers were consistently able to estimate the 100m strip width to within 10m accuracy. High population densities made the use of a range-finder impractical during transects, but bias introduced by inclusion of animals from outside the legitimate strip width was likely to be inconsequential. In order to minimize bias introduced by diurnal movement patterns (see Chapter 2), all transects were performed in the early morning (07:00-09:00). On one occasion, I performed 4 replicate transects throughout the day, to test the repeatability of the density estimates. Since totals varied relatively little between these replicates (coefficient of variation = 0.28), I assume that transects were a reliable index of kob population density.

Carcass density

Carcass density was determined in two ways. At Ajwara, total counts of carcasses were made over a 0.5km² area by a team of four observers on foot, separated by distances of 40 meters.

Thus, each observer was responsible for searching a strip 20 meters to either side. All carcasses encountered were marked with a numbered strip of red tape around a horn or limb. Of the marked adult carcasses, 61% were subsequently recovered 6 weeks following initial observation, while 39% of carcasses of calves were recovered, suggesting that while many carcasses remained from survey to survey, mortality estimates were biased downwards by carcass disappearance or mutilation by scavengers.

At all other study sites, carcasses were counted during 5km transects, by a two observer team from the back of a moving vehicle. In all cases, carcasses were counted along the same transect lines used for live population density estimates. I measured distance to each carcass using a tape measure, and all carcasses located outside 50 meters were disregarded in subsequent analyses.

Weekly mortality rates (m) were estimated by:

$$m = c / n t$$

where,

m=finite weekly mortality rate

c=number of carcasses/km² since previous survey

n=mean kob population density

t=time in weeks

Sex and age distribution

At regular intervals throughout the 1982 and 1983 dry seasons, I recorded sex ratio, calf/female ratio, and proportions of yearling and 2-year old males from large groups of kob. Sexes were easily distinguished since mature males have dark brown to ebony pelage and lyre-shaped horns, while females are hornless and tawny brown in color. Yearling males have short straight horns as long as the ears (Buechner 1974) and are slightly smaller than females. Two-year old males are larger than females (Fig. 6.3) and have slightly curved horns two to three times as long as the ears (Buechner 1974). Both yearling and 2 year old males are similar in color to females.

I estimated age structure of the population older than 2 years from a random shot sample of 38 individuals, since I could detect no visible differences between adults of different age. The usual hunting protocol involved selecting a group of kob from which to sample, slowly approaching in a vehicle, and then shooting the nearest animal of the sex I wanted. High population densities and ease of approach made sampling unusually simple. Under the circumstances, I consider it unlikely that hunter preference or avoidance behavior by certain sex or age classes greatly biased the results. I estimated the ages of 155 kob (from both the shot sample and from carcasses) by counting the cementum annuli from first incisors and first molars.

Tooth cementum lines

Whole teeth used for counting cementum annuli were first fixed in 10% formalin for five minutes prior to shipment from the field. They were then decalcified in 5% nitric acid until they reached a rubbery consistency (3-5 days) and immediately cut into 10-15 micr thick longitudinal sections through the pulp cavity, using a freeze microtome. After air drying for 24 hours, teeth were stained in Harris haematoxylin for 4 minutes, rinsed in tap water for 4 minutes, bathed in Scott solution for 3 minutes, and finally rinsed in tap water again for 4 minutes. After air drying for 24 hours, slides were then mounted in Permount.

I examined tooth sections under a compound microscope at both 10x and 40x magnification. The three clearest sections out of at least 9 sections per tooth were counted and recorded. A mean annuli count was determined for each tooth and rounded to the nearest whole number. Ring counts from yearling kob indicate that the first cementum rest line is laid down during the dry season following birth, thereafter followed by a single line per year. Cementum line counts required some degree of judgement, since lines were frequently difficult to distinguish. In order to assess the reliability of the technique, I recounted cementum lines from a random 20% sub-sample of the initial 155 individuals that were aged. Close correlation between the two counts ($r^2=0.85$, $p<0.05$) indicated that counting criteria remained consistent throughout the study.

Post-mortem examination

All shot animals and fresh carcasses encountered along transects were subjected to post-mortem examination. I weighed the total carcass, rumen (with and without contents), and the remaining alimentary tract using a spring balance. I measured head-tail length, heart girth, shoulder height, and tibia length. I also measured the horn length and distance between horn tips for all males.

Body condition in ungulates is commonly assessed by measurement of the fat content of bone marrow (Sinclair and Duncan 1972; Hanks 1981; Riney 1982). I estimated the fat content of femur bone marrow using a modification of standard procedures (Hanks 1981; Riney 1982). First, I extracted 5-10 gm of bone marrow from the center of the femur. This sample was weighed in an aluminum tray prior to being heated for a set time over hot coals. This procedure evaporated all the water present in the bone marrow sample, leaving a residue of fat and protein. Since mobilized marrow fat is replaced by water, the ratio of post-heating weight over pre-heating weight reflects the bone marrow fat content. Preliminary trials indicated little subsequent weight change following the first 5 minutes of heating; thereafter 5 minutes was maintained as a standard.

Results

Age distribution in the live population

The distribution of ages in the 1983 live population is shown in Fig. 3.1. Data were pooled from both sexes, due to the small sample size. Individuals 5 to 7 years formed the largest age classes. No individuals older than 10 years were found in the shot sample, although individuals up to 13 years old were observed among carcasses. Frequency of the 3 year age class was somewhat smaller than adjacent age classes. Recruitment of young to age 1 was approximately 10% of the total population in both 1982 and 1983.

Age distribution at death

The age distribution of carcasses (Fig. 3.2) was somewhat similar in shape to the standing age distribution. The most frequent age classes were from 5 to 7 years. However, subadults and young adults (1-4 years) were less common among carcasses than in the live population, while older age classes were more common.

Age distribution at death differed between sexes (Fig. 3.3, $\chi^2=15.0$, $p<0.01$). A greater proportion of 4 to 7 year old males died than similar aged females. Conversely, smaller numbers of old males were found than old females. These differences suggest that males suffered significantly greater

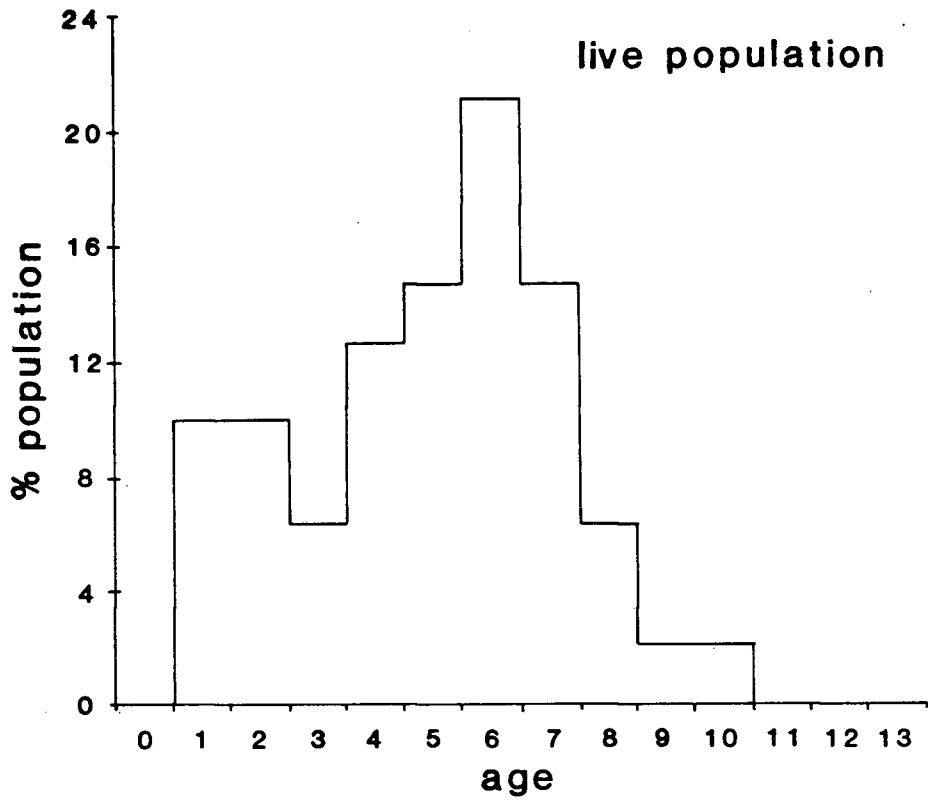


Figure 3.1 Age structure of the 1983 live population (1 year and older). Frequencies of individuals aged 1-3 estimated directly from observations of herd composition. Frequencies of age classes 3 years and older estimated from a random shot sample. Data from both sexes pooled (n=38).

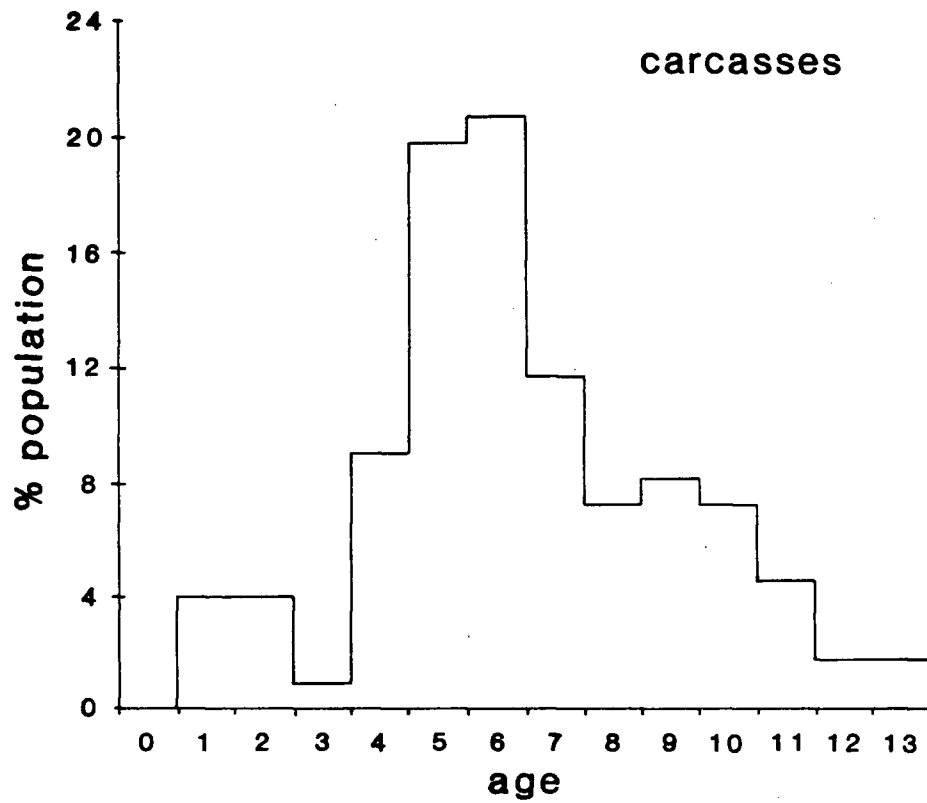


Figure 3.2 Age structure of the found carcass sample (1 year and older).
Data from both sexes pooled (n=103).

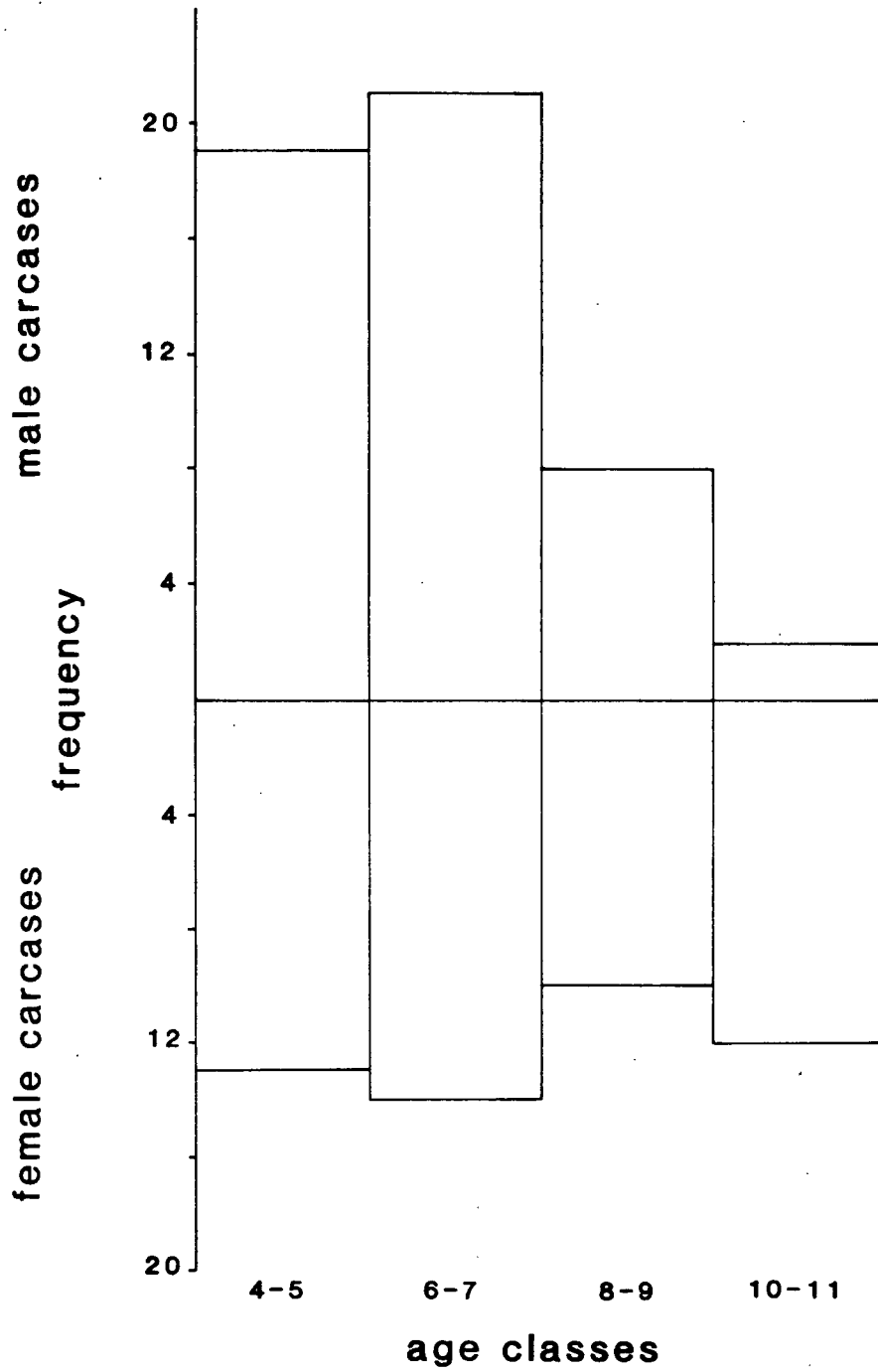


Figure 3.3 Age frequencies of male vs. female carcasses (males=50; females=45). Female total was adjusted to equal male total for statistical comparison ($\chi^2=15.0$; $p<0.05$).

risk of mortality as young to middle-age adults than females.

Age-specific mortality

The age-specific mortality, or q_x , curve is a useful means of illustrating differences in vulnerability to potential mortality agents according to age (Caughley 1966). The Boma kob q_x curve indicates high mortality of youngsters, relatively little mortality of young to middle-aged adults, and increasing mortality for older age groups (Fig. 3.4). This general form is consistent with previous published mammalian q_x curves (Caughley 1966). The curvilinear increase in q_x with increasing age appears more similar in form to published curves for domestic sheep, African buffalo, waterbuck, and dall sheep (Deevey 1947; Hickey 1963; Sinclair 1977; Spinage 1982) than the linear increase seen in thar (Caughley 1966).

Sex ratio

The sex ratio in the live population (excluding calves) in both 1982 and 1983 was skewed in favor of females (males=2550, females=3434; $\chi^2=130.8$, $p<0.001$). If we assume an equal sex ratio at birth, then mortality must differ between the sexes. Carcass totals during the dry season indicated that more males died than females. However, these results may have been biased since there was some evidence that male carcasses were more likely to be seen during transects. The frequency of both calf and female carcasses declined significantly at increasing

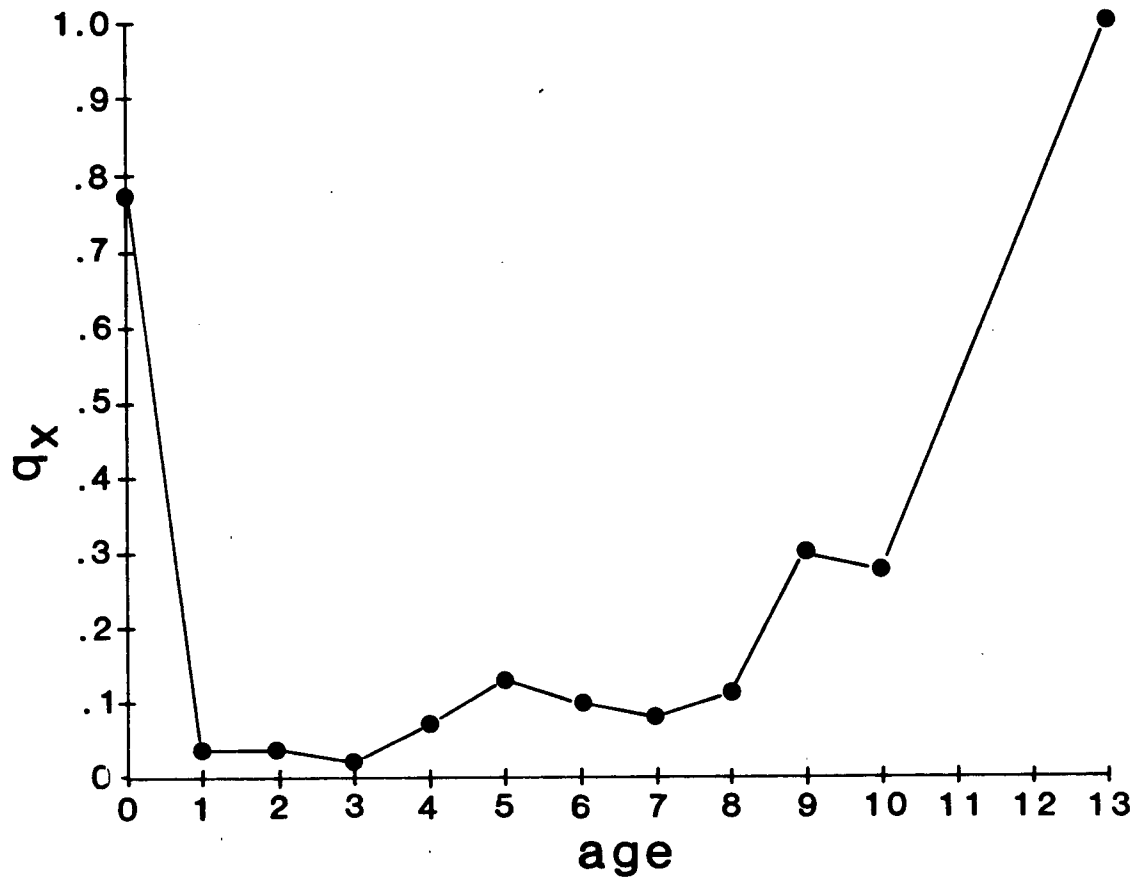


Figure 3.4 Kob age-specific mortality curve, from pooled data for both sexes. Age-specific mortality rates were calculated using equation 1, as explained in Chapter 6.

distance from the vehicle (Fig. 3.5)(females: $\chi^2=10.9$, $p<0.05$; calves: $\chi^2=96.8$, $p<0.05$), while the number of male carcasses observed at different distances from the vehicle varied little ($\chi^2=5.9$, n.s.). This suggests that males were more visible than females and calves during carcass transects, and that observed carcass totals for females and calves were biased downwards.

In order to account for this sightability bias, I multiplied carcass totals for youngsters and females by correction factors of 2.99 and 1.77^{*} respectively. These correction factors were derived by assuming that during transects all individuals less than 10m from observers were seen, consequently totals from greater distances should be equivalent in frequency to observations from the 0-10m range. After applying the correction factor, there were still significantly more male and less female carcasses than one would expect from the proportion of each sex in the live population (males=85, females(adjusted)=94; $\chi^2=4.18$, $p<0.05$). In addition, circumstantial evidence suggests that the skewed sex ratio in the live population may also result from preferential hunting of kob males by local tribesman. During 2 communal hunts that I observed, significantly more males and less females were taken than expected (males=134, females=72, $\chi^2=54.8$, $p<0.001$). These results suggest that the skewed sex ratio in the live population results from differential natural and hunting mortality between sexes.

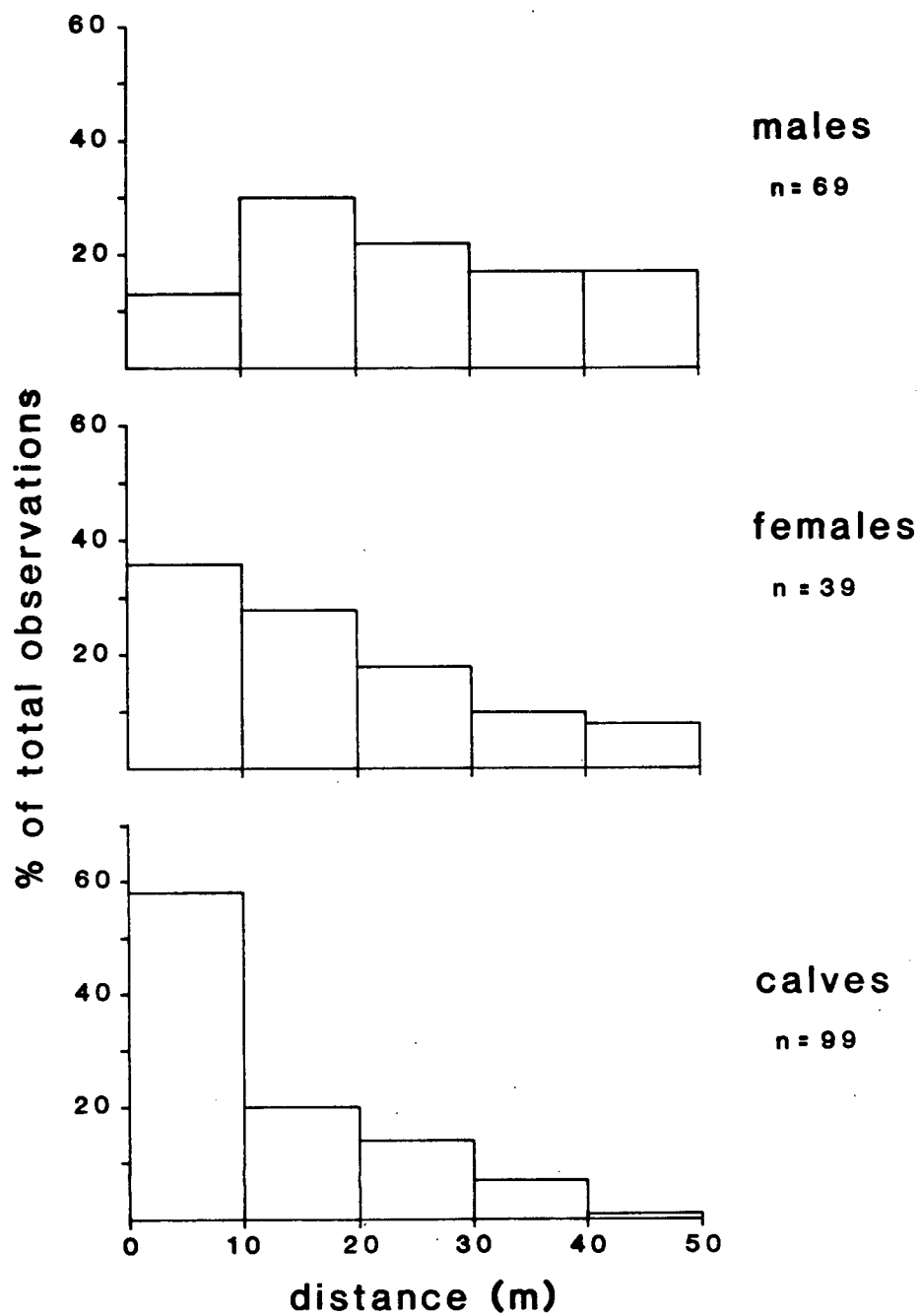


Figure 3.5 Numbers of carcasses observed at increasing distance from observers.

Seasonal changes in body condition

Several previous studies indicate that when ungulates are unable to maintain adequate food intake their fat reserves decline (Hanks 1981). Animals first use up their subcutaneous fat reserves, before mobilizing bone marrow fat at advanced stages of emaciation (Sinclair and Duncan 1972; Hanks 1981).

Body condition, as measured by bone marrow fat content, declined dramatically during the course of the 1983 dry season (Fig. 3.6b; Kruskal-Wallis, $H=16.4$, $p<0.05$). Males remained in comparatively better condition than females (Mann-Whitney, $U=90$, $p<0.05$), but both sexes showed similar rates of decline in body condition. Bone marrow fat content in carcasses compared to shot individuals suggests that individuals in poorest body condition were also the most likely to die. Decline in body condition probably reflects submaintenance supplies of high protein food; thus, stressed individuals were forced to mobilize body fat reserves to meet metabolic requirements.

Indices of body condition in the dry season differed between years. In 1982 (Fig. 3.6a), body condition indices did not decrease to levels seen in 1983 (Fig. 3.6b). In 1982, unusual amounts of rainfall (over 70mm) fell in late February, during the middle of the dry season. This rainfall produced a temporary flush of green growth over large areas in the kob dry season range (Chapter 2). Increased abundance of green grass resulting from this unusual dry season rainfall in 1982 may have increased kob green forage intake, preventing the precipitous decline in fat reserves seen in 1983.

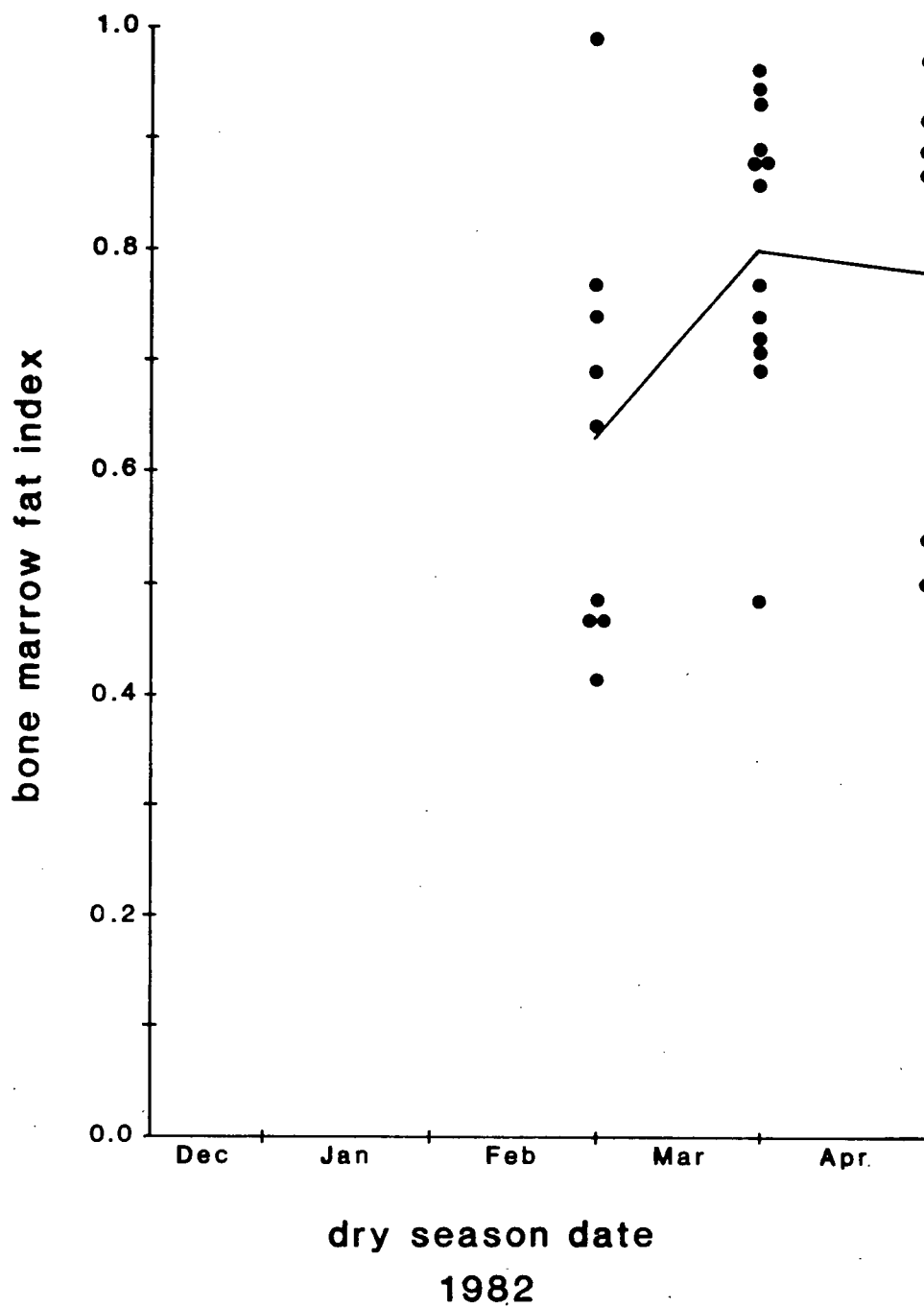


Figure 3.6a Dry season measurements of bone marrow fat content (1982). Data combined for both sexes. Solid line connects monthly mean values.

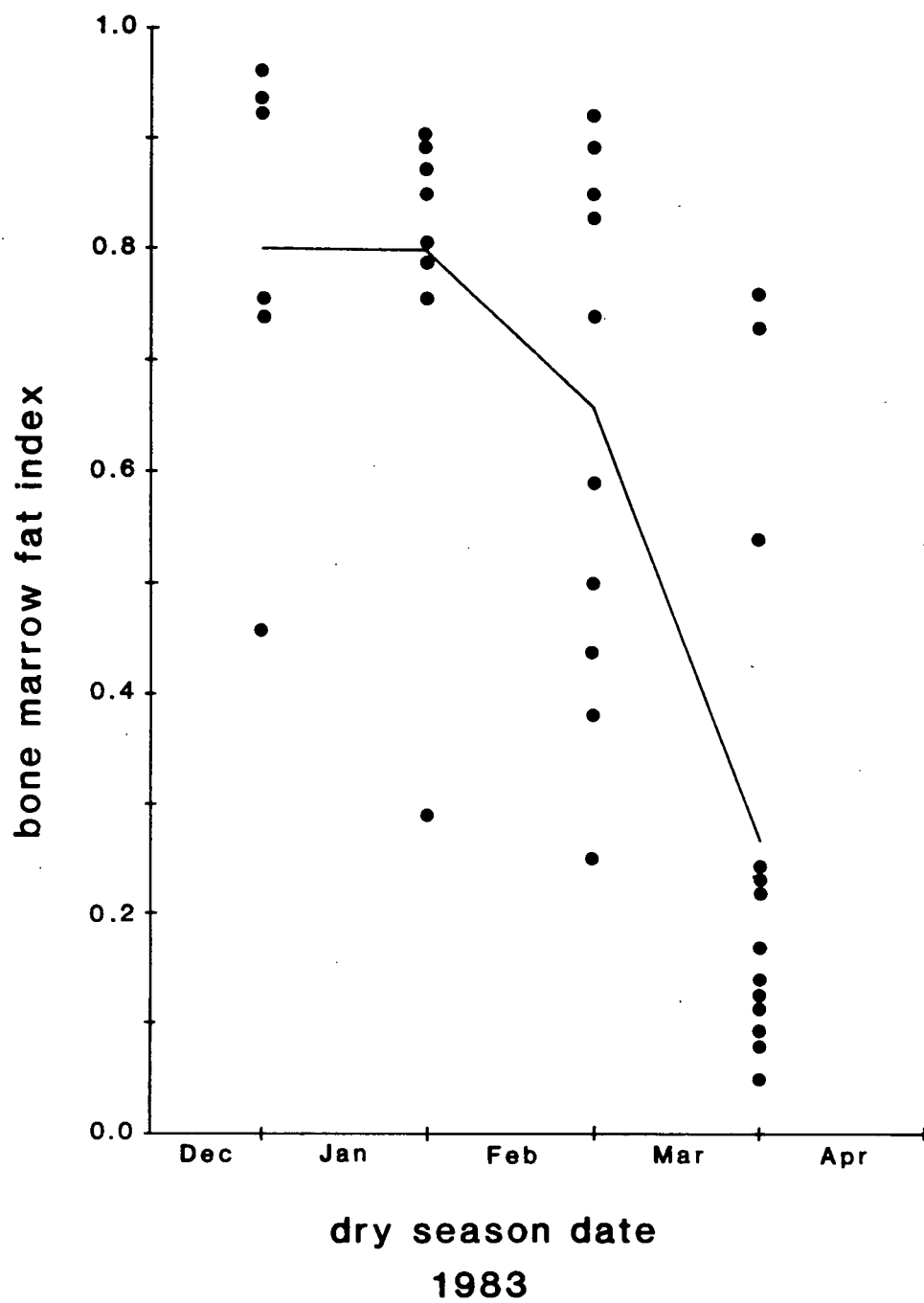


Figure 3.6b Dry season measurements of bone marrow fat content (1983). Data combined for both sexes. Solid line connects monthly mean values.

Seasonal changes in mortality rates

Weekly mortality rates for different localities and periods during the dry seasons of 1982 and 1983 are given in Table 3.1. During the 1982 dry season, adult mortality rates, expressed as a proportion of the initial adult population, varied between 0.0030 and 0.0044 per week, while 1983 values ranged from 0.0027 to 0.0195 per week. Calf mortality rates varied from 0.0070 to 0.0779 per week in 1983. Thus, there was a four fold difference in weekly mortality rates between calves and adults.

Adult mortality rates in the dry season differed between years. The mean weekly mortality rate in the 1982 dry season (0.0039) was significantly lower than the mortality rate in 1983 (0.0076) (Table 3.1; Mann-Whitney, $U=7$, $p<0.05$). This is consistent with the hypothesis that the dry season produces stressful conditions that are reflected in elevated mortality rates. The unusual dry season rainfall of 1982 caused increased production of green grass over much of the dry season range, which led to improved body condition and decreased adult mortality rates.

In 1983, mortality rates of adults increased significantly over the course of the dry season (Table 3.1; Mann-Whitney, $U=6$, $p<0.05$). Data from the most intensively monitored study site, Ajwara, illustrate this trend (Fig. 3.7). Adult mortality rates at Ajwara increased by a factor of 4 during the course of the dry season, at an apparently constant rate of increase. Estimates of calf mortality suggest a similar trend although not statistically significant (Table 3.1, Mann-Whitney, $U=3$, n.s.).

Table 3.1 Dry season weekly mortality estimates (1982 and 1983). Mean adult mortality rates differed between years (Mann-Whitney; $U=7$; $p<0.05$), but there was no significant difference between calf mortality rates in the 2 years.

location	date	adult weekly mortality rate	calf weekly mortality rate
Gom	Feb.-March 1983	0.0032	0.0155
Gom	March-April 1983	0.0068	0.0627
Wangchira	Jan.-Feb. 1983	0.0061	0.0650
Wangchira	Feb.-March 1983	0.0195	0.0741
Neubari	Jan.-Feb. 1983	0.0027	n.a.
Neubari	Feb.-March 1983	0.0054	n.a.
Ungwala	Jan.-Feb. 1983	0.0061	n.a.
Ungwala	Feb.-March 1983	0.0060	n.a.
Ajwara	Jan. 1983	0.0054	0.0070
Ajwara	Feb. 1983	0.0081	0.0779
Ajwara	March-April 1983	0.0143	0.0634
		$\bar{x} = 0.0076$	$\bar{x} = 0.0522$
		SE = 0.0032	SE = 0.0245
Ajwara	Jan.-Feb. 1982	0.0030	0.0206
Ajwara	March-April 1982	0.0039	n.a.
Gom	Jan.-Feb. 1982	0.0043	0.0508
Ungwala	Jan.-March 1982	0.0044	n.a.
		$\bar{x} = 0.0039$	$\bar{x} = 0.0357$
		SE = 0.0009	SE = 0.0107

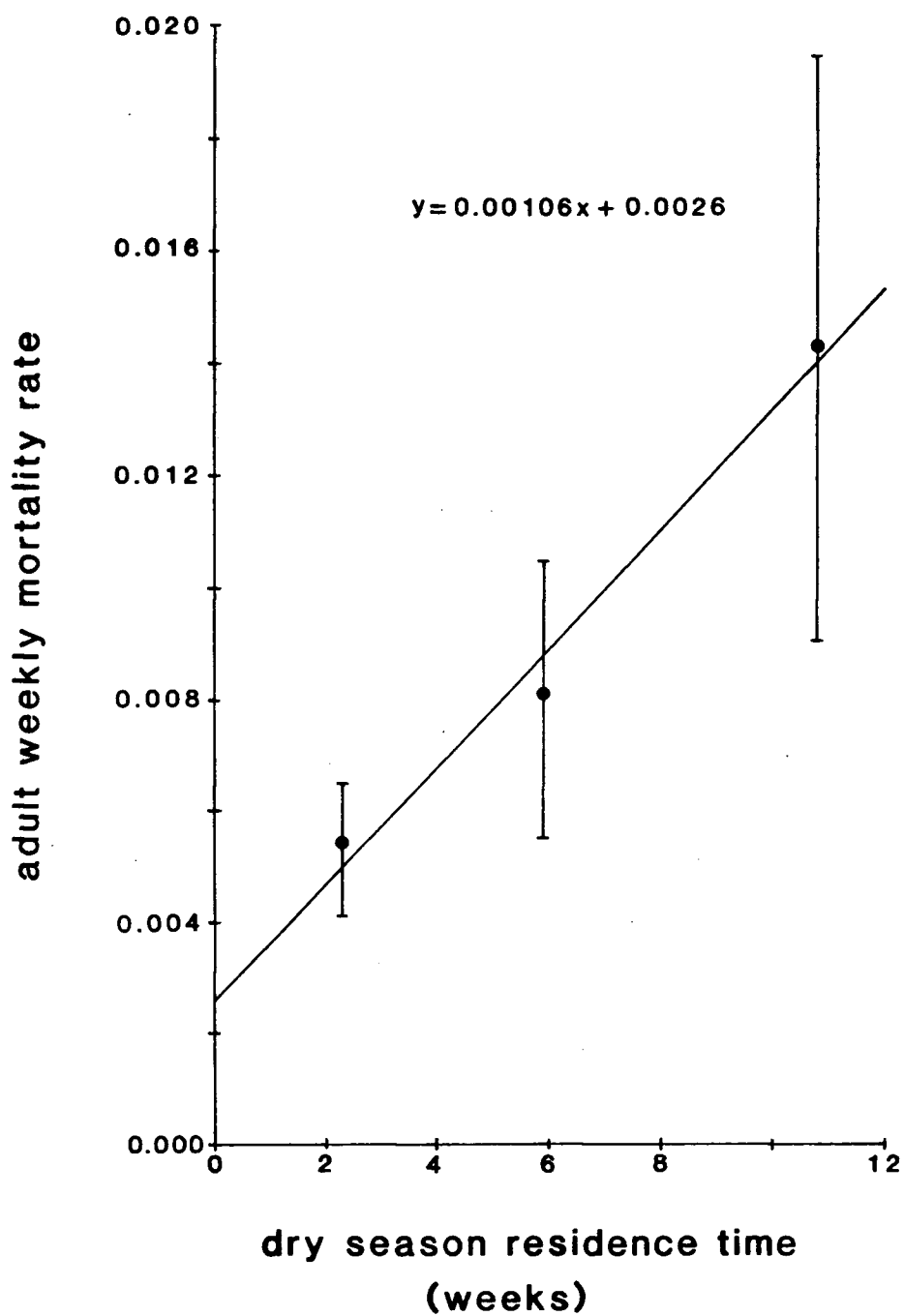


Figure 3.7 Dry season adult mortality rates at Ajwara (1983). Means indicated by solid dots, 95% confidence intervals indicated by vertical bars ($r^2=0.98$; $p<0.05$).

Calf mortality at the Ajwara study site increased rapidly during the dry season (Fig. 3.8).

What proportion of annual mortality occurs outside the dry season? I was unable to measure mortality rates directly during the wet season. However, simple calculations suggest that mortality during the wet season was probably much lower than that during the dry season. The average mortality rate of adults during the 1982 and 1983 dry seasons was 0.0039 and 0.0076 per week. If one applies these mortality rates over the entire year, then, at the 1982 rate, total mortality would have been 18%, and at the 1983 rate, total mortality would have been 33%. Since recruitment of young into the population was approximately 10% per year, annual adult mortality greater than 10% would have produced a decline in population numbers. Since censuses show no evidence of population decline over this period (Table 2.2), I argue that mortality rates were probably substantially higher during the dry season than during the remainder of the year.

Dry season mortality in relation to food intake

Food intake during the 1983 dry season was greater at Gom than Ajwara (Table 3.2). Estimated mortality of both adults and calves was higher at the location with lower food availability, although this inference could not be statistically tested due to the limited number of replicates (Ajwara $n=3$; Gom $n=2$). While inconclusive, these results provide additional supporting evidence that mortality rates during the dry season were related

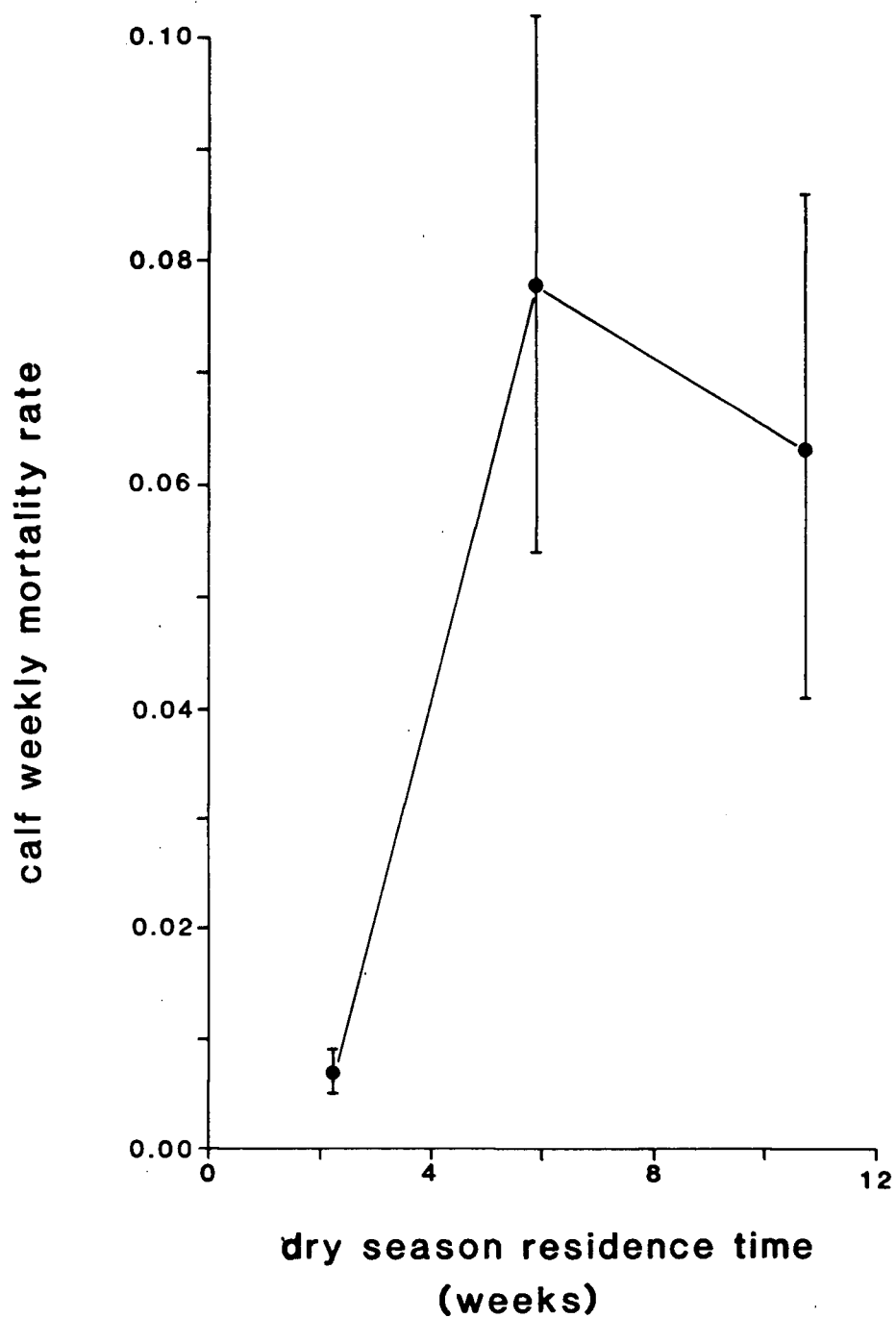


Figure 3.8 Dry season calf mortality rates at Ajwara (1983). Means indicated by solid dots, 95% confidence intervals indicated by vertical bars.

Table 3.2 Dry season mortality in relation to green grass consumption rates at Gom and Ajwara study sites.

location	grass consumed (kg/ind/day)	adult mortality	calf mortality	n
Gom	$\bar{x}$ 1.27	0.0050	0.0391	2
	SE 0.07	0.0013	0.0167	
Ajwara	$\bar{x}$ 0.71	0.0093	0.0494	3
	SE 0.26	0.0022	0.0177	

to food availability.

Cumulative dry season mortality

A linear increase in weekly mortality rates of adults implies a curvilinear increase in total adult deaths as the dry season progresses. The regression line drawn through estimates of weekly mortality rates from the Ajwara study site means that the number of adult deaths relative to initial numbers (y) was related to the dry season residence time (t) by:

$$\frac{dy}{dt} = 0.00106t + 0.0026$$

so that

$$y = 0.00053t^2 + 0.0026t + c$$

where

y = adult deaths/initial adult population size
 t = time in weeks
 $c = 0.0$, by definition

The resulting plot of total adult mortality as a function of dry season duration is shown in Fig. 3.9. Note, that while total adult mortality changed relatively little over the first 5 weeks of the dry season, thereafter mortality rapidly escalated. The exact parameters of this model should be strongly affected by year to year differences in both kob population density and habitat conditions. However, as long as there is a constant increase in weekly mortality rates as the dry season progresses, a curvilinear increase in total population mortality necessarily

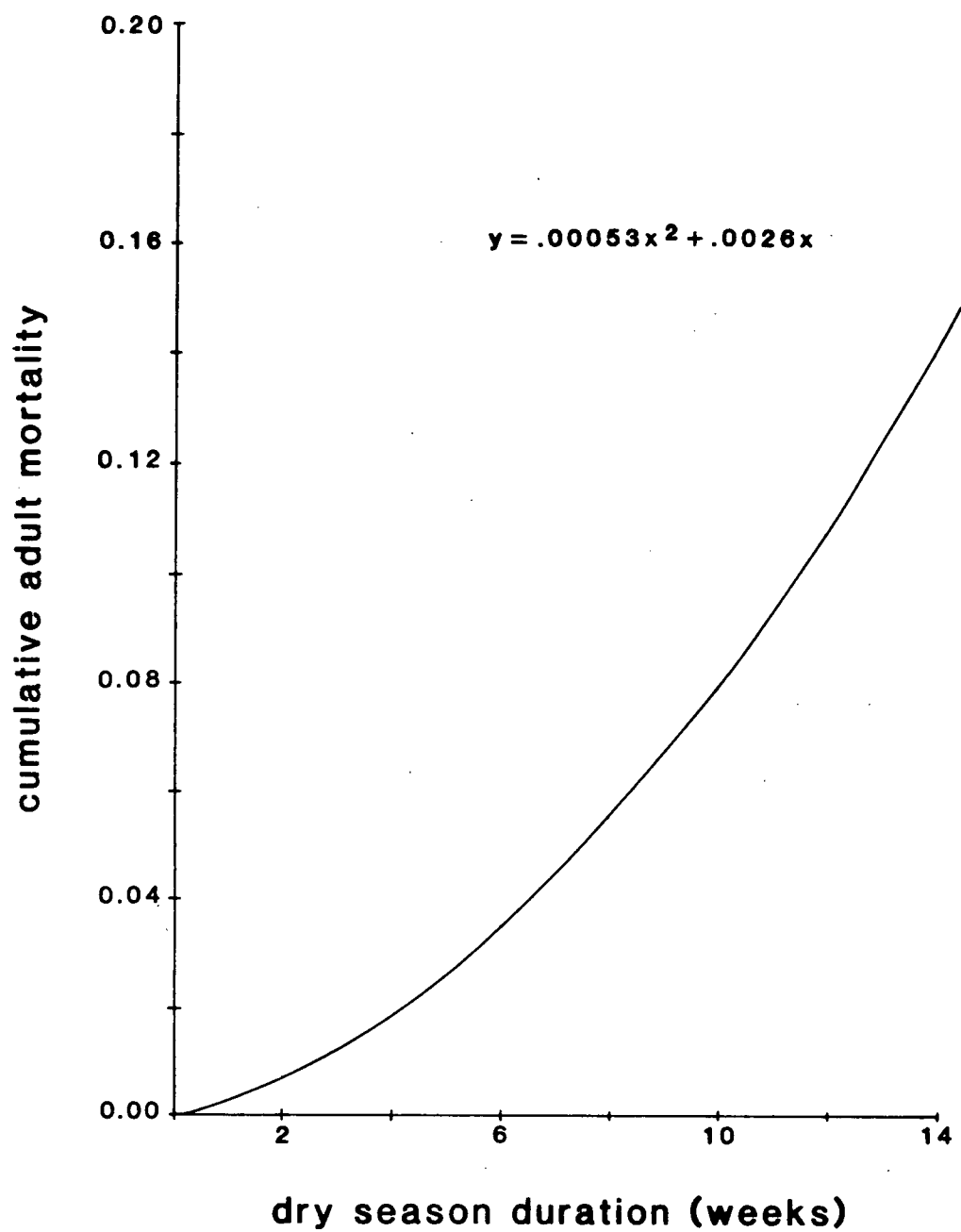


Figure 3.9 Cumulative adult mortality over the 1983 dry season, using Ajwara data.

follows.

This curvilinear increase in cumulative adult mortality may have resulted from increasing vulnerability to mortality agents as the dry season progressed, due to decline in body condition. Let us assume that at a given time the body condition of individuals within a population has a bell-shaped frequency distribution; that is, some individuals are in much better condition and some individuals are in much poorer condition than the bulk of the population. If, as shown in Fig. 3.6b, mean body condition of the population declines steadily during periods of food scarcity, then an increasing proportion of the population would become vulnerable to mortality agents, due to their weakened condition (Fig. 3.10). The vulnerable portion of the population would increase at an increasing rate, as in Fig. 3.9. This hypothesis predicts that cumulative adult mortality should increase curvilinearly until $1/2$ of the population has died (assuming a symmetrical distribution of body condition), thereafter cumulative adult mortality would show a diminishing rate of increase. Note that the hypothesis does not demand that food supplies become increasingly scarce, only that available food is less than the maintenance requirements of individuals within the population.

Unfortunately, there are no data to test the hypothesis adequately. Catastrophic dieoffs of ungulate populations have been documented a number of times (Christian et al. 1960; Klein 1968; Child 1972; Keep 1973) but none of these studies recorded mortality at intervals over the period of demise. Hillman and

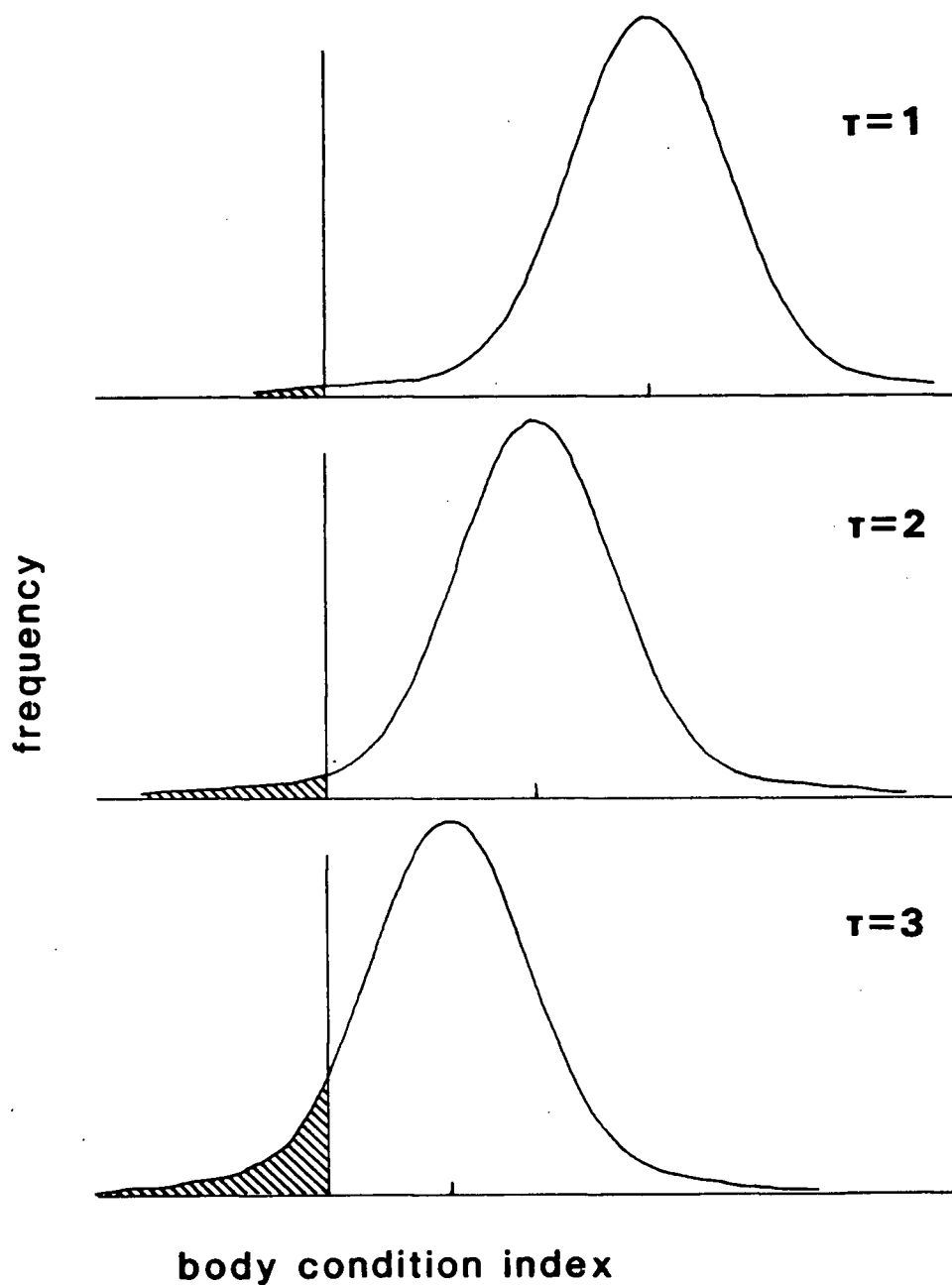


Figure 3.10 Graphical representation of the body condition/mortality hypothesis. As the body condition of individuals within a population declines during periods of food scarcity ($T=1$ to 3), an increasing proportion of the population becomes vulnerable to mortality agents (shaded portion under the curve).

Hillman (1977) estimated mortality at monthly intervals during an extended drought in Nairobi National Park (Fig. 3.11). Their results show the predicted curvilinear increase in cumulative adult mortality for kongoni and wildebeest, and possibly for zebra.

Discussion

Causes of mortality during the dry season

I now consider the three most obvious sources of kob mortality during the dry season: predation, disease, and malnutrition.

Predation

Predation by wild carnivores was probably inconsequential over most of the Boma kob dry season range. While a variety of carnivores occur in the area, including lion, hyena, leopard, and cheetah, their numbers were low. Leopard and cheetah sightings were confined to forested areas near the Boma Plateau. Kob used these areas during the southward migration, but only for a few days each year. Lion and hyena occurred in savannah areas frequented by kob during the dry season. However, in most locations, lion and hyena were rarely seen or heard. Social systems of lion and hyena preclude migration with the herds, because of the need to feed non-mobile young (Schaller 1972;

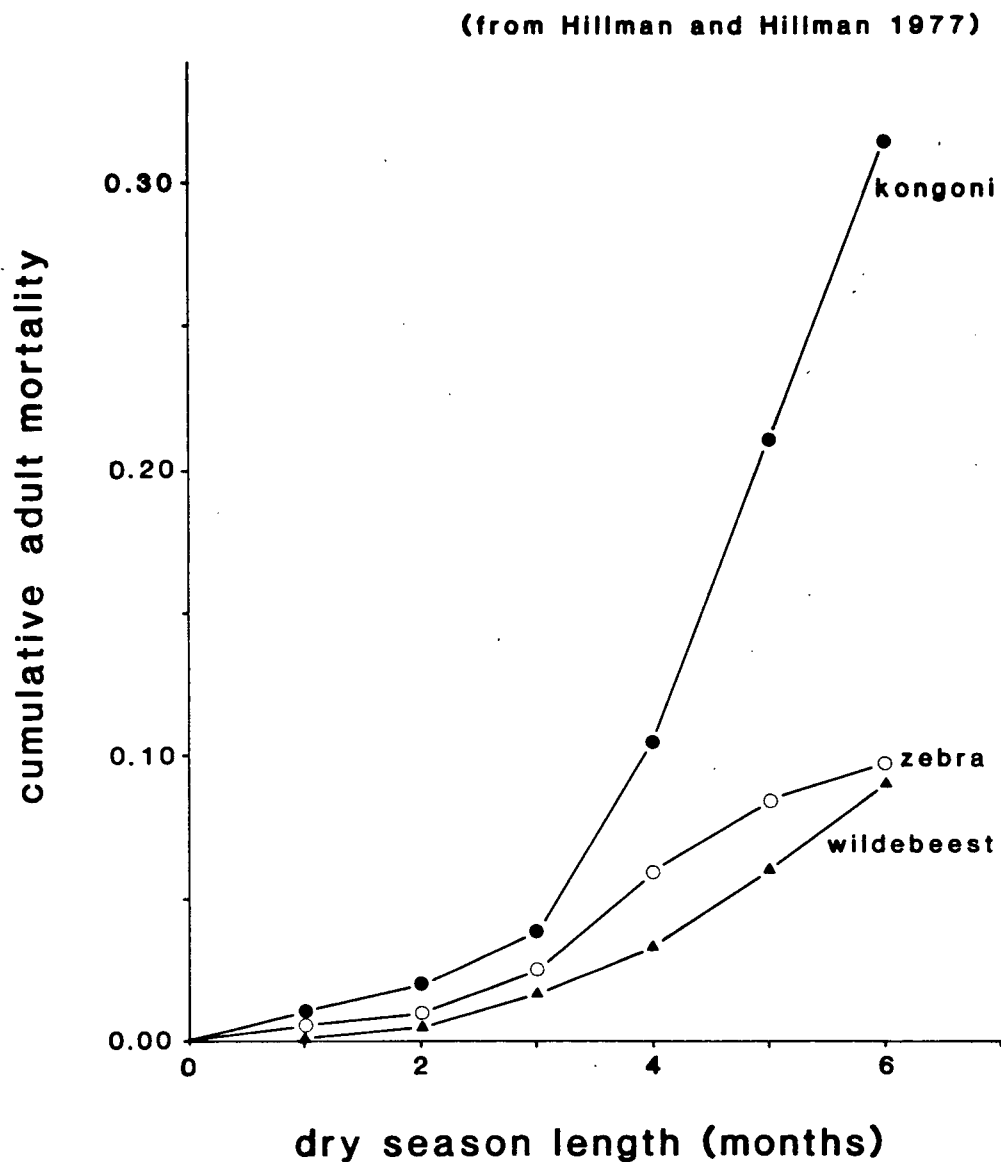


Figure 3.11 Cumulative adult mortality of kongoni, wildebeest, and zebra during a drought in Nairobi National Park, Kenya (from data in Hillman and Hillman 1977).

Hanby and Bygott 1979). Resident prey numbers were low in the northern grasslands, possibly because these areas become flooded each wet season. This suggests that Boma predators were rare because of a low biomass of prey available on a year-round basis. An alternative hypothesis is that carnivores are themselves actively persecuted by local tribesmen. This mortality is probably small, since local pastoralists tolerate carnivores unless they actually kill livestock or people (J.Arenson, pers. com.). The low carnivore density means that predation on kob was probably insignificant.

Predation of kob by man may be more substantial. During migration, 5000 kob were killed in communal hunts near Pibor Post by Murle tribesmen in 1982 and 1983. In many years, however, the migration does not come close enough to Murle settlements for successful communal hunts.

During the course of the dry season, subsistence hunting by both Murle and Anuak tribes occurred on a regular basis. There were 6 major villages with approximately 500 persons each that were in close contact with kob herds. Assuming that an adult kob would provide 20kg of meat, that each person ate 1kg of meat per day, and that kob hunters replenished their larders as needed, over a 3 month dry season perhaps 15,000 kob might have been slaughtered. In the wet season, kob were largely isolated from subsistence hunters, so offtake was probably minimal. Thus, I estimate that no more than 20,000 kob were harvested per year by human predators. By comparison, results indicate that at least 44,000 and 84,000 adult kob died of natural causes

during the respective dry seasons of 1982 and 1983. Thus, I estimate that 2-4 times as many kob died from natural causes as died from hunting.

Two points need to be stressed about hunting mortality. First, it is unlikely that the substantial mortality observed in the field was affected by hunting. Carcasses were only counted when there was no evidence of injury or mutilation by hunters. Second, it is fair to assume that subsistence hunters take relatively constant numbers of kob per year. There is no means of adequately preserving meat, there is no commercial trade in meat, and all hunt kills are for subsistence purposes. It is relatively easy to kill kob, because of their sheer abundance and behavior. Thus, it is likely that there is little density dependent predation by man.

Disease

There was no evidence that mortality during the dry season resulted from unusual disease occurrence. Post-mortem examinations of shot individuals showed no unusually high parasite loads or ubiquitous disease symptoms. There are comparatively few diseases of sufficient pathogenicity and high transmission rates to have large-scale effects, the few that do include bovine tuberculosis, pneumonia, rinderpest, and anthrax (L. Karstad, pers. com.). Since all study sites showed similar increases in mortality rates over the dry season, it is unlikely that widely separated kob herds would have been equally affected by disease outbreak.

Many pathogens are relatively harmless unless the nutritional condition of an affected individual declines to a critical level (Scrimshaw et al., 1968). Thus, disease may act as the proximate cause of death, when nutritional insufficiencies are ultimately responsible for making individuals vulnerable.

Age structure of the kob population

The age distribution of the kob population in 1983 showed a pronounced bulge in the 5-7 year old age groups. If a population has reached a stationary age distribution, the frequency of any given age class must be equivalent to or smaller than preceding age classes. Since 5 to 7 year old individuals were markedly more common than individuals 1 or 2 years old, this implies that the population must have undergone sizeable change previous to 1983. This bulge in the age distribution could have arisen from increased recruitment of young in 1976 to 1978, with a decrease in subsequent years. Alternatively, if the population decreased between 1978 and 1983 due to increased relative mortality of both calves and old adults, this would produce an increased relative proportion of young adult age classes in the surviving population. Without further information we can not discriminate between these hypotheses (Caughley 1977).

Much of the southern Sudan experienced drought conditions in 1979-80, immediately preceding this study. As a result, many

usually reliable watering points dried up and pastoralists in the Pibor township west of Boma National Park reported heavy cattle losses due to inadequate forage and lack of water (J.Arenson, pers. com.). Large numbers of dead kob near drying waterholes were reported by independent observers in February 1980 (G. Schaller and D. Western pers. com.). I estimated that there were over 80,000 kob carcasses during an aerial census in March 1980, late in the drought. Aerial censuses suggest no subsequent change in kob population numbers since March 1980, (Table 2.2; t-test, n.s.). Thus, it is likely that a sizeable reduction in kob numbers resulted from drought conditions in 1979 and 1980.

The white-eared kob q_x curve indicates that mortality risk is highest for both very young and very old kob. Under stressful environmental conditions these may be the most heavily affected age groups. Therefore, I suggest that the bulge in the standing age distribution observed in 1983 was due to increased mortality of both calves and older age classes during the 1980 population decline rather than a temporary increase in calf survival or birth rates from 1976 to 1978. Current frequencies of 5 to 7 year old age classes suggest a mean minimum recruitment in 1976-1978 of 145,000 yearlings per year (range=128,000 to 179,000). If one assumes that prior to 1980 yearlings similarly composed 10% of the total population (excluding calves), then this implies that the kob population prior to 1980 was about 1.5 million (Fig. 3.12). The 1980 drought may, therefore, have caused a 40% reduction in kob

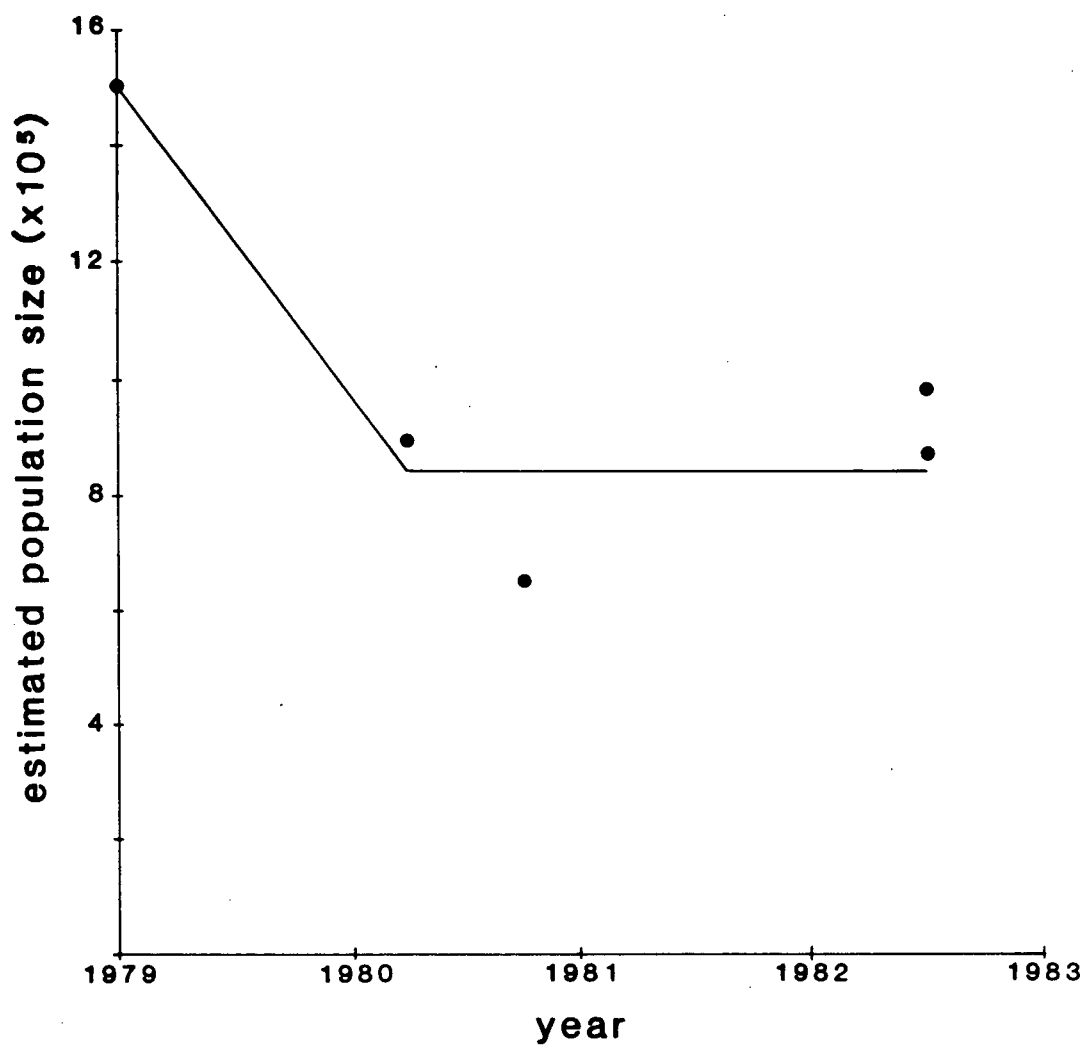


Figure 3.12 Kob population estimates 1979-1983. Population estimates after 1979 from aerial censuses. 1979 population estimate as explained in the text.

population numbers.

Evidence for food limitation

My results support the hypothesis that food availability limits the Boma kob population. At the beginning of this chapter I outlined a series of predictions to test the hypothesis.

The first prediction of the food hypothesis is that survival rates should decline during years of below-average food abundance and during seasonal periods of food scarcity. There was evidence that adult mortality rates varied considerably from year to year, depending on the severity of dry season conditions. The short dry season of 1982 produced considerably less adult mortality than the long dry season of 1983. I observed no significant differences between years in juvenile mortality or recruitment rates. Moreover, large-scale mortality during the 1979-80 drought is consistent with the food limitation hypothesis. During drought conditions, grazers are forced to concentrate near the few remaining waterholes and consequently can not obtain adequate food supplies (Corfield 1975). Thus, in many droughts, herbivores die of inadequate food rather than lack of water.

Mortality rates of both adults and calves increased during the dry season. As shown in Chapter 2, food intake during the dry season was insufficient to meet kob energetic requirements. Many previous studies have suggested that the dry season is the period of greatest nutritional stress in African savannah

grasslands (e.g. Western 1975; Sinclair 1977). In one of the few studies that have actually measured both food availability and mortality rates, Sinclair et al. (1985) found that dry season mortality in the Serengeti wildebeest was closely correlated with food availability.

The second prediction of the food hypothesis is that there should be an inverse correlation between mortality rates and body condition of herbivores. I found direct correspondence between body condition and elevated dry season mortality rates in the Boma kob population, which suggests that insufficient supplies of high protein food led to declining fat reserves, ultimately increasing the risk of mortality. Individuals in the poorest condition were also the most likely to die. Similar findings from African buffalo, wildebeest, and topi suggest this cause-effect relationship is common among African ungulates (Duncan 1975; Sinclair 1975; Sinclair 1977).

The third prediction of the food limitation hypothesis is that mortality rates should be correlated with food intake. Mortality rates differed between the 2 study sites for which I was able to estimate rates of food intake, but due to the small sample sizes, a statistical comparison was not possible.

These observations suggest that dry season food availability limits kob population numbers. Both adult and calf mortality rates increased during the dry season, but adult mortality was more clearly related to food availability than was calf mortality. A limited number of previous studies (Klein 1968; Grubb 1974; Sinclair 1977; Sinclair et al. 1985) have

also found that food availability determines mortality rates of adults. There is considerably more evidence that natality and/or calf survival are related to food availability (Woodgerd 1964; Gross 1969; Geist 1971; Grubb 1974; McCullough 1979; Clutton-Brock et al. 1982; Houston 1982). White-eared kob calves may be partially buffered against year to year variation in forage abundance because their mothers continue to provide milk throughout the dry season (Chapter 5). In contrast, all of the studies showing density-dependent responses in juvenile survival come from temperate populations that terminate lactation prior to the winter period of food scarcity.

One of the most intriguing results from this study is the apparently constant increase in mortality rates of adults as the dry season progresses. This would tend to confound any attempt to measure density-dependent mortality effects directly. Mortality is not only affected by the number of individuals competing for scarce resources, but also the length of time individuals are dependent upon sub-maintenance supplies. The longer individuals must rely on their own body reserves to meet a nutritional deficit, the lower these reserves become, and the more vulnerable they are to various potential mortality agents.

One of the consequences of a direct relationship between the duration of periods of food scarcity and mortality rates is that many large-mammal populations may be prone to large-scale population fluctuations (Klein 1968; Caughley and Lawton 1981; Sinclair and Norton-Griffiths 1979; Bayliss 1985). Populations similar to the Boma kob may be affected substantially by even

moderate droughts. Thus, resource limitation should come into play at frequent intervals (Schoener 1982) and we should expect to see large fluctuations over time in herbivore populations living in highly variable environments.

CHAPTER 4. KOB REPRODUCTIVE PHENOLOGY

Introduction

Many ungulate populations show seasonal peaks in calf production corresponding to periods of pronounced food abundance (reviews in Sadleir 1969; Schaller 1977; Bunnell 1982; Sinclair 1983a). Since high calf mortality is common in ungulates (Caughley 1966; Sinclair 1977; McCullough 1979; Fowler 1981; Clutton-Brock et al. 1982), breeding synchrony may have evolved as a means of improving the survival of vulnerable young. Females supply all the food for their newborn offspring through lactation and as a result, lactating females frequently suffer diminished fat reserves during the calving period relative to both non-lactating females and males in the population (Sinclair 1977; Clutton-Brock et al. 1982). By timing calf production to periods of the year when food is in greatest abundance, females should be better able to meet the demands of feeding dependent young, thereby increasing offspring survival. Thus, there is presumably strong selective pressure for populations living in seasonal environments to produce calves during the period of greatest food abundance.

In this chapter, I compare the reproductive phenology of the white-eared kob, Kobus kob leucotis, to the conspecific Uganda kob, Kobus kob thomasi. The migratory white-eared kob lives in savannah grasslands of the southern Sudan with markedly seasonal rainfall patterns (Chapter 2), while the Uganda kob is

non-migratory and lives in savannah areas with less pronounced seasonality (Buechner et al. 1966; Modha and Eltringham 1976). In response to climatic seasonality, the amount of green biomass available as food to white-eared kob varies predictably throughout the year (Chapter 2). During the rains, from April to October, forage is both abundant and widely distributed. However, during the dry season, from November to March, green grass becomes increasingly restricted to ephemeral swamps of limited extent. As a consequence of resource scarcity, mortality of both adult and juvenile white-eared kob is pronounced during the dry season (Chapter 3). In Chapter 2 I showed that food availability is highest during the late wet season. On the basis of this information, kob should time the production of young to coincide with the late wet season.

Methods

Seasonal changes in female reproductive condition were determined from a random shot sample. All shot females were examined for evidence of lactation (by mammary palpation and measurement of mammary gland wet weight), and pregnancy (by dissection of uteri). I measured fetal total weight and length, and described the fetal developmental stage. Conception dates were subsequently estimated from the regression of fetal weight on age reported by Buechner et al. (1966). Birth dates were estimated by extrapolating the 240 day gestation length of the Uganda kob (Buechner et al. 1966) from estimated conception

dates. I also noted the condition of the ovaries, particularly the presence of corpora lutea, based on the description in Morrison (1971).

Seasonal changes in the proportion of calves (individuals < 12 months old) in the kob population were determined from calf/female ratios in samples of the population observed both on the ground (December to April), and from photographs of migrating herds taken from low-flying aircraft (November and May). Sample sizes for ground observations ranged from 96 to 867 individuals, while aerial sample sizes ranged from 243 to 339 individuals. Adult males were easily distinguishable from females because of pronounced color dimorphism and presence of s-shaped horns (Chapter 6). Males 1 to 3 years old were also readily distinguished from females during ground observations due to presence of horns, even though males do not develop dark adult coloration until after 3 years. It was difficult to distinguish immature males from females on photographs, so I confined calculations to those counts from well defined, close up aerial photos (taken at flying heights of less than 30m above ground). Calves less than 6 months old are approximately one third the size of adult females (Chapter 6) and were easily distinguished both on the ground and from aerial photographs.

Diurnal activity budgets of adult kob during the dry season were estimated from large aggregations on swampy meadows. At 10min intervals, each individual within 40m was recorded as feeding, ruminating, reclining, standing, or other.

Results

Sixteen out of 17 fetuses examined were conceived between January and April (Fig. 4.1), implying a birth peak between September and December. The birth peak occurred at the end of the wet season, as predicted.

Female reproductive condition (Fig. 4.2) reflected the observed seasonal trend in calf production. In January and February, approximately 80% of females were lactating. Since kob lactate for approximately 180 days (Buechner 1974), Fig. 4.2 suggests that 80% of the females observed in January had produced calves in the preceeding 6 months. The proportion of lactating females declined over the course of the dry season (January to April), reaching approximately 25% by May.

In January and February, none of the sampled females were pregnant (Fig. 4.2). By the end of April, approximately 80% of the females were pregnant. These findings are somewhat inconsistent with the conception period (Fig. 4.1) estimated by the regression of fetal weight on age. It is possible that some of the females sampled in January and February might have had small fetuses that were undetected. Alternatively, the sampling procedure may have been biased such that non-pregnant females were more likely to be sampled than pregnant females. In any case, both Figs. 4.1 and 4.2 indicate that most conceptions occurred between January and May.

Approximately 80% of the female population conceived each year, and only one offspring was produced per female. Females were capable of conception as yearlings (2 females of age 2 were

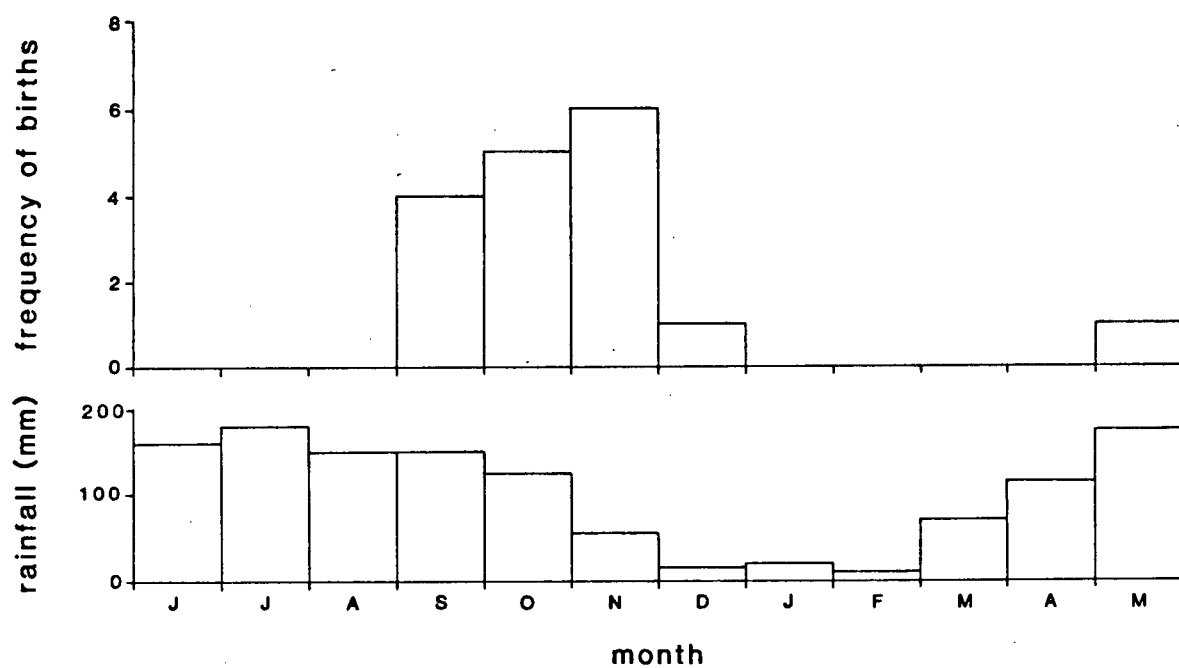


Figure 4.1 Upper histogram - frequencies of births by month, estimated from fetal weight ($n=17$). Lower histogram - mean monthly rainfall totals for Pachalla township (1953-1962).

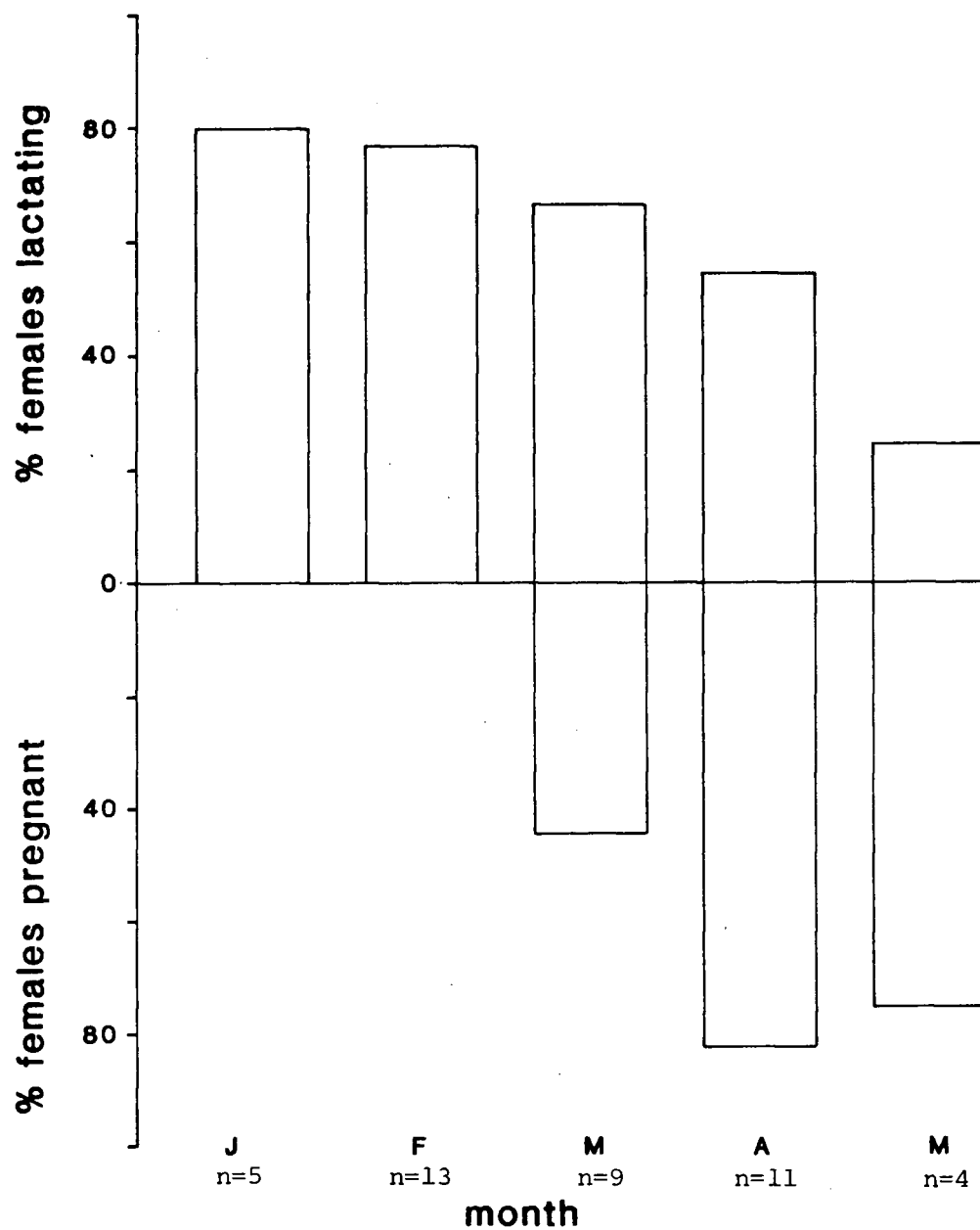


Figure 4.2 Female reproductive condition (January-May) from pooled data (1982 and 1983). Monthly sample sizes as indicated below histograms.

sampled and both were lactating, indicating that they conceived as yearlings). I observed no instances of multiple fetuses, in accordance with records from Uganda kob (Buechner et al. 1966). Like the Uganda kob (Buechner 1961b) white-eared kob embryos were invariably implanted in the right horn of the uterus.

Reproductive females were exposed to considerable nutritional stress during the latter stages of the lactation period, as it extended well into the dry season (Fig. 4.3). Lactating females in the dry season were in poorer body condition (as measured by bone marrow fat content; Sinclair and Duncan 1972; Hanks 1981), than non-lactating females (Mann-Whitney, $u=14$, $p<0.01$). Lactating females were also in poorer body condition than adult males (Mann-Whitney, $u=90$, $p<0.05$) despite the fact that females devoted a greater portion of the daylight hours to feeding than did males (Fig. 4.4). These findings indicate that lactation itself imposed increased demands on fat reserves at a time of year when kob were particularly vulnerable to nutritional stress (Chapter 3). During the dry season, calves were subject to high mortality: between 1.5-7.5% per week from late January to April (Chapter 3). Calf mortality in the dry season may have resulted in part from the limited capacity of females to feed young adequately. Although calves began to forage on their own before weaning, this food source was insufficient to make up for the loss of mother's milk.

Seasonal changes in calf/female ratio are shown in Fig. 4.5 (curve A). There was a steady increase in the proportion of

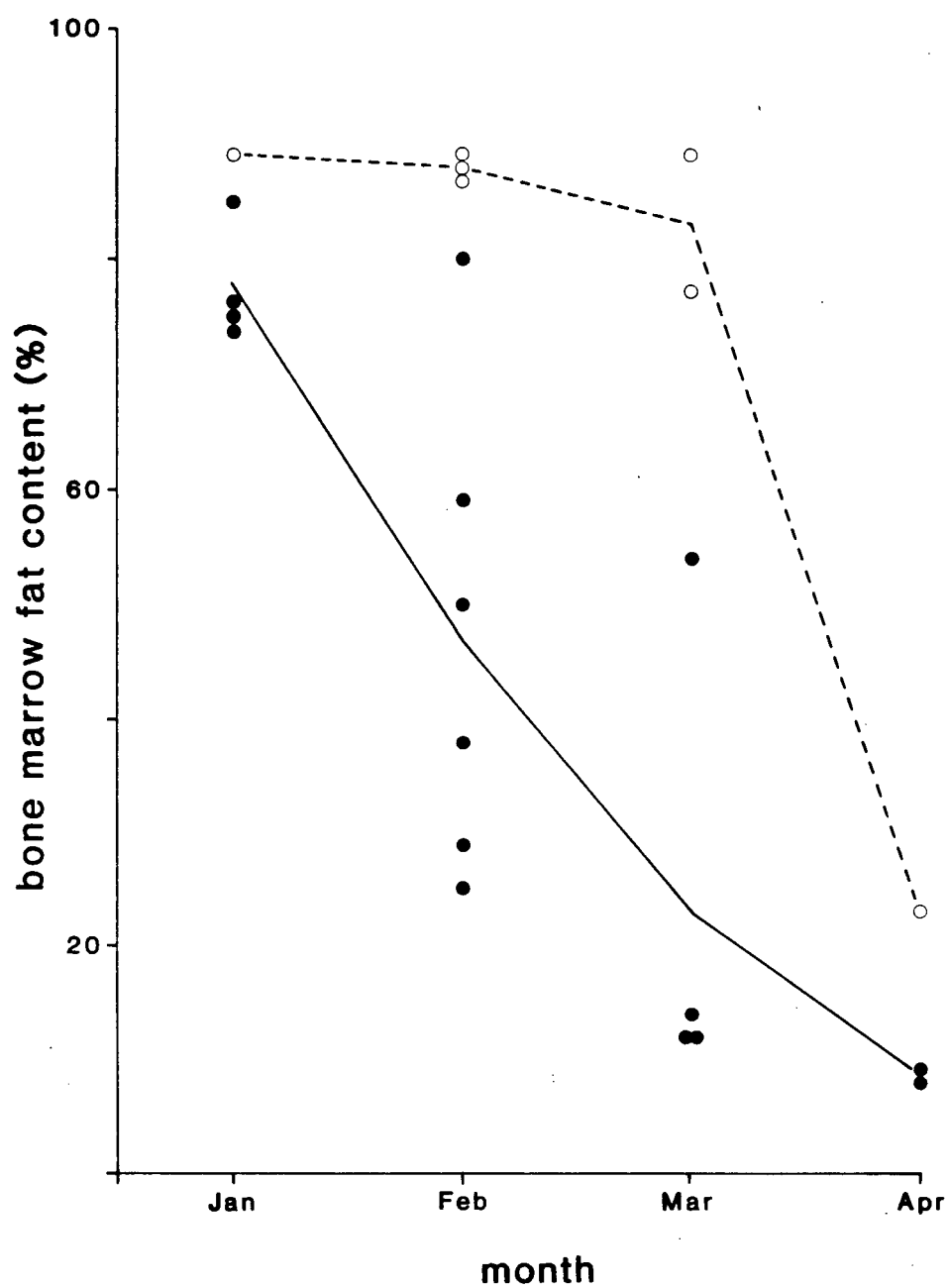


Figure 4.3 Dry season body condition of lactating (solid dots) vs. non-lactating (open dots) females (1983 data). Lines connect monthly mean values.

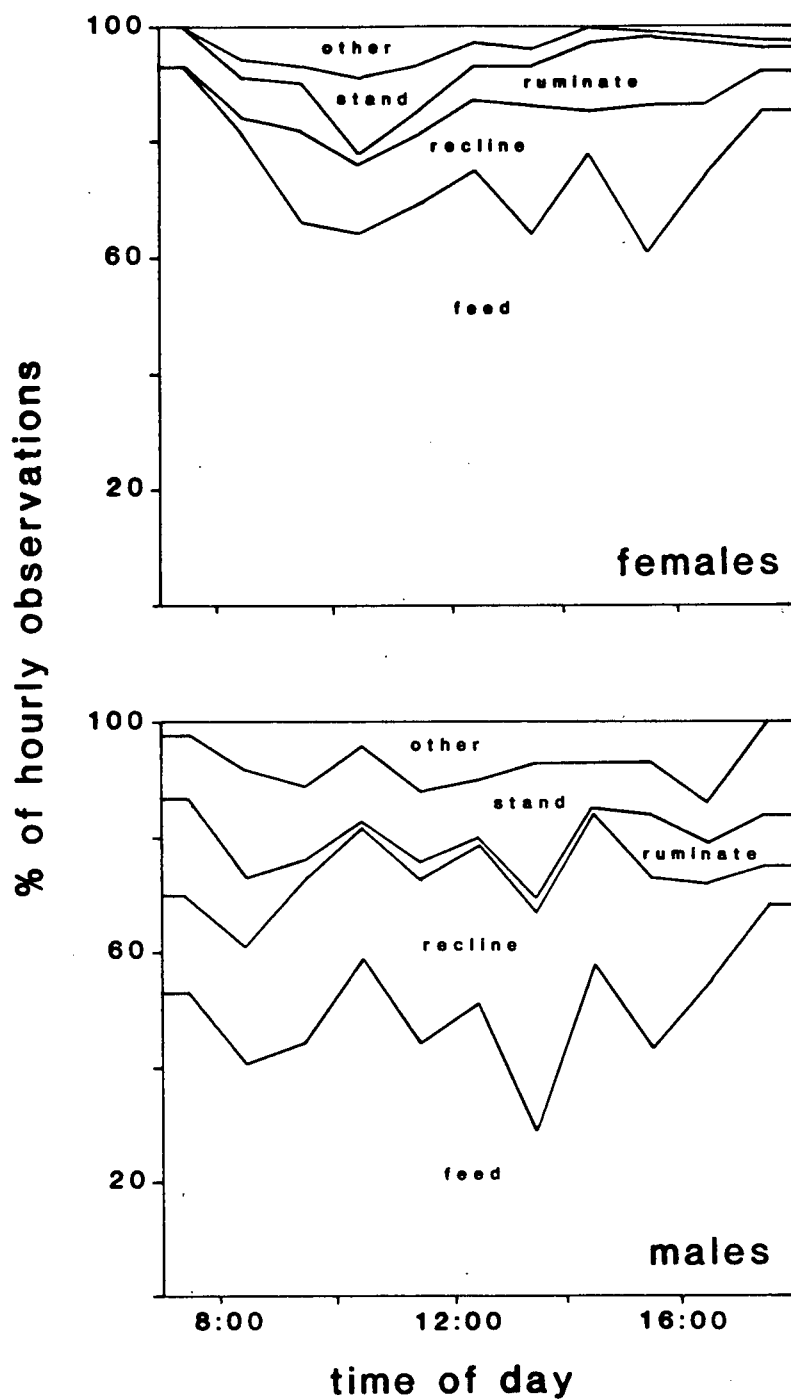


Figure 4.4 Activity budgets of male vs. female kob on meadows (male observations=1025; female observations=1379). Note that males spent significantly less time feeding than did females ($\chi^2=269.6$; $p<0.001$).

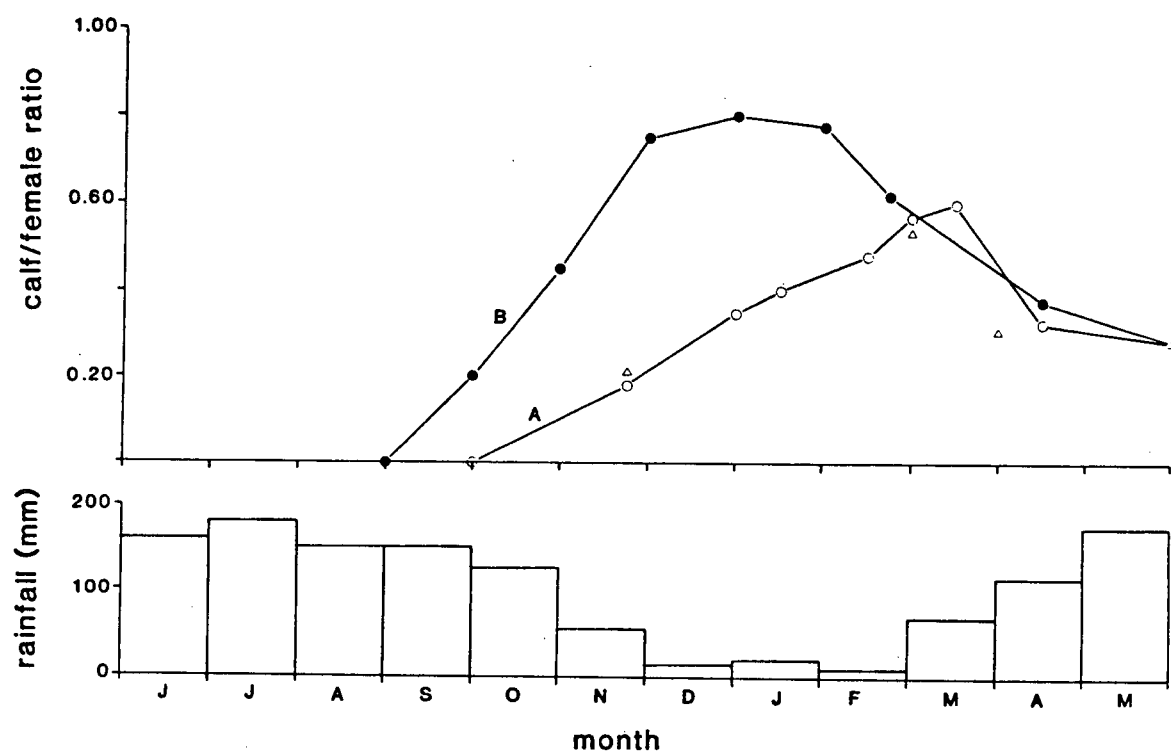


Figure 4.5 Seasonal changes in calf/female ratio, estimated in two ways. Curve A indicates calf/female ratio observed from field observations of herd composition (open triangles= 1981-1982; open circles= 1982-1983). Curve B indicates calf/female ratio predicted from frequencies of births by month (Fig. 4.1) and field estimates of calf mortality rates (Fig. 3.8). Lower histogram - mean monthly rainfall totals for Pachalla (1953-1962).

females with calves from October to mid-March, and a sharp decline in calf/female ratios from mid-March to May. Since virtually all calves were born between September and December (Fig. 4.1), one would expect the calf/female ratio to have increased only until the end of the calving period (December), in contrast to field observations. This discrepancy may have arisen because new-born kob hide in thickets and tall grass for some time, a common behavior in young of many African ungulates (Leuthold 1966). As a result, field observations of calf/female ratio may have been biased downwards prior to the date when all calves joined the adult herds following the hiding out period.

I calculated an expected seasonal curve of calf/female ratios (Fig. 4.5, curve B) from the frequency of births by month (Fig. 4.1), the fecundity rate among reproductive age females (80%, Fig. 4.2), and field estimates of mortality rates of calves during the dry season (Chapter 3). The expected curve peaks at the conclusion of the calving period (December) and declines over the dry season to levels close to observed calf/female ratios by the end of the dry season (April). Similarity between curves A and B in the late dry season suggest that by April all young have joined the adult herds. Calf mortality was apparently highest in the latter dry season period, levelling off with the onset of the rains. Similarity between field observations of calf/female ratio (Fig. 4.5) in 1981-82 (open triangles) and 1982-83 (open circles), suggests that natality rates and reproductive timing varied little between the two years.

Discussion

White-eared kob living in seasonal grasslands of the southern Sudan showed synchronous breeding resulting in calf production in the late wet season (September to December). There was a post-parturition interval of approximately 4 months before females conceived again. As a result, individual females gave birth to a single offspring per year. By contrast, Uganda kob produce calves throughout the year and females conceive within 2 months following parturition (Buechner et al. 1966; Buechner 1974). Consequently, female Uganda kob produce on average 1.35 young per individual per year (Buechner 1974), while white-eared kob females produced 0.80 young per year. Observations of lactation in 2 year old females in this study confirmed Buechner et al.'s (1966) view that Kobus kob females are capable of conception as yearlings. Thus, seasonal breeding reduced the annual reproductive potential of white-eared kob relative to Uganda kob.

White-eared kob calf production occurred in the late wet season, when food was both abundant and widespread. These results are consistent with a large number of studies on other ungulates living in seasonal environments (Sadleir 1969; Sinclair 1983a). However, females continued lactation well into the dry season, when food supplies were scarce. As a consequence, lactating females experienced greater depletion of fat reserves than non-lactating females. Since abundant food supplies were available early in the wet season, it is therefore puzzling that calf production did not occur earlier in the wet

season.

One possible explanation is that females require a substantial period to recover fat reserves lost during lactation before giving birth and feeding new young (Sinclair 1983a). If kob calves were born in the early wet season, females would have just emerged from the stressful dry season, possibly with inadequate fat reserves to sustain lactation even under abundant food conditions. Thus, the observed timing may reflect a trade-off between producing young during the wet season and ensuring that females have adequate recovery time prior to the next lactation. This hypothesis could be tested by measuring fat reserves of females throughout the wet season period. If females recover fat reserves quickly after the onset of the rains, this would be inconsistent with the condition recovery hypothesis.

Alternatively, it is possible that there are other selective forces acting on reproductive phenology. The white-eared kob population migrates each year from low rainfall, short grass areas in the south each wet season to high rainfall, ephemeral swamped grasslands in the north in the dry season (Chapter 2). Calf production takes place largely during the northward migration from October to December. The observed timing of calf production may function as an anti-predator adaptation. There are apparently few predators present in the northern grasslands, possibly due to the lack of year round resident prey species (Chapter 3). Thus, calf production during migration into the dry season range may reduce the likelihood of

predation on vulnerable young and females.

There is a clear way in which the predation hypothesis might be tested. In the Boma ecosystem, several ungulate species have north-south migratory movements similar to the white-eared kob (e.g. tiang, zebra, and eland), while others are non-migratory (e.g. buffalo, lelwel, and oribi). If kob produce calves during the northward migration as an anti-predator adaptation, then I predict that other migratory species should adopt a similar strategy, while non-migratory species should exhibit calving peaks in the early wet season. Thus, there should be a clear difference in the timing of calf production between non-migratory and migratory populations.

CHAPTER 5. BREEDING SYNCHRONY AND MALE AGGRESSION

Introduction

Four features characterize lek mating systems (Bradbury 1981): (1) males congregate at communal display sites for the sole purpose of attracting females; (2) males do not care for young; (3) display sites contain no defensible resources of interest to females; and (4) females choose males to mate with from the display site. As a consequence of these conditions, lek systems constitute an extreme form of polygyny and, since female choice depends mainly on the display qualities of males, there is presumably intense sexual selection on males (Emlen and Oring 1977; Borgia 1979; Bradbury and Gibson 1983). Thus, lekking species are particularly well suited to testing hypotheses about the evolution and adaptive function of mate choice (Emlen and Oring 1977; Borgia 1979; Wittenberger 1978; Wrangham 1980; Bradbury 1981; Bradbury and Gibson 1983; Foster 1983).

A critical element in lek systems is that males compete aggressively for occupation of preferred lek territories, or courts. In most lekking populations, matings are largely restricted to males that are lek members, and satellite males are excluded from breeding activities. Moreover, most matings are achieved by holders of a small number of central courts within the lek (Buechner 1961a; Wiley 1973; Lill 1974, 1976; Robel and Ballard 1974; but see Leuthold 1966; Floody and Arnold

1975). As a result, there is a highly skewed distribution of mating success among males in the population (Emlen and Oring 1977; Borgia 1979; Bradbury and Gibson 1983).

Among lekking ungulates, males can control preferred central courts for only a few days, while they can control peripheral courts for several weeks (Buechner et al. 1966). This difference in site occupancy could arise from central males expending more energy on defense and courting of females (Buechner and Schloeth 1965). There is some evidence that only a few males have access to central positions because dominant males return repeatedly for brief periods of tenure within leks following temporary periods of association with surrounding bachelor herds (Buechner et al., unpublished MS, cited in Bradbury and Gibson 1983).

Little attention has been paid to the effect of synchronized breeding on lek mating systems. Emlen and Oring (1977) suggested that extreme breeding synchrony should diminish the degree of polygyny, since individual males can only obtain a few matings when many females come into breeding condition simultaneously (Fig. 5.1). Pronounced polygyny may be expected at intermediate degrees of breeding synchrony, since individual males would be able to obtain many matings during the short period of tenure in a preferred lek position. Asynchronous populations should be less polygynous, since it would be difficult for males to retain a dominant position for extended periods of time, providing new opportunities for other males. Therefore, one would predict more polygyny and intense sexual

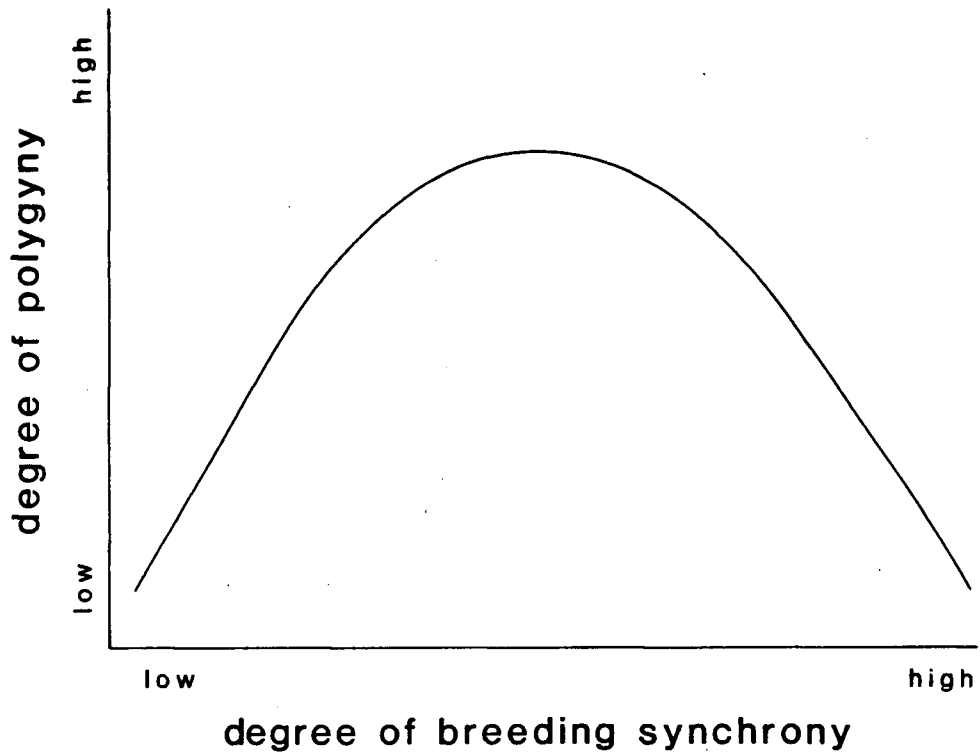


Figure 5.1 Hypothetical relationship between degree of breeding synchrony and degree of polygyny (from Emlen and Oring 1977).

selection in populations with intermediate breeding synchrony.

Two predictions arise from this hypothesis. First, if sexual selection is greater in moderately synchronous populations, sexual dimorphism should also be more pronounced. Second, dominant males should obtain greater benefits under conditions favoring polygyny (i.e. for moderately synchronous populations). Natural selection should favor individuals that are able to obtain greater benefits relative to costs, so competing males on leks should be more aggressive in moderately synchronous populations (Fig. 5.2).

In order to test this hypothesis, I examined lek behavior in a migratory population of the white-eared kob, Kobus kob leucotis, in the southern Sudan. The behavior of the white-eared kob on leks is similar to that of the Uganda kob, Kobus kob thomasi (Buechner and Schloeth 1965), so I shall concentrate on quantitative differences between the two races. The chief difference is that mating is restricted to a 4 month period in white-eared kob (Chapter 5) while Uganda kob breed year-round (Buechner 1974). Thus, a comparison of the populations will test the hypothesis that sexual selection is more intense in moderately synchronous than in asynchronous lekking populations. This hypothesis predicts a greater degree of sexual dimorphism in the white-eared kob and more intense competition among males.

I also investigated the consequences of aggression between males on leks. Previous studies on the Uganda kob suggest only that lek aggression determines dominance relations between males (Buechner 1961a). However, recent work suggests that disruptive

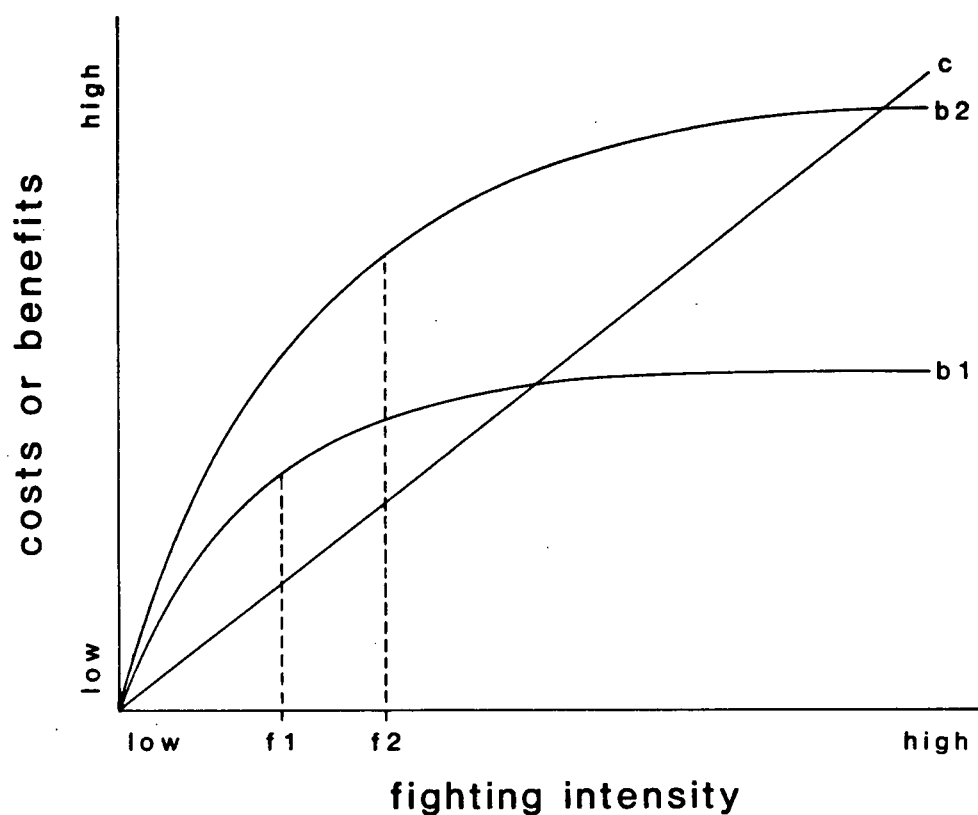


Figure 5.2 Postulated male cost/benefit curves in relation to fighting intensity (b_1 = benefits to males in highly synchronized or asynchronous populations; b_2 = benefits to males in moderately synchronized populations; c = costs to males; f_1 = fighting intensity at which $b_1 - c$ is greatest; and f_2 = fighting intensity at which $b_2 - c$ is greatest).

behavior is common in some lekking species (Wrangham 1980; Foster 1983; Trail 1985). This suggests an alternative hypothesis, that male aggression may serve to disrupt the mating activities of neighboring males.

Methods

Sexual dimorphism

I measured size dimorphism in adult kob from a random shot sample of 18 males and 24 females. Animals were weighed, and a variety of other body measurements were recorded. A non-random (with respect to age) sample of 10 immature males and 11 calves were also taken. These age groups were easily recognizable by horn shape, horn length, and coat color. Ages of adults were determined by counts of tooth cementum annuli (Chapter 3).

Lek observations

Observations of lek behavior were compiled from 8 hours of observations per month for January to April, 1983. Because kob populations were transient, no leks were active throughout the entire 4 month period. I therefore combined observations from 5 different leks, each numbering between 20 and 65 males.

I made recorded observations for 10 minute periods on a tape recorder, separated by 10 minute intervals during which I transcribed the records onto data sheets. For each observation

period I counted the total number of males and females present at the beginning of the interval, and noted the locations of females on the lek. During the observation periods I noted all incidences of the following behaviors: (a) mount attempts - a mount in which the penis is erect and the male actually makes physical contact with the female, although penetration may not occur; (b) sexual solicits - male exhibits precoital behaviors such as "prancing", "lip-curling", or "leg-striking" (Buechner and Schloeth 1965); (c) threats - males engage in agonistic displays with heads lowered and ears extended, and prepare for complete sparring activity; (d) chases - male chases another male, usually when a second male moves onto the court of the first, or as a result of threat or fight behavior; (e) fights - males make physical contact with the horns, usually after threat behavior. Only the most escalated agonistic behavior was recorded for each incident. Since virtually all fights terminated in a retreat by the loser and chase by the victor, I simply scored such events as a fight.

In addition, I recorded the location of all fights and mount attempts within 3 concentric zones of equal width on the lek: central, intermediate, and peripheral. Since leks were roughly circular in shape, the ratios of the relative areas of the three zones were approximately 1:3:5. I used these ratios to calculate expected values for the spatial distribution of females and of aggressive encounters on the lek. For example, if females were distributed at random on the lek, one would predict five times as many females in the perimeter zone as in

the central zone.

Results

Sexual dimorphism

Adult white-eared kob differ markedly from Uganda kob in degree of color dimorphism. Adult leucotis males are ebony colored, with highly contrasting white patches on the face, ears, and throat, and are entirely white ventrally. By contrast, thomasi males are an even tawny brown color. Females of both races resemble thomasi males in color. The pronounced color dimorphism in leucotis first appears at 3 years of age, when males are approaching full body size and sexual maturity (Buechner et al. 1966). There is no difference in weight dimorphism between the two races (Fig. 5.3) (leucotis adult male/female weight = 1.37; thomasi male/female weight = 1.41 (Buechner and Golley 1967)). White-eared kob are, however, smaller than Uganda kob (mean live weight of leucotis males = 55kg, mean live weight of thomasi males = 90kg).

Temporal change in mating and agonistic behavior

The number of females observed on leks declined slightly between January and April (Table 5.1). However, mount attempts per hour did not change significantly over the 4 month breeding

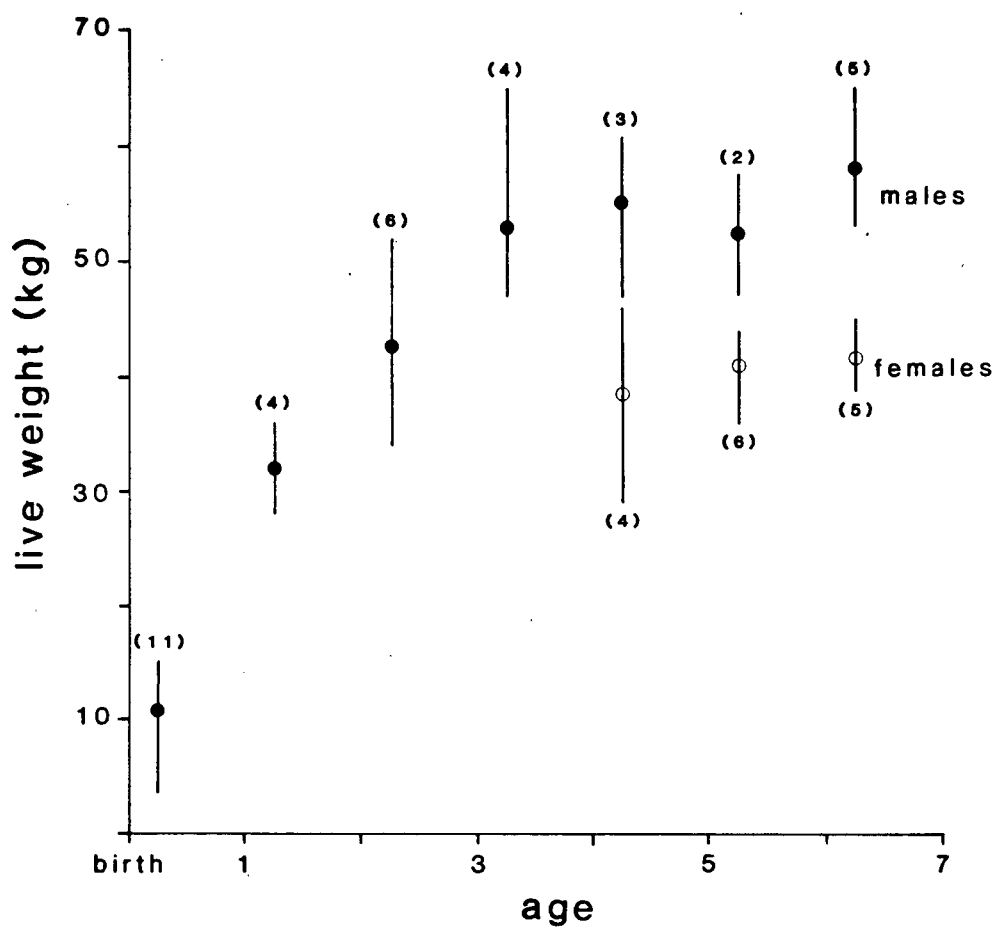


Figure 5.3 Kob live weights at age (males=solid dots; females=open dots). Mean values indicated by dots, range by vertical bar, and sample sizes in brackets.

Table 5.1 Changes in mating behavior over the breeding season (January-April, 1983) (mean values per hour, SE of mean shown in parentheses). Differences between means evaluated by Kruskal-Wallis Test (df=3; *:p<0.05; **:p<0.001).

	January	February	March	April	differences between means?
no. males	28.7(1.7)	26.4(0.9)	51.5(4.2)	18.4(0.7)	H=42.5, **
no. females	7.6(1.7)	7.0(0.7)	4.8(0.3)	5.3(0.4)	H=11.0, *
no. mounts	21.1(4.0)	20.6(3.9)	17.1(3.5)	19.6(5.1)	H=3.5, n.s.
no. fights per male	2.06(0.33)	0.98(0.17)	0.39(0.07)	0.42(0.03)	H=30.7, **
no. chases per male	0.64(0.09)	0.26(0.05)	0.12(0.03)	0.13(0.03)	H=26.6, **
no. threats per male	0.25(0.08)	0.09(0.03)	0.13(0.03)	0.08(0.03)	H=4.7, n.s.

season. These results suggest that matings were evenly spread over the entire breeding period, as in the Uganda kob (Buechner 1974).

However, the mean number of fights per male per hour did decrease significantly over the breeding season, ranging from a peak of 2.06 fights per hour in January to 0.39 fights per hour in March (Fig. 5.4). The mean value for the 4 month period was 1.07 fights per hour. When fights are combined with a threat rate of 0.13 per hour, there was a mean agonistic encounter rate of 1.20 per hour over the breeding season, which is much greater than the value of 0.38 per hour for the Uganda kob, calculated in the same way from Floody and Arnold's (1975) data. Agonistic encounters were therefore three times as frequent in the white-eared kob population as the Uganda kob population. However, the agonistic encounter rate declined to a comparable value by the end of the white-eared kob breeding season.

Spatial distribution of females and agonistic encounters

More than 3 times as many females as expected concentrated in the central area of the display grounds (Fig. 5.5, $\chi^2=296$, $df=2$, $p<0.001$). This is consistent with the behavior of female Uganda kob (Buechner 1961b; Floody and Arnold 1975), as well as that of most other lekking species (Bradbury 1981). Although central areas were preferred, and as many as 12 different females were on occasion located with a single male, females were generally not highly clumped (Fig. 5.6). Clumping of females was even less common away from central or intermediate

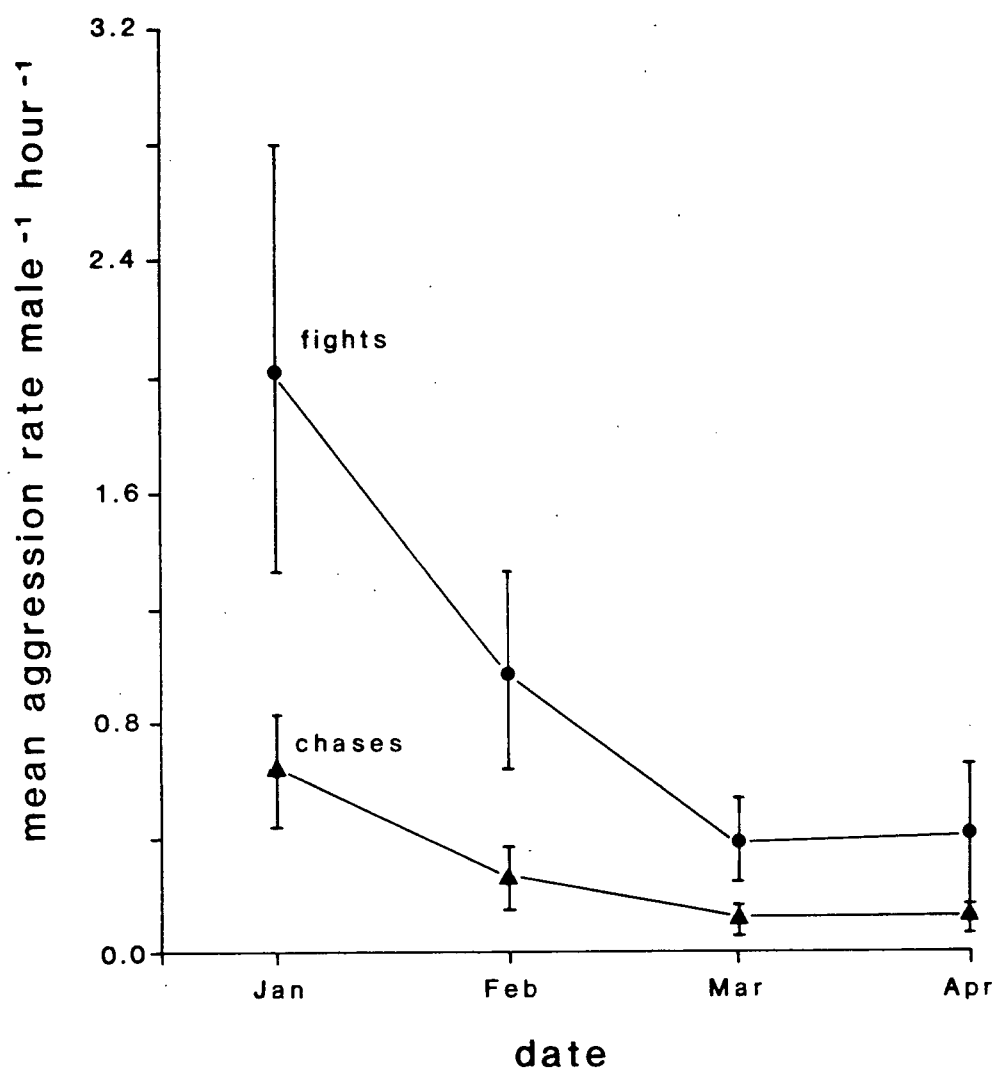


Figure 5.4 Changes in aggressive behavior over the breeding season (dots=means, vertical bars=95% confidence intervals).

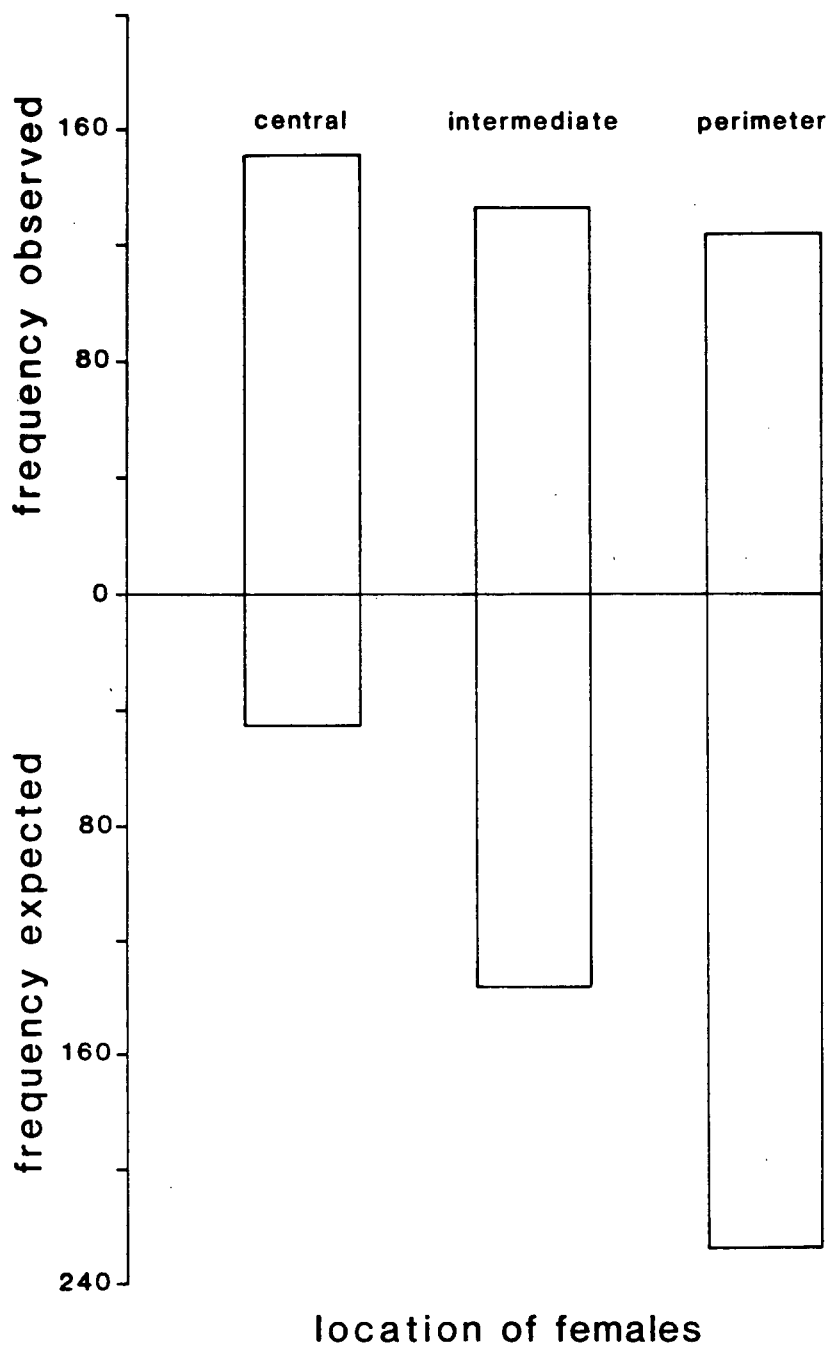


Figure 5.5 Female spatial distribution on leks. Upper histogram shows observed values, lower histogram shows expected frequencies under the null hypothesis that females choose position at random.

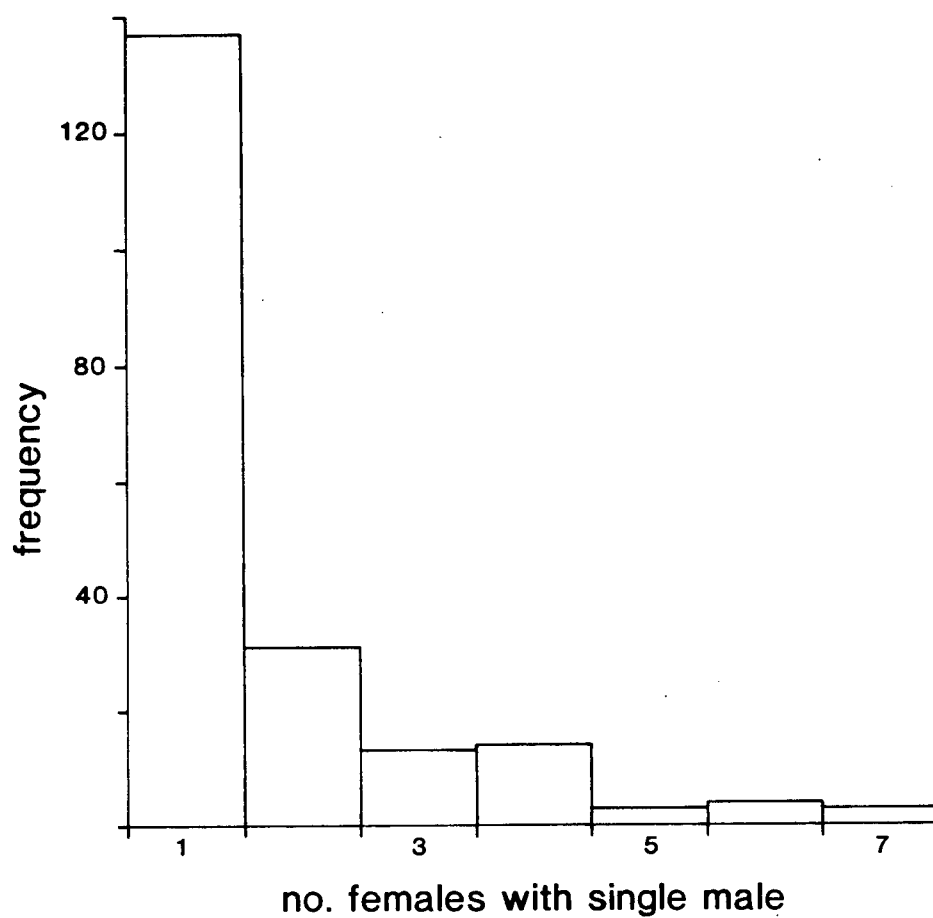


Figure 5.6 Female group sizes with individual courting males.

areas. A mean of 5.7 females were located on the lek for each observation period, and these females were on average distributed among 3.2 different males.

Agonistic encounters were more frequent than expected on central positions on the lek (Fig. 5.7, $\chi^2=116.1$, $df=2$, $p<0.001$), although males also fought in peripheral areas. Spot checks of male distribution indicated that males were spread out relatively evenly over the lek (based on expected numbers in the 3 concentric zones). Thus, the increased agonistic encounter rate in the center of the lek did not simply result from more males being present.

These results are consistent with Floody and Arnold's (1975) observations of a close correlation between the number of mating attempts and the number of agonistic encounters by individual Uganda kob males. Both behaviors were concentrated in central areas in Uganda kob, as is the usual case for other lekking species (Bradbury 1981). In addition, fights in central areas tended to be both more prolonged and more energetic than those in more peripheral areas.

Functions of fighting behavior

Buechner (1961a) suggested that aggressive behavior in the kob contributes to the establishment of dominance positions on the display ground. Males compete strenuously for possession of central courts and agonistic encounters frequently escalate into full-scale fights. In 204 of 305 fights observed (67%), no females were present with either combatant, suggesting that

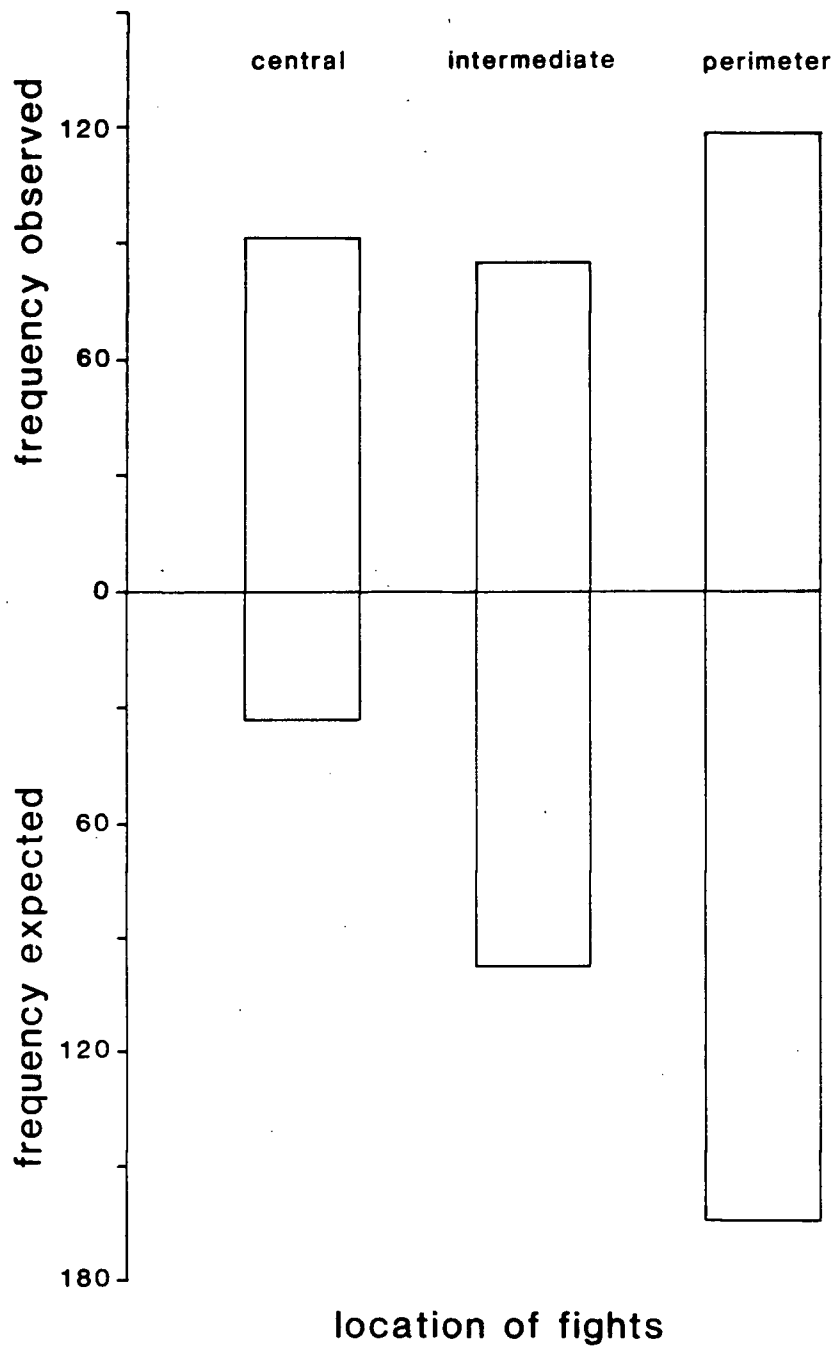


Figure 5.7 Spatial distribution of male fights. Upper histogram shows observed values, lower histogram shows the expected frequencies under the null hypothesis that the number of fights is related to the number of males in zones of different sizes.

these fights were concerned solely with deciding the lek positions of the males involved. However, in the other 33% of fights, at least one female was present in the court of one of the combatants. This suggests that many fights may disrupt mating activities of neighboring males.

To examine this hypothesis, I compared the relative probabilities of a male being engaged in a fight given that a female was or was not present. If fighting was not oriented towards disruption, fighting should be equally likely in both cases. I calculated the conditional probabilities of a fight occurring, given that a female was or was not present, according to Bayes' rule (Scheaffer and Mendenhall 1975), using the following probabilities calculated from 91 observations periods:

$$\begin{aligned} A &= p(\text{fight}) = 0.18 \\ A' &= p(\text{no fight}) = 0.82 \\ B &= p(\text{female present} \mid \text{fight}) = 0.33 \\ B' &= p(\text{female present} \mid \text{no fight}) = 0.07 \\ C &= p(\text{no female present} \mid \text{fight}) = 0.67 \\ C' &= p(\text{no female present} \mid \text{no fight}) = 0.93 \end{aligned}$$

$$p(\text{fight} \mid \text{female present}) = \frac{(A)(B)}{(A)(B) + (A')(B')} = 0.509$$

$$p(\text{fight} \mid \text{no female present}) = \frac{(A)(C)}{(A)(C) + (A')(C')} = 0.137$$

Thus, the probability of a fight occurring was approximately four times greater if a female was present than not. This suggests that neighboring males may initiate fights in order to either disrupt mating or to steal females.

During 14 out of 91 observation periods (15%) females changed location subsequent to fights. On these 14 occasions, the male that was challenged was courting on average 4.1 females before the fight and 0.9 females after the fight. As a result of this disruptive behavior, a total of 57 females moved to new locations, while 22 females changed position during the 77 observation periods (85%) characterized by no disruptive behavior. Subsequent movements of females are summarized in Table 5.2. Nearly twice as many disrupted females moved to a neighboring male (40%) than returned to their original partner (21%), and 39% left the lek entirely. The majority (64%) of movements of non-disrupted females resulted in females leaving the lek, while 36% resulted in females moving to neighboring males. These findings indicate that disruptive behavior greatly increased the frequency of movements by females on the lek, although a substantial proportion of females returned to their original partners. The data are inadequate to test whether the challenging male subsequently mated with females scattered by fighting. At worst, however, disrupting males temporarily forced females back into a "pool" from which they might later gain.

Consequences of fighting

Vigorous competition for access to females may expose males to substantial risks. During 16 hours of observations at leks, I recorded 4 instances of serious wounding during 305 fights;

Table 5.2 Movements of disrupted vs. non-disrupted females (proportion of total observations in parentheses).

	returned to origin	moved to neighbour	left lek	total no. females
disrupted	12 (0.21)	23 (0.40)	22 (0.39)	57
not disrupted	0 (0.00)	8 (0.36)	14 (0.64)	22

all of these were horn wounds to the sides or abdomen of combatants. Agonistic encounters between 2 males were frequently joined by a third male, who often directed his initial blows to the unprotected flanks and abdomen of the other combatants. Also, 3 out of 5 male carcasses found near leks showed symptoms of recent horn wounds. Moreover, the distribution of ages at death (obtained during the breeding season) differed significantly between the sexes (Fig. 3.8, $\chi^2=15.0$, $df=3$, $p<0.01$). A larger proportion of male than female carcasses were young to mid-aged adults, and these are the age classes most active on the display ground (Leuthold 1966). Aggressive competition between males may explain the skewed sex ratios observed in both white-eared kob (58-62% females) and Uganda kob (59% females; Buechner 1974) populations.

Discussion

Emlen and Oring's (1977) hypothesis that species with moderate breeding synchrony should be more polygynous than either asynchronous or highly synchronous breeders predicts that sexual selection should be greater for the moderately synchronous white-eared kob than the asynchronous Uganda kob. One consequence of increased sexual selection is increased sexual dimorphism in size and coloration. White-eared kob differed markedly from the conspecific Uganda kob in the degree of color dimorphism, but not in size dimorphism.

Dark coloration has no known adaptive value other than male advertisement. Few savannah-dwelling antelope species are

characterized by extreme melanism, presumably because of the disadvantages of being highly visible to predators. Moreover, dark pelage absorbs considerably more solar radiation than light pelage, making individuals more prone to heat stress in tropical climatic conditions (Finch 1972). Mean daily maximum temperatures in the Sudan study area range from 30-39° C., so the potential for thermal stress is considerable. Previous studies in hot savannah grasslands suggest strong selection against dark coat color in African cattle herds (Finch and Western 1977). I argue that contrasting black and white coloration of males may serve largely for sexual advertisement. Recent theoretical work has shown that otherwise non-adaptive traits of males may evolve, if they are used by females as arbitrary mating cues (Lande 1980, 1981; Kirkpatrick 1982). Thus, dark coloration in white-eared kob males may constitute an example of "runaway" sexual selection (Fisher 1958).

A second prediction from increased sexual selection is that white-eared kob males should compete more vigorously than Uganda kob for possession of preferred lek courts. Results from this study suggest that the overall frequency of agonistic encounters is significantly higher for the moderately synchronous white-eared kob than for the asynchronous Uganda kob, supporting the hypothesis. However, fighting frequency declined substantially over the course of the breeding season, and by the end of the period the white-eared kob aggression rate was similar to values reported for Uganda kob. The significance of this decline is not clear. It may simply reflect that dominance relations on

the display grounds are gradually established over the course of the breeding period. Alternatively, males may simply have less to gain by supplanting males in preferred courts late in the mating season when most females have already been served, while the risks of injury remain the same. Thus, the most successful male mating strategy may involve fighting vigorously early in the mating season when potential fitness gains are highest, and less vigorously later on. The data from this study are inadequate to discriminate between these hypotheses.

Lekking males incur a high risk of mortality as a consequence of intrasexual competition for access to females. I observed several instances of serious wounding, and lekking males frequently attacked the undefended flanks of other males engaged in territorial disputes. Distribution of ages at death differed significantly between the sexes, suggesting that strong intrasexual selection may result in predictable changes in age-specific mortality patterns and a skewed sex ratio. Clutton-Brock et al. (1985) have recently suggested that juvenile mortality is higher for males than females in species with high sexual dimorphism. I argue, in addition, that mortality of reproductive-aged males may be higher than that of females under conditions of strong sexual selection. This may explain the adult sex ratios skewed towards females frequently observed in ungulates (Cowan 1950; Clutton-Brock et al. 1982).

Aggressive behavior not only influences dominance relations of males on display grounds, but it also disrupts the mating activities of neighboring males. Males that were courting

females were much more likely to be engaged in fights than unattended males. Thus, much of the observed aggression was directed towards successfully mating males. Females were scattered immediately following disruptive fights, although a substantial proportion of females subsequently returned to their original male partners. Disruptive fighting periodically redistributes females onto new courts, which is advantageous to challenging males.

Such disruptive behavior has not been previously described for mammalian leks, although it occurs in some insect and bird species (Foster 1983; Trail 1985). I suggest that disruption may be a successful strategy in lekking populations like the white-eared kob with restricted breeding seasons. In species that breed year-round, peripheral males on leks may do better by waiting for the owners of preferred central courts to weaken, rather than incur the substantial risks of fighting.

Recent reviews of lek behavior have examined the importance of disruptive behavior in the evolution of lek mating choice systems (Wrangham 1980; Foster 1983). Results from this study suggest that disruptive behavior may be more prevalent than previously assumed, particularly under conditions of increased sexual selection associated with a restricted mating season as in white-eared kob.

CHAPTER 6. AGE-SPECIFIC MORTALITY: AN ALTERNATIVE APPROACH

Introduction

Age-specific survivorship is basic to many population models used by ecologists (Leslie 1945; Beverton and Holt 1957; Gadgil and Bossert 1970; Schaffer 1974; Stearns 1976; Gulland 1977). Since it is rarely possible to monitor the fates of true cohorts over their entire life spans (Lowe 1969; Connell 1970; Sherman and Morton 1984), many studies estimate survivorship from samples of the population age structure (Seber 1973; Ricker 1975; Caughley 1977). These indirect methods of calculating "static" life tables assume that the population rate of increase (r) has remained constant for several generations, producing a stable age distribution. Despite the widespread use of these methods, few published life table studies meet adequately the underlying assumptions on which they are based (Caughley 1966).

Two of the most frequently used methods estimate age-specific survivorship from (A) the standing age distribution (s_x , the number of age x individuals in a population at a specified time relative to the number of new-born young), or (B) the standing distribution of ages at death (s'_x , the relative frequencies of individuals of age x that die over a specified time interval, usually 1 year). For method A, the standing age distribution is converted to an l_x schedule by multiplying s_x values by e^{-rx} , to discount the effects of the population rate of increase on the observed age distribution. For method B, the standing distribution of ages at death is likewise converted to

a d_x schedule by multiplying the s'_x values by e^{rx} . This d_x schedule is then used to calculate the corresponding l_x schedule, and the ratio d_x/l_x is used to estimate the age-specific mortality rate, q_x . Both methods A and B rely on the assumption that the population has a stable age distribution, and require precise estimates of population numbers over several generations in order to calculate r .

I propose an alternative method of estimating age-specific mortality rates based on Pielou's (1977) approach, that is free of these restrictive assumptions, and compare it to methods currently in use.

The model

Simply put, q_x values indicate the probability of dying for individuals in each age class over the time interval from t to $t+1$. Thus, it is the proportion of individuals of age x that die over a given time interval relative to the number alive at the beginning of the interval. As indicated by Pielou (1977),

$$q_x = \frac{c_x}{n_x},$$

where c_x = number of age x individuals that die during the year, and
 n_x = initial number of age x individuals.

In field studies it is rarely possible to count all

individuals of known age in a population or even to count all those that die in a given year. However, these values may be estimated by multiplying the sampled frequencies of each age class for both live and dead populations by overall population estimates. Note that

$$\begin{aligned} c_x &= C f_x \text{ and} \\ n_x &= N g_x , \end{aligned}$$

where $C = \sum c_x$,
 $N = \sum n_x$,
 f_x = sampled proportion at age x among carcasses, and
 g_x = sampled proportions at age x among live initial population.

$$\text{Thus } q_x = \frac{k f_x}{g_x} , \quad \text{equation 1}$$

where $k = C / N$.

In some field situations, the initial standing age distribution may be unavailable for one reason or another. However, it is possible to derive these values from the standing age distribution at the end of the interval. Suppose

h_{x+1} = sampled proportions at age $x+1$ among live population subsequent to annual mortality and
 N' = total population size at end of interval.

Then $n_x = N'h_{x+1} + Cf_x$ and equation 1 can be rewritten as

$$q_x = \frac{C f_x}{N' h_{x+1} + C f_x} \quad \text{equation 2}$$

In order to calculate a q_x schedule using equations 1 or 2, one requires an estimate of annual mortality, standing distribution of ages at death, and the standing age distribution either at the beginning or the end of the period in which mortality was monitored. Equation 2 also requires an estimate of population numbers at the end of the observation period. There are no further assumptions of a stable age distribution and constant rate of population increase.

Methods

To investigate the utility of the proposed technique, three approaches were employed. First, I compared estimates of age-specific mortality derived by the proposed technique to published values (Sinclair 1977) for the African buffalo, Syncerus caffer. Second, I performed a series of computer simulations, using Sinclair's buffalo data, to estimate the sampling variation resulting from three alternative methods of estimating age-specific mortality. Third, I tested the accuracy of the three methods when the underlying assumption of a stable age distribution is violated, by calculating age-specific mortality following a temporary perturbation of a hypothetical African buffalo population.

Calculation of age-specific mortality

Sinclair (1977) derived a life table for female buffalo in the Serengeti ecosystem from a found sample of 246 carcasses 2 years and older. Survival of calves (age 0 to 1) and yearlings (age 1 to 2) was estimated independently by counts of these age classes per 100 females from aerial photographs (Sinclair 1977). At the time of the study the population was increasing at a constant rate ($r=0.077$), so Sinclair calculated d_x by multiplying the standing distribution of ages at death by e^{rx} to incorporate the effect of population increase. The resultant q_x schedule is shown in Fig. 6.1.

Sinclair also shot a random sample of 80 females 2 years and older over the same three year period (1967-1969) that the skull sample was collected (Sinclair unpublished). The ages of the shot sample and the carcass sample were determined from counts of tooth cementum annuli.

The standing age distribution from the live population was converted to a g_x distribution by dividing the frequency of each age group in the shot sample by the total sample size, as shown in Table 6.1. The standing distribution of ages at death was converted to an f_x distribution by dividing the number of carcasses of age x in the found sample by the total number of carcasses (246). For subsequent calculations of age-specific mortality, I smoothed both the f_x and the g_x distributions by taking a three point running average for sequential age classes.

I estimated q_x from the ratio of f_x over g_x , multiplied by the annual mortality rate of adults (0.0596) averaged over the

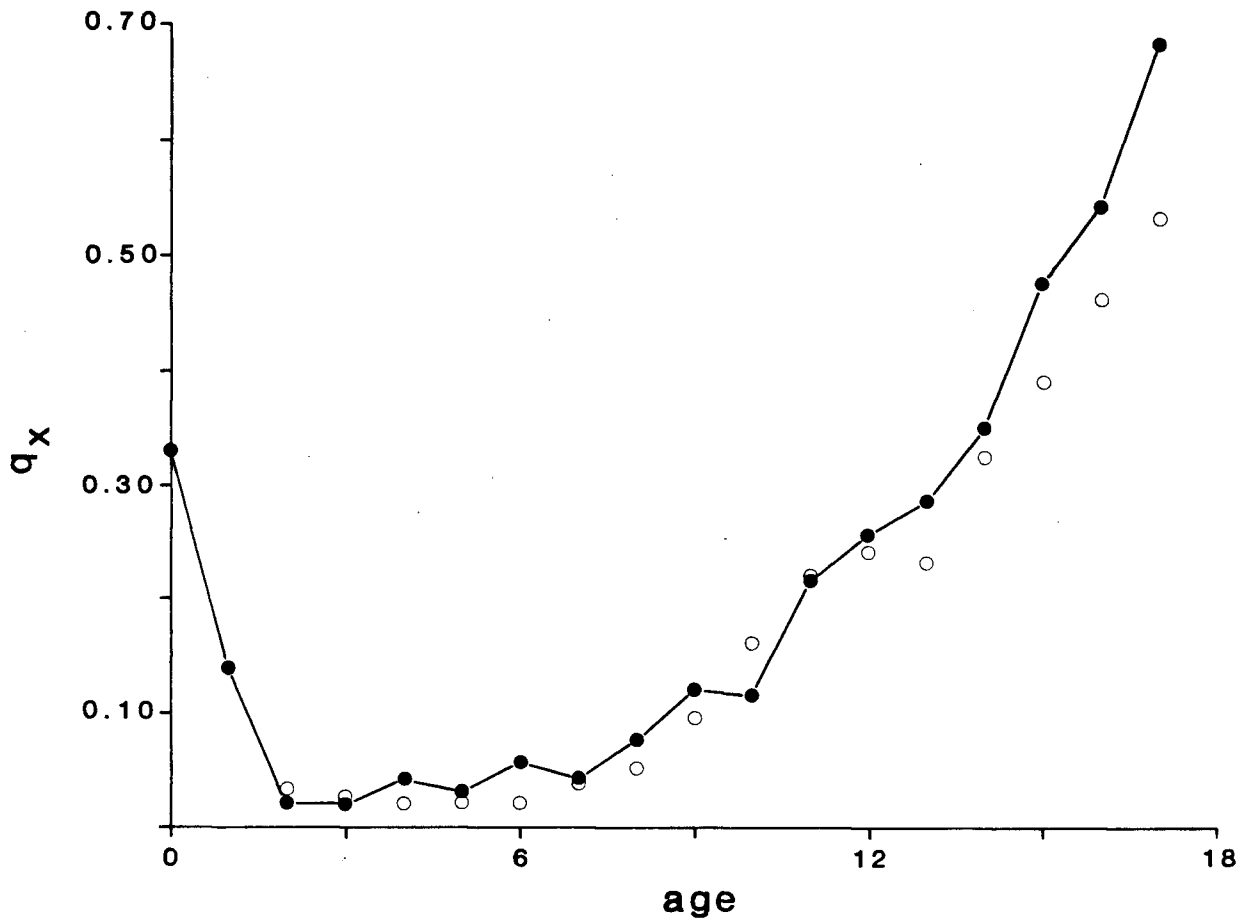


Figure 6.1 African buffalo age-specific mortality curve estimated using methods B and C. Solid dots indicate q_x estimates obtained using method B (data from Sinclair 1977). Open dots indicate q_x estimated using the new method, C.

Table 6.1 Age distribution data for female African buffalo, from a found carcass sample (Sinclair 1977) and a live sample (Sinclair personal communication). Age-specific mortality rate, q_x , calculated according to the new method, C (*: estimated from polynomial regression of q_x values for age classes 2-13; $q_x = 0.0564 + 0.0214x + 0.00290x^2$; $r^2=0.950$).

age	carcass sample	live sample	smoothed f_x	smoothed q_x	q_x
2	9	5	0.037	0.075	0.029
3	9	7	0.045	0.109	0.025
4	15	14	0.046	0.154	0.018
5	10	16	0.057	0.163	0.021
6	17	9	0.052	0.141	0.022
7	11	9	0.062	0.096	0.038
8	18	5	0.072	0.084	0.051
9	24	6	0.083	0.054	0.092
10	19	2	0.099	0.038	0.155
11	29	1	0.100	0.029	0.206
12	25	4	0.100	0.025	0.238
13	19	1	0.081	0.021	0.230
14	16	0	0.065	n.a.	0.325*
15	13	0	0.049	n.a.	0.388*
16	7	0	0.032	n.a.	0.456*
17	4	1	0.016	n.a.	0.531*
18	1	0	0.004	n.a.	0.611*

three year period of study (Sinclair 1977). Although the standing age distribution was not collected prior to the found sample, equation 1 is still appropriate because the buffalo population had been increasing at a constant rate for several years prior to the collection period, presumably producing a stable age distribution. Due to the relatively small size of the shot sample, only one individual older than 13 years was taken. I therefore estimated q_x values for age classes 14-18 using a polynomial curve fitted to data for ages 2-13 ($r^2=0.950$).

Sampling distributions

The methodology employed follows Polacheck's (1985) procedure for simulating sampling distributions for specified survival vectors. A series of computer simulations were executed to assess the sampling variation of age-specific mortality estimates derived from three different methods: (A) age-specific survivorship estimated from the ratio of adjacent age frequencies from the standing age distribution; (B) age-specific mortality estimated from the standing distribution of ages at death; and (C) age-specific mortality estimated from equation 1 above. Demographic data from Sinclair's (1977) African buffalo study were used for each method. Age-specific mortality rates were calculated according to the following equations (Caughley 1977):

method A: $q_x = 1 - (s_x / s_{x-1})$

method B: $q_x = d_x / 1 - \sum_{i=0}^{x-1} d_i$

method C: $q_x = k f_x / g_x$

Sinclair's (1977) schedules for l_x and d_x , corrected for the population rate of increase, were used to calculate the expected standing age distribution (s_x) and standing distribution of ages at death (s'_x). The smoothed f_x and g_x distributions were taken as the expected values for method C.

Simulated age distributions were created by generating pseudorandom numbers from a uniform distribution between 0 and 1.0 and assigning each random number to a specific age class by comparing the random number to the cumulative relative frequencies of s_x , s'_x , f_x , or g_x . For example, if a random number between 0 and 0.138 was drawn, one individual would be assigned to age class 0 in the simulated standing age distribution, if a number between 0.138 and 0.230 was drawn, one individual would be assigned to age class 1, and so on. For methods A and B, age distributions were simulated for 1000 sampled individuals. For method C, each of the f_x and g_x distributions were simulated for 500 individuals, giving a total sample of 1000. Age-specific mortality rates were calculated for each simulated age distribution, and this procedure was repeated 400 times to generate sampling distributions of age-specific mortality rates using each of the three methods. All

simulations were programmed in C Language and were executed on a Digital VAX 11/750 computer, running under a Berkeley UNIX 4.2 operating system.

Effects of an unstable age distribution

I first calculated the stable distribution that would result from Sinclair's (1977) l_x and d_x schedules, assuming a constant rate of increase ($r=0.077$). Then, for a hypothetical female population of 50,000 buffalo, I calculated the standing age distribution produced by 2 years of increased mortality, followed by a third year in which age-specific mortality rates returned to normal. During the 2 years of increased mortality, I arbitrarily set each q_x at twice the values shown in Table 1. This scenario produced (1) a temporary decrease in buffalo population numbers from 50,000 to as low as 45,000, before increasing in the third year to 49,000; and (2) an unstable age distribution. This scenario would mimic the effects of temporarily harsh weather conditions, for example a drought, on an otherwise increasing population. I then calculated q_x using methods A, B, and C for the hypothetical population at the end of the third year.

Results

Age-specific mortality estimates derived using methods B (from Sinclair 1977) and the new method C are shown in Fig. 6.1. There is close agreement between the two q_x curves, indicating that the proposed method (C) yields comparable results to the traditional method (B). The fit between the two curves is close for age classes up to age 13, and diverges thereafter for older age classes whose q_x values were estimated using a fitted polynomial curve.

Fig. 6.2 shows the standard deviations for q_x derived by the three alternative methods. Method A had the greatest variation, particularly for younger age classes, while method B had the lowest variation at all ages. Method C was comparable to B for age classes 2 through 9, but sharply increased for older age classes. Method A had an order of magnitude greater variability than method B, even for younger age classes.

Both methods A and C produced sampling distributions that were significantly skewed and kurtotic (Table 6.2). All of the sampling distributions for methods A and C were positively skewed. 71% of method C and 44% of method A distributions were significantly kurtotic. In contrast, distributions derived from method B were neither skewed or kurtotic. Thus, sampling distributions derived using method B are approximately normal, while methods A and C produce distributions that, while bell-shaped, show some departure from normality.

The comparative robustness of the three methods is demonstrated in Fig. 6.3. Age-specific mortality curves

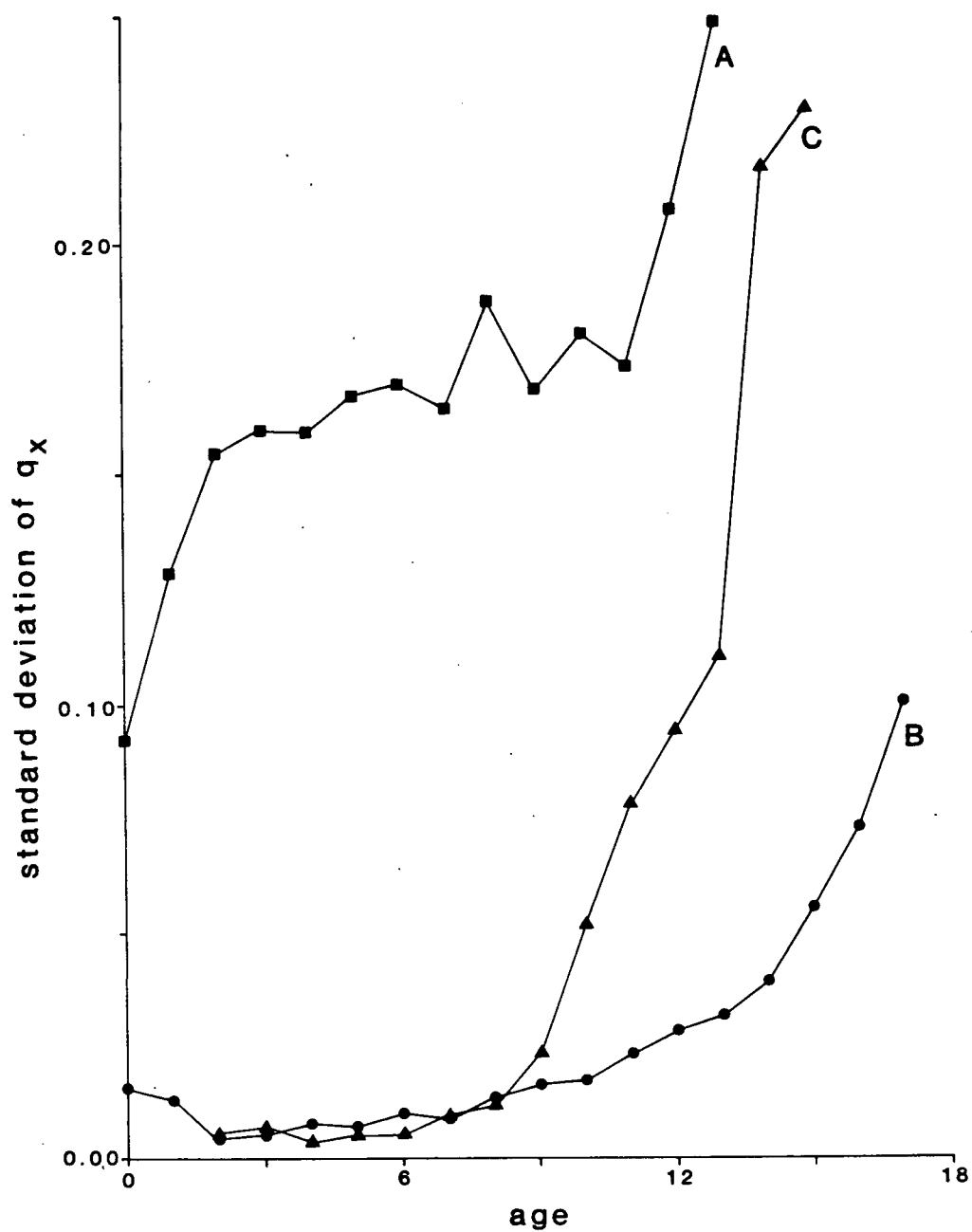


Figure 6.2 Sampling variation resulting from the use of 3 alternative methods for calculating q_x .

Table 6.2 Skewness and kurtosis of simulated sampling distributions, as indicated by g_1 and g_2 statistics (Snedecor and Cochran 1967). Values significantly different from 0.0 ($p \leq 0.05$) indicated by *.

Age	Method A		Method B		Method C	
	g_1	g_2	g_1	g_2	g_1	g_2
0	0.60*	0.52*	0.03	-0.19	n.a.	n.a.
1	0.33*	0.14	-0.01	-0.25	n.a.	n.a.
2	0.37*	0.25	-0.03	-0.06	0.31*	-0.03
3	0.41*	0.43	0.23	0.07	0.39*	-0.02
4	0.72*	0.87*	0.02	-0.38	0.31*	-0.06
5	0.71*	1.64*	0.32*	0.02	0.57*	0.15
6	0.46*	0.20	0.15	-0.05	0.60*	0.62*
7	0.22	-0.30	0.23	-0.15	0.70*	0.52*
8	0.44*	0.26	0.16	-0.33	0.48*	-0.13
9	0.52*	0.39	0.10	-0.22	0.65*	0.67*
10	0.50*	0.56*	0.02	-0.06	1.42*	3.64*
11	0.56*	0.37	0.05	-0.04	1.29*	2.82*
12	0.61*	0.31	0.03	0.09	1.74*	6.08*
13	1.14*	2.05*	-0.05	0.11	2.04*	7.66*
14	0.82*	0.81*	0.02	0.01	1.50*	1.51*
15	2.81*	14.57*	-0.06	-0.17	1.26*	0.87*

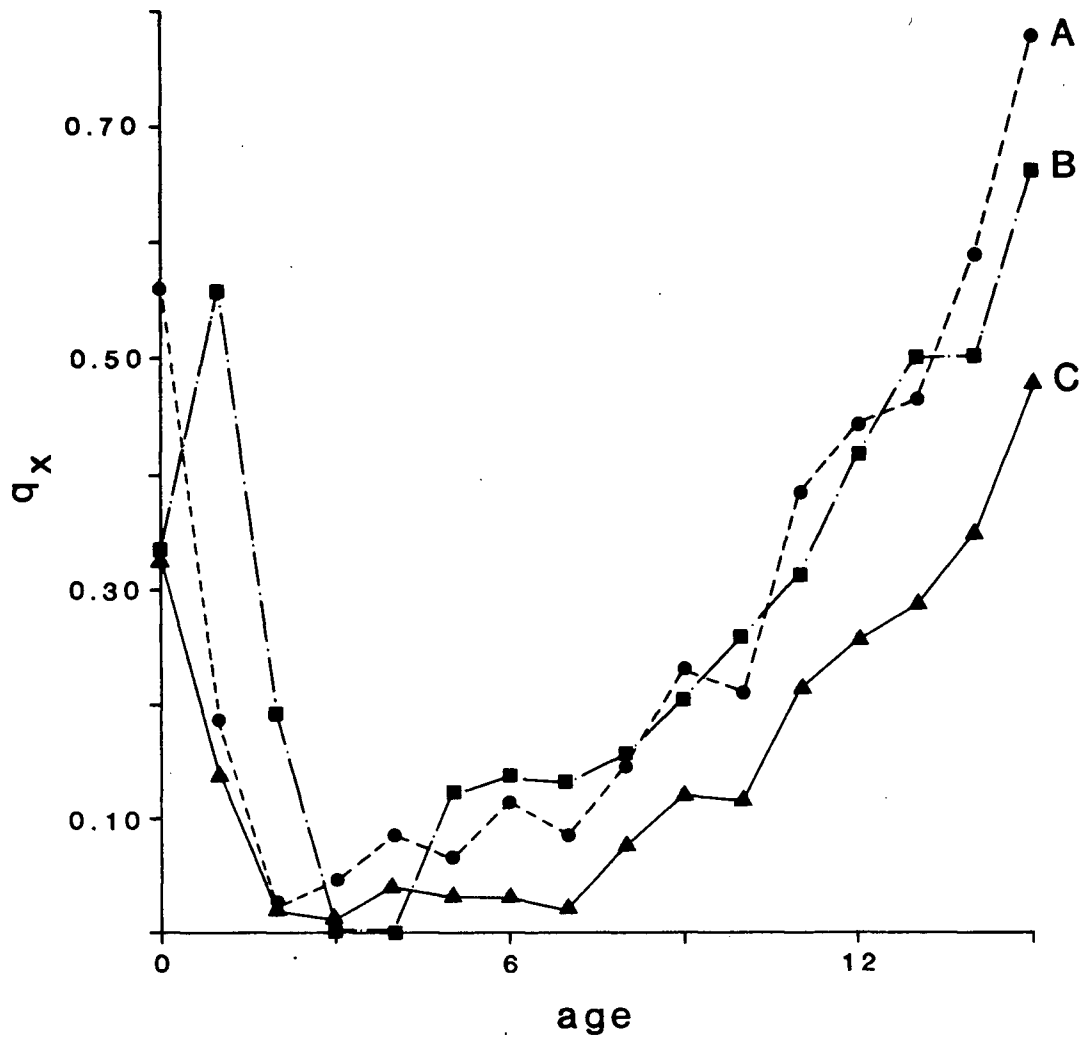


Figure 6.3 Age-specific mortality curves estimated from an unstable age distribution, as described in the text, using 3 alternative methods. (assuming that the fates of all members of the population are known, i.e., there is no sampling variation).

estimated using methods A or B were biased by a slight departure from the underlying assumption of a stable age distribution, while method C was not affected. The scenario producing Fig. 6.3 involved a short (2 year) period of increased mortality, much like the presumed effect of a temporary drought, with a subsequent return to normal conditions. Such perturbations may be frequent in many natural populations (Wiens 1977, Schoener 1982). To the degree that such perturbations do occur, we should expect few natural populations to exhibit a stable age distribution, seriously limiting the usefulness of methods A and B.

Discussion

Advantages of the proposed method

Under circumstances familiar to most field biologists, life table calculations using conventional techniques are rarely justified because of restrictive assumptions. One way to avoid this problem is to use independently obtained estimates of the standing age distribution and the standing distribution of ages at death. Because age-specific mortality rates are calculated directly from population deaths relative to those potentially vulnerable, there is no need to know long-term trends in population size, or whether the age distribution is stable. As

in other methods of estimating age-specific mortality, there is an underlying assumption that sampled age frequencies are representative of the population as a whole. If social factors promote the uneven spatial distribution of certain age classes, then either a shot sample or a carcass sample may be biased.

Equations 1 and 2 do require an estimate of total population mortality, expressed as a proportion of initial numbers. This is often a difficult statistic to obtain. However, it requires less effort to obtain a single precise estimate of total annual mortality than to measure precisely population numbers over an extended time period. Moreover, there is no underlying assumption that the population has reached a stable age distribution.

One advantage of the proposed technique is that the shape of the q_x curve is determined only by the ratio of the f_x and q_x distributions. If k (total annual mortality) is estimated inaccurately, the q_x curve will be displaced upwards or downwards, but the shape of the curve will remain the same. As Caughley (1966) suggested, the shape of the q_x curve is perhaps the most robust basis for comparisons of age-specific selection pressures experienced by different populations. From this point of view, the proposed method is preferable to traditional techniques that rely on underlying assumptions that can fundamentally change the shape of the q_x curve.

Another benefit of the proposed technique is that it allows the calculation of age-specific mortality rates at frequent intervals during periods of rapid population fluctuation, which

is not possible using current methods. Such data may yield new insights into changes in age-specific selection pressures coincident with population fluctuations.

Using the proposed method C it should also be possible to determine whether a population is increasing or decreasing simply from the age distributions and a single estimate of annual mortality. Let us assume that data on both the standing age distribution and standing distribution of ages at death are collected for a given population, and a q_x curve is estimated using method C. Then, suppose that the s'_x data is then used to calculate q_x values using method B, under the null hypothesis that population numbers have remained constant. If the q_x curve generated using method B lies below the curve generated using method C (i.e. age-specific mortality under the assumption that $r=0.0$ is less than an unbiased estimate of age-specific mortality), then this implies that the population is decreasing. Conversely, if q_x values calculated under the null hypothesis of $r=0.0$ are greater than the unbiased estimates, then this implies that the population is actually increasing.

This reasoning is valid only if age-specific natality remains unchanged. If natality rates increase at the same time that age-specific mortality rates are increasing, then by using the above procedure one might falsely conclude that a population was decreasing when, in fact, it was remaining constant or even increasing. Such situations, however, may be rare in nature. If increased age-specific mortality rates result from a relative shortage of resources (e.g. during a drought or as a result of

large-scale habitat changes) then this process, if anything, should similarly cause a decrease in natality. The only realistic circumstances under which such a scenario seems likely is when mortality changes are due to an unusual event, such as the outbreak of an epidemic or introduction of predators, coincidental with an increase in natality rates.

Comparisons between methods

The simulated sampling distributions allow us to judge the relative precision of the three procedures for estimating age-specific mortality. Method B, based on the d_x schedule derived directly from the standing distribution of ages at death, is less subject to sampling variation than either method A or the proposed method C. Moreover, using method B it is impossible to generate biologically unrealistic q_x values (i.e. greater than 1.0 or less than 0). Method A can generate q_x values less than 0 and method C can generate q_x values greater than 1.0. Strictly on the basis of sampling variation, method B should be preferred to method C, which is in turn preferable to method A.

Method C is similar in precision to Method B for younger age classes, but is less precise for older age classes. There are several reasons why imprecise estimation of survival for older age classes using method C may not cause serious problems. First, in most populations the number of individuals in the older age groups is much less than numbers in younger age groups, so that sampling errors would be small relative to the

whole population. Second, in many species older individuals are no longer reproductively active, so inaccuracies in estimating their frequencies will have little bias effect on population models. Third, if q_x values for younger age classes are known with precision, curve-fitting procedures may be employed to discount the effect of high sampling variation for older age classes (e.g. Chapman 1964, Caughley 1966, 1977).

Sampling variation becomes more pronounced for older age classes using all three methods. This is because age-specific mortality is derived from ratios of two frequencies, that are themselves subject to sampling variation. The denominator in each of the equations used for methods A, B, and C, becomes increasingly smaller as a function of age. The smaller that the expected frequency is, the greater the effect of random variation (Fig. 6.4). As a consequence, sampling variation increases for older age classes.

Methods A and B produce inaccurate q_x curves when a stable distribution has not been reached, while the proposed method C is not affected. This problem will be most serious for long-lived species, since it would take many years at a constant rate of population increase to produce a stable age distribution. Thus, method C is more robust than either methods A or B.

When the underlying assumptions are met, q_x estimation from the standing distribution of ages at death (method B), is the most precise procedure available. However, when the underlying assumptions of a stable age distribution and constant rate of population increase are not met, method C offers an alternative

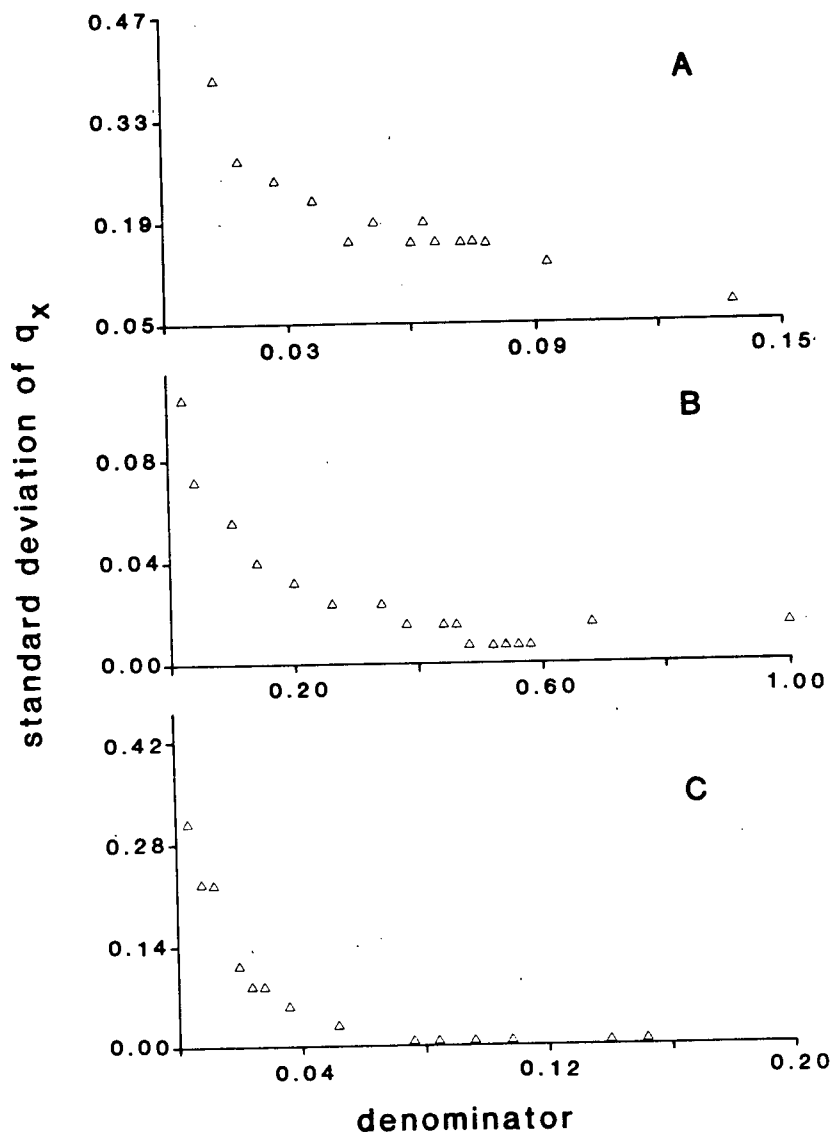


Figure 6.4 Sampling variation of q_x estimates as a function of denominator value in the equations used.

approach with a tolerable loss in precision.

CHAPTER 7. GENERAL DISCUSSION

Food limitation

Several factors are known to limit ungulate populations: (1) food availability (Bobek 1977; Sinclair 1977; McCullough 1979; Fowler 1981; Clutton-Brock et al. 1982; Houston 1982), (2) predation (Mech and Karns 1977; Caughley et al. 1980; Gasaway et al. 1983), and (3) disease (Christian et al. 1960; Sinclair 1977; Berry 1981). Moreover, a given population may be limited at different times by different factors (May 1977; Peterman et al. 1979). For example, long-term studies indicate that Serengeti wildebeest and buffalo populations were limited by rinderpest prior to a successful eradication program in the early 1960's (Sinclair 1977; Sinclair and Norton-Griffiths 1979). A temporary period of increase followed rinderpest eradication, and these populations are now apparently limited by food availability (Sinclair 1977; Sinclair and Norton-Griffiths 1982; Sinclair et al. 1985). Similarly, Gasaway et al. (1983) reported that some Alaskan moose populations are regulated at low population densities by wolf predation, following a series of harsh winters that depressed prey population numbers. These results indicate that multiple equilibria may be more prevalent than previously assumed.

At the outset of this study, extreme seasonal climatic variation suggested that the white-eared kob population might be limited by food availability during the dry season period. I

tested this hypothesis by attempting to falsify a number of its predictions. Results indicated that kob mortality during the dry season, when food intake was below requirements, was considerably greater than at other times of the year. Fat reserves (a measure of body condition) declined dramatically during the dry season at the same time that mortality was increasing. Finally, unusual rainfall during the 1982 dry season, which produced increased food availability, resulted in decreased adult mortality. On the basis of this evidence, there is no reason to reject the food hypothesis.

Food availability during the dry season is affected by both environmental conditions and herbivore population density. If environmental conditions were to remain constant for an extended period of time, increased mortality resulting from intra-specific competition for food should serve to regulate kob population numbers. However, most savannah ecosystems show considerable year to year variation in rainfall. Results from this study suggest that total adult mortality is highly sensitive to the duration of sub-maintenance dry season conditions. This predicts that savannah herbivore populations should fluctuate considerably from year to year.

Seasonal migration

Two hypotheses have been advanced to explain the adaptive function of migration by large herbivores. The first hypothesis suggests that herbivores migrate in order to take advantage of ephemeral distributions of food supplies (Pennycuik 1975; Maddock 1979). The second hypothesis (Western 1975) suggests that herbivores unable to meet their metabolic water requirements from forage are obliged to migrate during dry periods to permanent water supplies. During wet periods, herbivores disperse into surrounding areas to forage at will.

Migration patterns of white-eared kob were consistent with both hypotheses, since during the dry season water was restricted to the same areas that offered the greatest abundance of green forage. Like many problems in ecology (Krebs 1985), the examination of distribution patterns was greatly affected by the scale of observation. Data from aerial surveys indicated poorly that kob dry season movements tracked the availability of food and water supplies, while ground surveys demonstrated this relationship more clearly. Choice of the wrong scale of observation could easily lead one to falsely reject either of the resource acquisition hypotheses.

In addition to the problems of scale, it is often difficult to measure resources in terms that are meaningful for the animals involved. Not all vegetation may be available to herbivores, due to the effects of vegetation structure (Bell 1971). Furthermore, as shown in this study and elsewhere (McNaughton 1984), continual cropping is a common feature of

many grazing ecosystems. Thus, simple measures of resource abundance are not necessarily valid indices of resource availability.

Many studies have concluded that animal migration tracks shifting resource distributions (Dingle 1980; Sinclair 1983). However, most studies (including this one) have been based on indirect, correlative evidence. Animal migration may have an entirely different primary function, such as avoiding predators or reducing parasite loads by periodic movement into new habitats, and only secondarily track resources. Consider an hypothetical population under strong selective pressure to remain transient. It should then be of selective advantage to secondarily "choose" a migration route that also tracks resources.

For example, results from this study and elsewhere in Africa (Pennycuik 1975; Western 1975) suggest that migration tracks resources. This pattern is most apparent in the dry season, when resources are scarce. However, there is currently no convincing explanation why these same populations move elsewhere during the wet season, since the dry season ranges also have abundant forage during the wet season. There is some supporting evidence that migratory ungulates in the Serengeti can not be regulated by predators, since the predators are unable to follow the herds because of the need to feed immobile young during a long period of dependency (Schaller 1972; Hanby and Bygott 1979). Thus, migration may have evolved primarily as an anti-predator adaptation, with a secondary selection pressure

to cue movements to resource distribution. Since in these same ecosystems other species (and sometimes population sub-groups) persist without migration, it is clear that migration in search of scarce resources is not obligatory for survival.

Breeding phenology

Mammals living in seasonal environments should time production of young to the period of the year when food is most abundant (Sadleir 1969; Sinclair 1983a). Results from this study are consistent with this hypothesis, since kob gave birth during the late wet season, when food availability was highest. However, white-eared kob continued to lactate throughout the dry season, when food limitation was most pronounced. As a consequence, females were exposed to considerable nutritional stress, and had lower fat reserves than either non-lactating females or males in the population. Since food was also abundant early in the wet season, it is puzzling that calf production did not occur earlier.

It is possible that females are not able to produce young in the early wet season because of an obligatory time lag for replenishing fat reserves following the onset of the rains (Sinclair 1983a). This hypothesis implies that kob reproductive phenology has evolved to ensure adequate female body condition prior to birth rather than food intake during lactation (Sinclair 1983a). Alternatively, birth timing may reflect other selection pressures. Kob calves are born largely during the northward migration to the dry season range. I propose that

calving at this time may serve as an anti-predator strategy, since there are few predators present in the northern areas. By delaying calf production until the late wet season, kob may avoid predation on vulnerable young and females in the immediate post-calving period.

Breeding synchrony and male aggression

The white-eared kob has a lek mating system (Bradbury 1981), in which males aggressively compete for position on specialized display grounds, from which females choose their mates. Emlen and Oring's (1977) breeding synchrony hypothesis predicts that male aggression and sexual dimorphism should be higher in the moderately synchronous white-eared kob than in the asynchronous Uganda kob. Results from this study were consistent with these predictions: white-eared kob males were more aggressive (particularly in the early part of the breeding season) and exhibit pronounced color dimorphism relative to the conspecific Uganda kob.

In addition, I considered the consequences of male aggression. Previous studies (Buechner 1961a) have suggested that lek aggression in ungulates serves primarily to establish dominance relations among lek males, but recent evidence for other species (Foster 1983) suggests that male aggression may also disrupt the breeding activities of neighboring males. Results from this study showed that the majority of male conflicts occurred in the absence of females, and were presumably concerned with establishing dominance relations.

However, males fought more frequently when females were present, causing a redistribution of females on the lek, indicating that disruption is an important feature in kob leks. Fighting was related to increased mortality of young adult males, suggesting that competition for mates causes the skewed adult sex ratio in the kob population.

Age-specific mortality patterns

Most conventional methods of estimating age-specific mortality rates rely on restrictive assumptions of a constant rate of population increase and a stable age distribution. In practice, these assumptions are seldom met (Caughley 1966), limiting the usefulness of these approaches.

I devised an alternative method for estimating age-specific mortality rates based on the annual population mortality rate and age distributions from both the live population and naturally occurring deaths that is free of these restrictive assumptions. The method was illustrated using demographic data for the African buffalo (Sinclair 1977). I compared the proposed to two conventional methods using Monte Carlo simulation techniques.

The advantages of the proposed method are: (1) it is more robust than conventional methods because it has less restrictive underlying assumptions, (2) it can be applied at frequent intervals to fluctuating populations, and (3) under some circumstances it may be used to estimate whether a population is increasing or decreasing. The proposed method is, however, less

precise than calculating q_x values directly from the age distribution of carcasses, provided that the underlying assumptions are adequately met.

General conclusions

Evidence from this study suggests that the Boma white-eared kob population is limited by the availability of green forage during the dry season. White-eared kob exhibit a number of adaptations in response to this selection pressure. Seasonal migration allows kob to utilize refuge areas that supply green forage and water when these resources are scarce elsewhere in the ecosystem. Year-round residency is precluded by flooding of these refuge areas during the wet season. Kob time the production of young to coincide with peak forage abundance in the late wet season. Thus, adaptation to seasonal resource limitation explains several important aspects of kob life history.

These findings suggest that other savannah-dwelling herbivores may be limited similarly by food abundance. However, there are 2 features of the Boma ecosystem that are probably uncommon in most other savannah ecosystems. First, during the dry season adequate forage is restricted to a relatively small proportion of the Boma ecosystem. Kob population densities in the dry season range commonly exceed 1000 individuals/km². Very few other ungulate populations occur at such high densities, even in natural reserves. Second, predators are rare in the Boma ecosystem, unlike most other savannah ecosystems in Africa.

Thus, in many other savannah ecosystems predation may exert a much greater impact on herbivore numbers.

In the course of this study, several useful lines of future work became apparent. First, although food inadequacy was ultimately responsible for much of the dry season mortality, the proximate cause of death in many cases was probably nutrition-related disease. There has been a good deal of research into the relationship between nutrition and resistance to disease in man and domesticated animals (Scrimshaw et al. 1968) but little work has been done on natural ungulate populations. Such research might provide a useful means of predicting how a given herbivore population will respond to changes in food abundance.

Second, Caughley (1966) has shown that many vertebrate populations have similar age-specific mortality curves. However, we know little about how age-specific mortality rates are affected during periods of rapid population change. For example, in this study I speculated that during the 1980 drought both very young and very old kob were probably more affected than young adults. Using the new technique I outlined in Chapter 6, it should be possible to determine the relative impact of perturbations on specific age groups. This information would be of particular use in age-structured population models.

Third, although natural predators in the Boma ecosystem are rare, hunting pressure may be of much greater significance. I inferred that hunting is probably less important than nutrition-related mortality in the Boma kob, but this assertion needs to

be tested. There have been few studies to my knowledge that have examined man as a predator, but this information may be of particular importance in the many ecosystems, like Boma, where harvesting by man is essentially unrestricted.

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APPENDIX 1. PLANT SPECIES COLLECTED

<u>Acacia nubica</u> Benth.	Mimosaceae
<u>Acacia polyacantha</u> Willd.	Mimosaceae
<u>Acacia senegal</u> (L.) Willd.	Mimosaceae
<u>Acacia seyal</u> DC.	Mimosaceae
<u>Acacia sieberiana</u> DC. var. <u>sieberiana</u>	Mimosaceae
<u>Acacia zanzibarica</u> (S. Moore) Taub.	Mimosaceae
<u>Achyranthes aspera</u> L.	Amaranthaceae
<u>Alysicarpus glumeceus</u> (Vahl) DC.	Leguminosae
<u>Asparagus africanus</u> Lam.	Liliaceae
<u>Balanites aegyptiaca</u> (L.) Del.	Balanitaceae
<u>Balanites rotundifolia</u> (Van Tiegh.) Blatter	Balanitaceae
<u>Butyrospermum paradoxum</u> (Gaertn.) Hepper	Sapotaceae
ssp. <u>niloticum</u> (Kotschy) Hepper	
<u>Cadaba farinosa</u> Forssk. ssp. <u>farinosa</u>	Capparaceae
<u>Capparis tomentosa</u> Lam.	Capparaceae
<u>Celtis toka</u> (Forssk.) Hepper & Wood	Ulmaceae
<u>Combretum fragrans</u> F. Hoff.	Combretaceae
<u>Cordia sinensis</u> Lam. forma vel sp. aff.	Boraginaceae
<u>Crateva adansonii</u> DC.	Capparaceae
<u>Dichrostachys cinerea</u> (L.) Wight & Arn.	Mimosaceae
ssp. <u>cinerea</u>	
<u>Diospyros mespiliformis</u> A. DC.	Ebenaceae
<u>Dobera glabra</u> (Forssk.) R. Br.	Salvadoraceae
<u>Echinochloa pyramidalis</u> (Lam.) Hitchc. & Chase	Gramineae
<u>Echinochloa stagnina</u> (Retz.) P. Beauv.	Gramineae

<u>Eragrostis cilianensis</u> (All.) F.T. Hubb.	Gramineae
<u>Ficus lutea</u> Vahl	Moraceae
<u>Ficus sur</u> Forssk. forma vel sp. aff.	Moraceae
<u>Fuerstia africana</u> T.C.E. Fr.	Labiatae
<u>Gardenia ternifolia</u> Schumach. & Thonn.	Rubiaceae
<u>Gardenia volkensii</u> K. Sch.	Rubiaceae
<u>Grewia bicolor</u> Juss.	Tiliaceae
<u>Grewia mollis</u> Juss.	Tiliaceae
<u>Grewia tenax</u> (Forssk.) Fiori	Tiliaceae
<u>Harrisonia abyssinica</u> Oliv.	Simaroubaceae
<u>Heteropogon contortus</u> (L.) Roem. & Schult.	Gramineae
<u>Hyparrhenia filipendula</u> (Hochst.) Stapf	Gramineae
<u>Hyparrhenia rufa</u> (Nees) Stapf.	Gramineae
<u>Hyperthelia dissoluta</u> (Nees ex Steud.)	Gramineae
W.D. Clayton	
<u>Lonchocarpus laxiflorus</u> Guill. & Perr.	Papilionaceae
<u>Loudetia arundinacea</u> (A. Rich.) Steud.	Gramineae
<u>Maerua angolensis</u> DC.	Capparaceae
<u>Maerua oblongifolia</u> A. Rich.	Capparaceae
<u>Maerua pseudopetulosa</u> (Gilg & Bened.) De Wolf	Capparaceae
<u>Maytenus senegalensis</u> (Lam.) Exell	Celestraceae
<u>Mimosa pigra</u> L.	Mimosaceae
<u>Nauclea latifolia</u> Smith	Rubiaceae
<u>Ozoroa insignis</u> Del. ssp. insignis	Anacardiaceae
<u>Panicum coloratum</u> L.	Gramineae
<u>Piliostigma thonningii</u> (Schumach.) Milne-Redh.	Caesalpiniaceae
<u>Pseudocedrela kotschy</u> (Schweinf.) Harms	Meliaceae

<u>Rhus natalensis</u> Krauss	Anacardiaceae
<u>Securinega virosa</u> (Willd.) Baill.	Euphorbiaceae
<u>Sehima nervosum</u> (Willd.) Stapf	Gramineae
<u>Setaria incrassata</u> (Hochst.) Hack.	Gramineae
<u>Sorghum purpureo sericeum</u> (Hochst. ex A. Rich.) Aschers & Schweinf.	Gramineae
<u>Sporobolus helvolus</u> (Trin.) Dur. & Schinz.	Gramineae
<u>Sporobolus ioclados</u> (Trin.) Nees	Gramineae
<u>Steganotaenia araliacea</u> Hochst. forma vel. aff.	Araliaceae
<u>Stereospermum kunthianum</u> Cham.	Bignoniaceae
<u>Tamarindus indica</u> L.	Caesalpinaceae
<u>Terminalia brevipes</u> Pampan	Combretaceae
<u>Triumfetta rhomboidea</u> Jacq.	Tiliaceae
<u>Ximenia caffra</u> Sond.	Olacaceae
<u>Ziziphus mauritiana</u> Lam.	Rhamnaceae