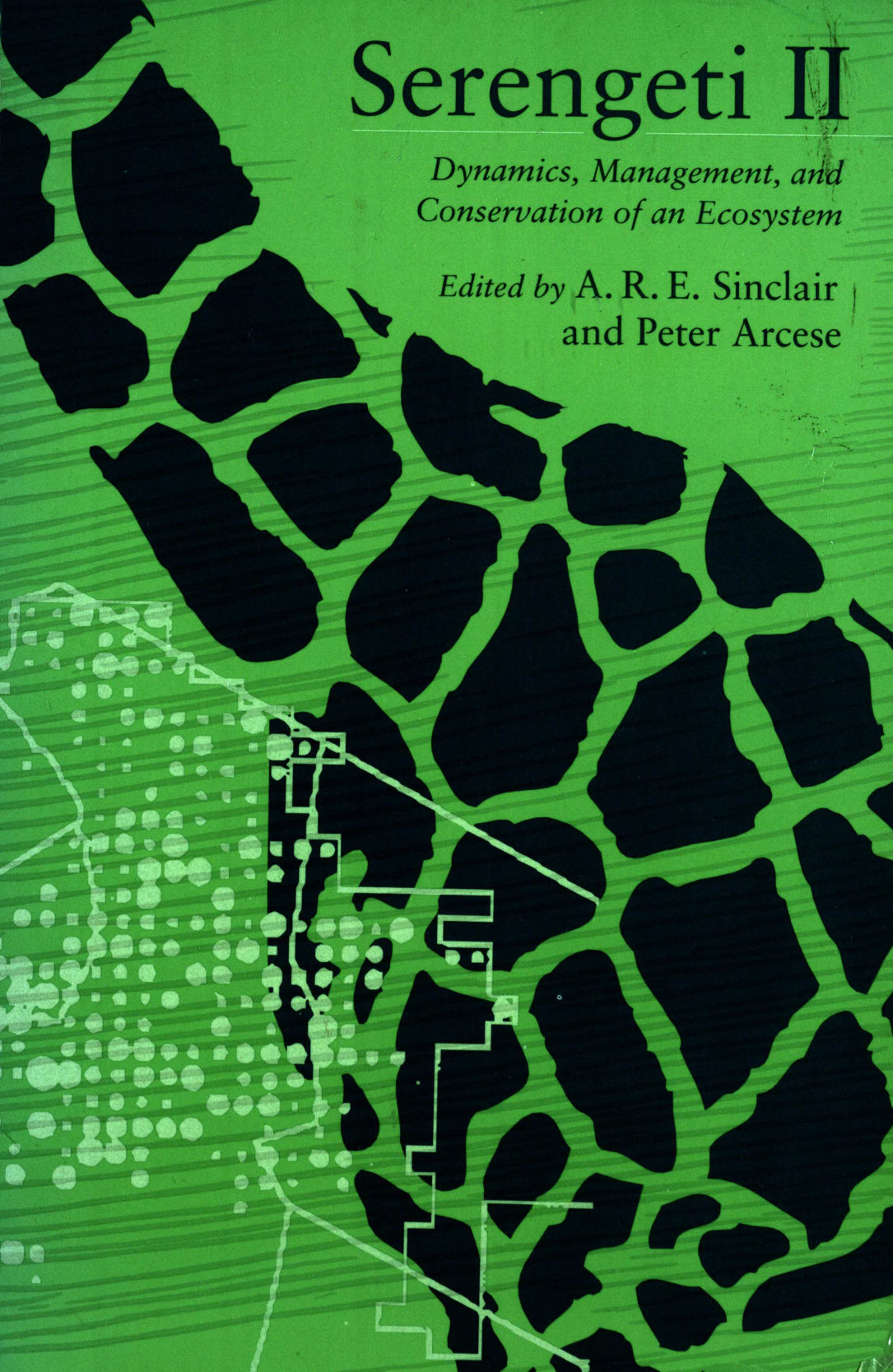# Serengeti II

Dynamics, Management, and
Conservation of an Ecosystem

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and Peter Arcese

ELEVEN

Specific Nutrient Requirements and Migration of Wildebeest

Martyn G. Murray

With the arrival of heavy rainstorms, African ungulates seek out new pastures, leaving their dry season refuges by way of well-worn paths and trails. Usually they concentrate near permanent water during dry periods and disperse, often moving upward into neighboring "dry country," during wet periods. So the annual cycle of movement typically consists of contraction and concentration in the dry season followed by expansion and dispersion in the wet season (Dasmann and Mossman 1962; Lamprey 1964; Jarman 1972; Stanley Price 1974; Western 1975; Afolayan and Ajayi 1980; Sinclair 1983). In certain exceptional cases, the pattern of movement differs in that concentrations of game take place in both the wet and dry seasons (Bell 1969; Murray 1982). In many cases, it seems that some additional factor, related to breeding, concentrates these populations on wet season calving grounds (Sinclair 1983). Where the two concentration areas are sufficiently far apart, the movements are called seasonal migrations.

Despite the major influence of migrations on ecosystem dynamics (Sinclair and Norton-Griffiths 1979), the acute vulnerability of migrations to human developments in land use (Borner 1985; Williamson and Mbano 1988; Howell, Lock, and Cobb 1989), and the scientific interest in describing and understanding the phenomenon itself, the reasons for migratory movements of African ungulate populations remain inadequately known. In their study of migratory kob (*Kobus kob leucotis* Lichtenstein and Peters), Fryxell and Sinclair (1988) point out that movements onto the wet season concentration area (which they share with the migratory tiang, *Damaliscus lunatus tiang* Heuglin) cannot be explained by the need to avoid annual flooding, or by selection of habitats with greater forage abundance. They conclude that the grasslands of the wet season range must be attractive "for more subtle reasons." These more subtle reasons form the subject matter of this chapter, in which I investigate seasonal habitat selection by white-bearded wildebeest in the Serengeti-

Mara ecosystem of Tanzania and Kenya. In particular, I examine the possibility that wildebeest migration is driven by seasonal demands for specific nutrients.

Each year some 1 million wildebeest migrate across the Serengeti-Mara ecosystem, traveling 10 km per day averaged over a whole year (D. Kreulen, pers. comm., cited in Pennycuick 1979). The crude cost of this movement, relative to neighboring resident populations of wildebeest, is a 3% increment in mortality per year (Sinclair 1983), possibly combined with reduced fertility in young females (Watson 1969). The overall migratory pattern is thought to be related to food supply, which is itself dependent on an uneven distribution of rainfall (Grzimek and Grzimek 1960; Talbot and Talbot 1963; Anderson and Talbot 1965; Pennycuick 1975; Maddock 1979). It has been suggested that the principal northwesterly movement at the start of the dry season is in response to the need to find surface water (Sinclair and Fryxell 1985), but according to Watson (1967), in some years the movement may begin before the wet season has ended and despite continued growth of grass and abundant supplies of drinking water. The unique movement south and east that returns the wildebeest to their wet season calving ground is the most predictable feature of the migration, and its explanation is crucial to an understanding of the migration as a whole.

The wet season range of wildebeest, situated on the short and medium-length grasslands of the Serengeti plains, is thought to provide the best grazing in the ecosystem (Bell 1971; Braun 1973; Sinclair and Fryxell 1985). Usually taller grasses are more fibrous, have lower protein concentrations, and are less digestible (Van Soest 1982), so selection by wildebeest of short grassland could be due to the requirements of lactating females for metabolizable energy and protein (Watson 1967; McNaughton 1985). Grasses prone to heavy grazing have evolved a variety of specialized growth traits (McNaughton 1984). An alternative hypothesis for why wildebeest select their wet season habitat is that grasses on the dry season range are unable to sustain production of new growth if heavily grazed, as they lack appropriate genetic adaptations (R. Ruess, pers. comm.). Long-distance movements have also been attributed to the wildebeest's dislike of wet and sticky ground (Talbot and Talbot 1963; Anderson and Talbot 1965), escape from predation pressure by large predators confined to territories (Fryxell, Greever, and Sinclair 1988), reduction of competition for food with resident grazers, and avoidance of areas with tsetse fly (Maddock 1979).

Wildebeest movements could also be influenced by changes in requirements for specific nutrients. Kreulen (1975) noted that Serengeti wildebeest on their wet season range preferred a short-grass over a long-grass habitat, and that calcium concentrations were higher on the short

grassland. By extrapolation from livestock data, he showed that the elevated requirement for calcium in lactating females could be met only by forage gathered from the short grassland, concluding that this could explain habitat selection. Recent surveys of element concentrations in Serengeti grasslands reveal that most minerals have substantially higher concentrations in short grasslands on the wet season range of migratory wildebeest than in other Serengeti grasslands (McNaughton and Banyikwa, chap. 3; McNaughton 1989). Movements of lactating wildebeest were related to forage levels of Cu, Mg, N, Na, and P, and to the Ca:P ratio (McNaughton 1990). These findings indicate that cyclic requirements for one or more elements by female wildebeest could account for localized movements and seasonal migration in the Serengeti-Mara ecosystem.

In this chapter, habitat preferences of wildebeest are investigated in relation to (1) the availability of specific nutrients in different habitats, (2) seasonal variation in dietary requirements of female wildebeest, and (3) the evidence for mineral deficiency in lactating females from assays of serum and urine electrolytes. These data are used to test among six hypothetical constraints that could account for seasonal movements. It is hypothesized that wildebeest select wet season habitats to (1) increase their daily intake of green leaf; (2) increase the concentration of metabolizable energy in their diet; (3) increase the concentration of protein in their diet; (4) meet minimum requirements for dietary sodium; (5) meet minimum requirements for dietary calcium; (6) meet minimum requirements for dietary phosphorus. The first two hypotheses are also considered by Fryxell (chap. 12).

STUDY REGION

Bounded to the north by the Isuria escarpment and Loita plains, on the east by the Loliondo highlands and the western wall of the Rift Valley, to the south by the Crater Highlands and Eyasi escarpment, and to the west by Lake Victoria and expanding human cultivation, the Serengeti-Mara ecosystem extends over some 25,000–35,000 km^2 (fig. 11.1). In April 1989, the population of migratory wildebeest was estimated to be 1.6 million, with a smaller population of 25,000 resident wildebeest on grassland plains at Kirawira in the west of Serengeti National Park (Campbell 1989). The ecosystem contains a diverse assemblage of other grazing herbivores, including substantial numbers of zebra, buffalo, kongoni, topi, and Thomson's gazelle. Major predators of these species are hyena, wild dog, lion, leopard, and cheetah.

The migratory wildebeest typically spend wet season months (November to May) on treeless plains to the southeast (fig.11.1), which in-
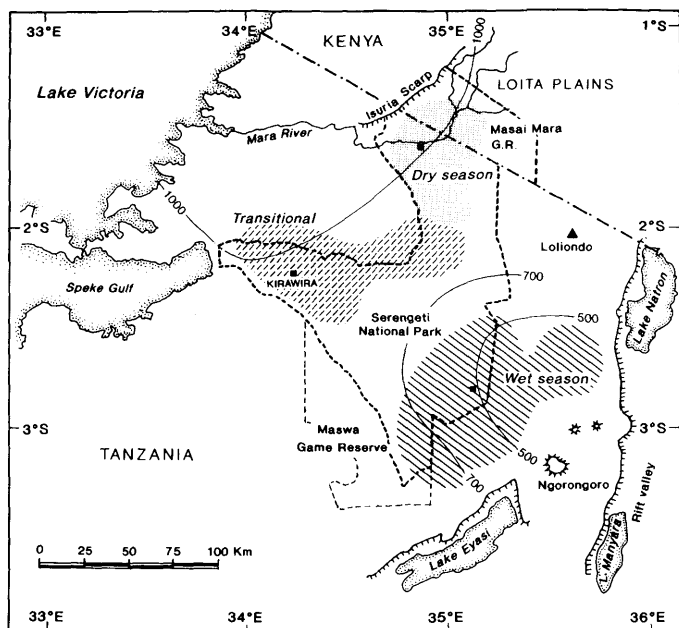
Figure 11.1 The seasonal ranges occupied by migratory wildebeest in the Serengeti-Mara ecosystem. Mean annual rainfall is shown by isohyets (in mm). The locations of sample sites are indicated by solid squares.

clude extensive areas of short grassland on saline and alkaline soils, dominated by *Sporobolus ioclados, S. kentrophyllus, S. fimbriatus, Digitaria abyssinica, D. macroblephara,* and *Kyllinga nervosa* (Cyperaceae) (McNaughton 1983). Rainfall is largely confined to the wet season, annually averaging 400 mm in the southeast to 800 mm in the northwest of the plains (Norton-Griffiths, Herlocker, and Pennycuick 1975).

In the early dry season, migratory wildebeest occupy a transitional range in the western part of the ecosystem that overlaps with areas used by the resident population at Kirawira. The range is wooded but is broken by extensive plains on which *Themeda triandra, Panicum coloratum, Chrysochloa orientalis,* and *Eriochloa fatmensis* are common grass species. Taller grasses (such as *Panicum maximum* and *Echinochloa hapoclada*) occur in swamps and along major rivers (Duncan 1975). Rainfall is more evenly distributed through the year, averaging 900–1,000 mm per annum. In wet months, the resident wildebeest at Kirawira prefer short grasslands on the well-drained catena top, dominated by *Digitaria macroblephara, Sporobolus ioclados, Cynodon dactylon,* and *Chrysochloa orientalis.*

In the late dry season, the migratory wildebeest move northeast to

their dry season range in the northwest of Serengeti National Park, spilling over into the Masai Mara National Reserve of Kenya. The area contains forest and thicket patches in open, relatively tall grassland with scattered *Acacia* trees. Common grass species are *Themeda triandra, Setaria sphacelata, Sporobolus fimbriatus, Pennisetum mezianum,* and *Digitaria macroblephara* (Sinclair 1977). The dry season range has a comparatively high annual rainfall of 1,000–1,200 mm, often with appreciable rainfall in the dry season (June to October).

METHODS
Structural and Chemical Composition of Pastures
Aboveground plant biomass and the proportional representation of green leaf in the sward were studied from December 1988 to July 1989 at two sites, one located on the short-grass plains in the wet season range and the other on open *Themeda* grassland in the dry season range of the migratory wildebeest (see fig. 11.1). Each study site had three permanent exclosures (5 by 5 m), one each on catena top, mid-catena, and just above catena bottom. The sites were visited twice per calendar month (as close as possible to the 1st and 16th day of each month).

Three permanent plots of 60 by 40 cm were located within each exclosure and clipped to 2 cm twice per month to measure net primary aboveground production. One other plot of the same dimensions was moved at each visit onto an untreated area within the exclosure and also clipped to 2 cm, to measure the standing crop. Clipped samples were sorted by hand to separate green leaf from the remainder, and the sorted fractions were oven-dried at 65°C and weighed.

Samples of green leaf were analyzed for crude protein (CP), neutral cellulase digestibility (NCD), sodium, calcium, and phosphorus by the Agricultural Development and Advisory Service (ADAS) of the Ministry of Agriculture, Fisheries, and Food, U.K., using their methods (MAFF 1986); NCD was determined using method e of Dowman and Collins (1982). Degradable nitrogen (DN) was estimated from a regression equation for digestible crude protein (DCP) of tropical green forages (Minson 1982):

$$DCP \ (g/kg) = 0.96CP(g/kg) - 38,$$

($R^2 = 0.98$), and DN = DCP/6.25. Metabolizable energy content (ME) was estimated from a regression equation for spring-grown herbage in the U.K. (Givens, Everington, and Adamson 1990), after confirming similar relationships between NCD and CP in the U. K. and Serengeti forage samples (Murray 1991):

$$ME \ (MJ/kg) = 0.0111NCD(g/kg) + 3.24.$$

(SE = 0.65 MJ/kg). In addition to the samples collected from within enclosures, a single collection of forage species was gathered from unprotected swards in February 1989, when the growth stage of the grass was immature. These samples were collected along 2 km transects, from the upper to the lower catena, at the two study sites for migratory wildebeest and also at two sites within wet and dry season habitats of resident wildebeest at Kirawira (see fig. 11.1). Samples of green leaf were gathered from the two dominant grass species at 50 m intervals along each transect; these were oven-dried and analyzed for crude protein, sodium, calcium, and phosphorus, as described above.

Mineral Requirements

Given the uncertainties involved in calculating requirements for wildebeest based on those recommended for cattle, only two extreme cases are considered: (1) the female wildebeest in the early to middle stage of pregnancy, maintaining body weight and ingesting a low-quality forage, which is assumed to be typical of conditions in the dry season in an extended period without rainfall; and (2) the female wildebeest maintaining body weight at peak lactation while ingesting a high-quality forage, which is assumed to be typical of conditions in the wet season in a period with abundant rainfall.

During extended periods without rain, wildebeest graze pastures of mature or senescent growth with little green leaf; a common forage species is *Themeda triandra*. In recent feeding trials conducted in the Serengeti, two yearling male wildebeest, with body masses of 86 and 108 kg, were provided a forage of mature *Themeda* with metabolizable energy concentration of 7.20 MJ/kg (Murray 1993). The animals maintained constant body weight with an average daily intake of metabolizable energy of 0.512 MJ/kg $W^{0.75}$. Extrapolating from these results, the intake of metabolizable energy for wildebeest of 143 kg live weight (the average for adult females in the migratory population; Watson 1967) would be 21.17 MJ/day. If this "average" animal walked 3 km/day, an additional intake of 1.15 MJ would be required, or 22.32 MJ/day in all (Kreulen 1975). Dry matter intake for maintenance of body weight would then be 3.10 (22.32/7.20) kg/day.

Peak lactation in the Serengeti wildebeest occurs during the wet season when the animals graze on short pastures of young green leaf and stem. Under these conditions, the intake of dry matter by an adult female wildebeest of 143 kg live weight was estimated by Kreulen (1975) to be 4.54 kg/day.

There is a wide range in the recommended allowances of calcium and phosphorus for sheep and cattle (ARC 1965, 1980; INRA 1978; NRC 1985), which has stimulated debate and new research into the actual re-

quirements for these minerals (MAFF 1984; Brodison et al. 1989). In revising previous estimates, AFRC (1991) introduced two new principles: that the obligatory component of endogenous fecal loss of calcium, E(Ca), and of phosphorus, E(P), is related to the level of food intake, and in the case of E(P) also to the proportion of roughage in the diet. Their new equations for cattle, on a diet containing at least 50% roughage, are applied here to wildebeest:

$$E(Ca) \text{ g/day} = -0.74 + 0.0079W + 0.66DMI, \qquad (11.1)$$

and

$$E(P) \text{ g/day} = 1.6 (-0.06 + 0.693DMI), \qquad (11.2)$$

where W is live weight (kg) and DMI is dry matter intake (kg). By substitution into equations (11.1) and (11.2), estimates for endogenous fecal losses of calcium and phosphorus in wildebeest are E(Ca) = 2.44 g/day and E(P) = 3.34 g/day.

The minimum dietary intake of both calcium and phosphorus at maintenance is obtained by dividing E by the appropriate absorption coefficient (ARC 1980). Minimum concentrations of minerals in forage are determined by dividing the daily requirements by the estimated intake of dry matter per day (table 11.1).

The new factorial models recommended for estimating the dietary requirements of lactating cattle are

$$\text{Ca (g/day)} =$$
$$(-0.74 + 0.0079W + 0.66DMI + m \times c)/0.68, \qquad (11.3)$$

and

$$P \text{ (g/day)} = 1.6(-0.06 + 0.693DMI + m \times p)/0.58, \qquad (11.4)$$

where m is the milk yield (kg/day), and c and p are the Ca and P concentrations of milk (g/kg) respectively.

From equations (11.1) and (11.2), the endogenous fecal losses of Ca and P in lactating wildebeest are 3.39 g/day and 4.94 g/day respectively. The average composition of milk collected from fifteen lactating wildebeest on their wet season range in the Serengeti was 1.9 g Ca/kg and 1.4 g P/kg. Peak milk yield was estimated by Kreulen (1975) from secondary sources to be 3.77 kg/day, giving losses of 7.16 g Ca/day and 5.28 g P/day in milk.

Dietary requirements of sodium were estimated in a similar way, and once again the estimations for cattle were used for wildebeest. On a low dietary intake of sodium, beef cattle at maintenance are estimated to lose sodium at a daily rate of 6.8 mg/kg live weight (ARC 1980). The absorption coefficient of sodium is estimated to be 0.91, so the dietary requirement at maintenance is

$$0.0068W/0.91 \text{ g/day.} \qquad (11.5)$$

The dietary requirement of sodium during lactation, with the animal maintaining body weight, is estimated to be

$$0.0068W + m \times s/0.91 \text{ g/day}, \tag{11.6}$$

where s is the concentration of sodium in milk (g/kg). For wildebeest sampled in the Serengeti, $s = 0.31$ g Na/kg, giving losses of 1.17g Na/day in milk.

Requirements for minerals at peak lactation (equations [11.3], [11.4], and [11.6]) are listed in table 11.1, together with the minimum concentrations in forage that would be necessary to meet dietary requirements assuming the DMI estimated above.

Serum and Urine Electrolytes and Proteins

In April 1989, seventeen adult female wildebeest were immobilized for sample collections on the wet season range of migratory wildebeest; in July, nine animals were immobilized on the transitional range and five more on the dry season range. Samples of serum, urine, and milk were taken from each animal and stored temporarily in the Serengeti at $-10°C$. In addition, the age of the mother's calf was estimated from its horn length, and the visual condition of the mother was estimated from the profile of pelvic bones, vertebrae, and ribs. Serum and urine electrolytes and proteins were analyzed by Rossdale and Partners, Newmarket, U.K. Sodium and potassium were assayed with a Corning Flame Photometer, model 435 (supplied by Corning Medical, Halstead, Essex, U.K.); all other assays were conducted with a Hitachi 705 Automatic Biochemistry Analyser (supplied by Boehringer Mannheim U.K., Lewes, East Sussex, U.K.). Milk samples were analyzed by the Agricultural Development and Advisory Service, U.K., who assayed the major minerals by atomic absorption spectrophotometry (MAFF 1986).

A general linear model procedure was used to determine what proportion of the variation in serum electrolytes and creatinine clearances was due to differences in location of sampled animals, and what proportion was due to differences in the reproductive stage and physical condition of the animals.

Table 11.1   Calcium, phosphorus, and sodium intake requirements, and minimum dietary concentrations in forage for an adult female wildebeest maintaining a constant live weight of 143 kg.

Reproductive status	Intake (g/day)			Minimum concentration (% DM)		
	Ca	P	Na	Ca	P	Na
Early–mid-pregnancy	3.59	5.76	1.07	0.12	0.19	0.035
Peak of lactation	15.51	17.61	2.35	0.34	0.39	0.052

RESULTS
Structure and Nutritional Composition of Pastures
Primary production peaked sharply on the wet season range of migratory wildebeest during February 1989 following heavy rain in January. It declined through the remainder of the growth season (fig. 11.2a). Production over the same period on the dry season range was less variable (fig. 11.2b). Over the entire growth period, overall production and green leaf production did not differ significantly between the wet and dry season ranges (table 11.2). Standing crop within the fenced exclosures increased steadily over the growth season in both areas, with a substantial rise on the dry season range in April and May (fig. 11.3). Over the entire growth
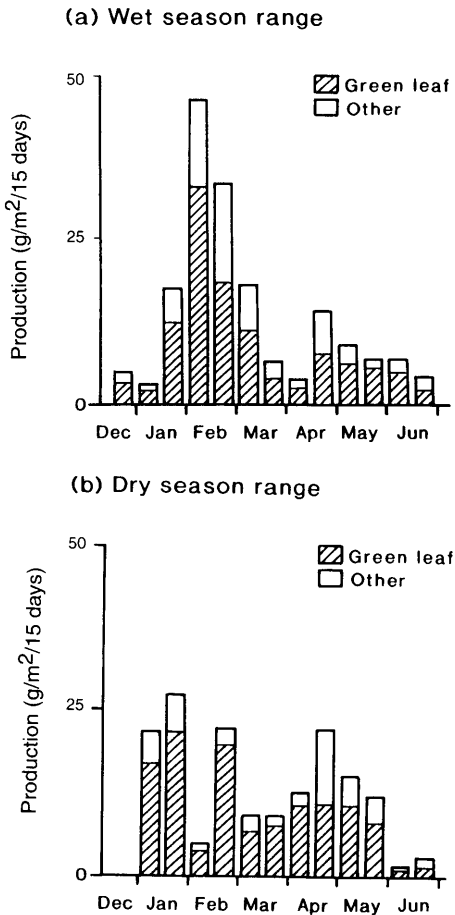
Figure 11.2   Total production and leaf production at bimonthly intervals on (*a*) the wet season range (calving ground) and (*b*) the dry season range of migratory wildebeest.

Table 11.2.   Sward characteristics on the wet and dry season ranges of migratory wildebeest in the Serengeti.

Range	Standing crop			Production per 15 days		
	Green leaf (g/m^2)	Total (g/m^2)	Green leaf (%)	Green leaf (g/m^2)	Total (g/m^2)	Green leaf (%)
Wet season	31.2	100.4	39.7	8.7	13.6	63.3
	(5.2)	(20.2)	(4.2)	(2.4)	(3.5)	(2.4)
Dry season	75.0	207.0	45.9	10.9	14.7	71.8
	(12.2)	(42.7)	(4.7)	(2.0)	(2.5)	(3.7)

Note: Means and standard errors (in parentheses) taken from 14 bimonthly measures over the growing season.
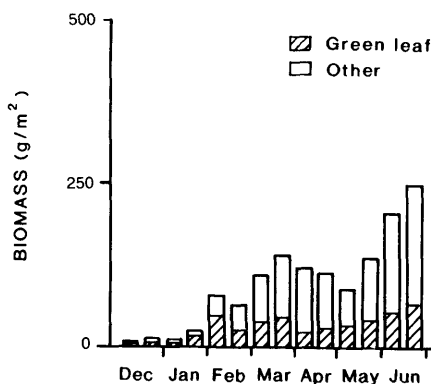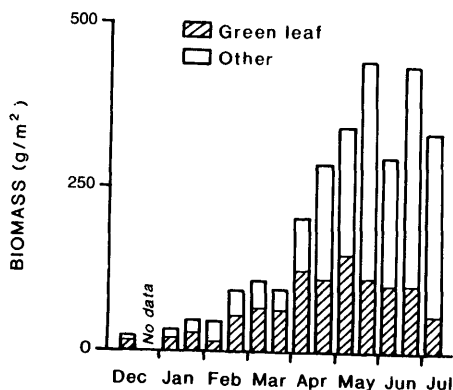
Figure 11.3   Standing crop and green leaf crop within exclosures situated in (*a*) the wet season range and (*b*) the dry season range of migratory wildebeest.

period, the total standing crop and the standing crop of green leaf were significantly higher in the dry season range ($P < .01$ and $P < .05$, respectively). The proportion of green leaf in wet and dry season ranges did not differ significantly, either in clipped or in control plots.

Digestibility of green leaf remained high over the growth season, and there was no consistent difference between samples gathered from the wet and from the dry season ranges of migratory wildebeest (fig. 11.4a; table 11.3). This result indicates that metabolizable energy was equally avail-

(a) Digestibility of leaf

(b) Protein content of leaf
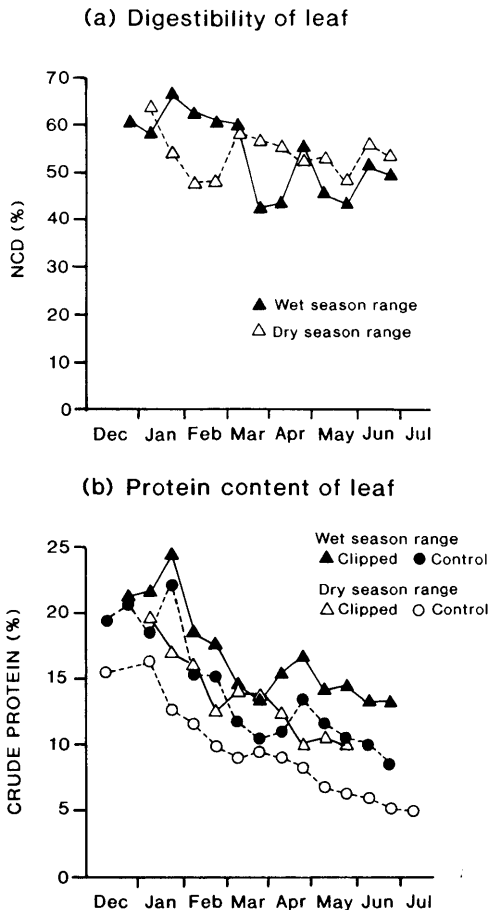
Figure 11.4   Bimonthly variation in (*a*) digestibility of clipped and (*b*) protein content of both clipped and control green leaf samples on seasonal ranges of migratory wildebeest.

Table 11.3 Nutritional composition of green leaf collected from within exclosures on the wet and dry season ranges of migratory wildebeest in the Serengeti.

Range	Treatment	NCD	CP	Sodium	Calcium	Phosphorus	Ca:P	n
Wet season	Clipped	53.93	16.77	0.13	0.56	0.54	1.15	12
		(8.26)	(3.65)	(0.06)	(0.08)	(0.13)	(0.57)	
Dry season	Clipped	53.91	13.58	0.13	0.40	0.26	1.53	10
		(4.66)	(3.20)	(0.06)	(0.05)	(0.05)	(0.18)	
		NS	*	NS	***	***		
Wet season	Control	52.31	14.19	0.22	0.50	0.52	1.01	14
		(5.98)	(4.42)	(0.08)	(0.13)	(0.09)	(0.43)	
Dry season	Control	50.60	9.30	0.09	0.37	0.19	2.06	14
		(7.03)	(3.61)	(0.06)	(0.06)	(0.06)	(0.39)	
		NS	**	***	**	***		

Note: All measures are expressed as a percentage of dry weight. Means and standard deviations (in parentheses) are given for the growth period (December through June). Clipped, plot clipped every 15 days; control, plot not previously clipped. NCD, neutral cellulase digestibility; CP, crude protein; Ca:P, calcium to phosphorus ratio; n, minimum sample size. Significance levels refer to Mann-Whitney tests of differences in nutritional composition between samples collected from the wet and dry season ranges.
*$P < .05$; **$P < .01$; ***$P < .001$; NS, not significant.

able in both areas. The crude protein content of green leaf declined throughout the growth period (fig. 11.4b), averaging 3% higher in clipped plots on the wet season range (table 11.3). In samples collected from unprotected sites, the concentration of crude protein was not significantly different between wet and dry season ranges (table 11.4), nor was there a significant difference between the wet and dry season ranges of resident wildebeest. The availability of protein in grass leaf for fermentation (g degradable nitrogen/MJ of metabolizable energy) declined during the growth period, but reached levels likely to constrain dry matter intake (< 1.0 gN/MJ; see "Discussion" below) only toward the end of the growth period, in the standing crop of the dry season range (fig. 11.5).

Mineral Concentrations in Grass Leaf

In samples collected from inside exclosures, major minerals were usually more concentrated on the wet than on the dry season range of migratory wildebeest (table 11.3). For example, green leaf from clipped plots on the wet season range contained twice as much phosphorus, 1.4 times as much calcium, and equivalent quantities of sodium. Sodium concentrations were above the required level for lactating wildebeest in all but three samples, which were collected from the standing crop on the dry season range toward the end of the growing season. Calcium concentrations fell just below the required level for lactating wildebeest in one clipped and six control samples taken from the dry season range (table 11.1; fig. 11.6a, b). Phosphorus concentrations were below the required level for lactating wildebeest in all 24 samples gathered from the dry season range, but in
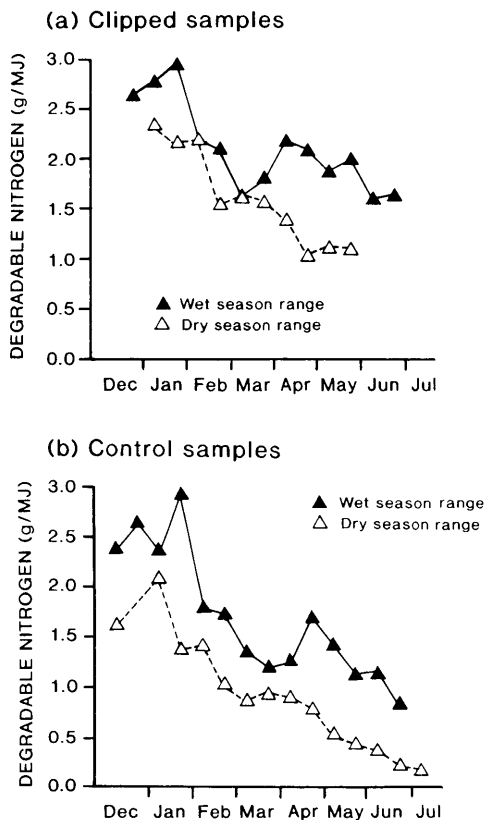
(a) Clipped samples

(b) Control samples

Figure 11.5   The availability of protein for rumen fermentation in green leaf collected inside exclosures on the wet and dry season ranges of migratory wildebeest: (*a*) clipped plots; (*b*) control plots.

only 4 of 26 samples from the wet season range (table 11.1; fig. 11.6c, d). There was also a seasonal trend, with calcium concentration declining over the growth period on both ranges, but phosphorus concentration declining on the dry season range and increasing on the wet season range.

In samples collected from unprotected sites, calcium and phosphorus were again more concentrated on the wet season range of the migratory population (table 11.4). Sodium was lower on the wet season range, but not significantly so. Differences in mineral concentrations on the wet and dry season ranges of resident wildebeest were less marked and failed to achieve statistical significance. However, sodium concentrations were several times greater than on the wet and dry season ranges of the migratory

(a) Calcium, clipped

(b) Calcium, control

(c) Phosphorus, clipped
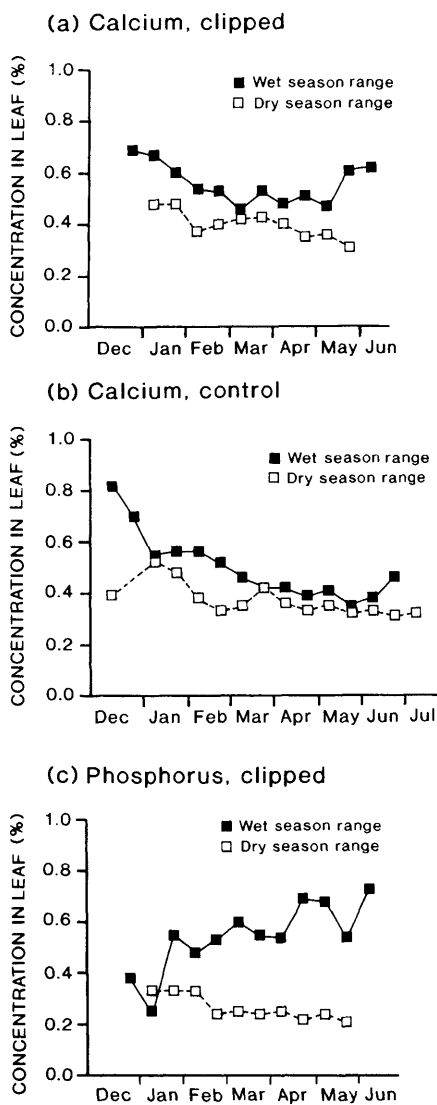
Figure 11.6 Bimonthly variation in concentration of calcium and phosphorus in green leaf collected within exclosures on the wet and dry season ranges of migratory wildebeest. (*a*) calcium, clipped sample; (*b*) calcium, control sample; (*c*) phosphorus, clipped sample; (*d*) phosphorus, control sample.

(d) Phosphorus, control
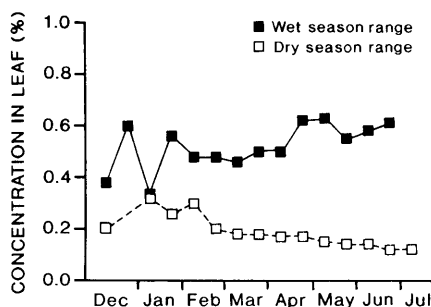
Table 11.4 Nutritional composition of green leaf collected from unprotected sites on the wet season and dry season ranges of migratory and resident wildebeest.

Population	Range	CP	Sodium	Calcium	Phosphorus	Ca:P	n
Migratory	Wet season	18.13	0.10	0.66	0.52	1.28	30
		(4.55)	(0.13)	(0.19)	(0.12)	(0.41)	
Migratory	Dry season	16.09	0.19	0.47	0.31	1.58	33
		(3.60)	(0.34)	(0.11)	(0.06)	(0.43)	
		NS	NS	**	***		
Resident	Wet season	15.97	0.55	0.41	0.45	0.99	23
		(3.42)	(0.38)	(0.09)	(0.14)	(0.38)	
Resident	Dry season	13.68	0.73	0.42	0.36	1.22	30
		(3.44)	(0.57)	(0.06)	(0.08)	(0.36)	
		NS	NS	NS	NS		

Note: All measures are expressed as a percentage of dry weight. Means and standard deviations (in parentheses) refer to single collections from each site. Significance levels refer to Kolgomorov-Smirnov two-sample tests of nutrient concentrations within populations and between ranges.
$**P < .01; ***P < .001$; NS, not significant.

population (table 11.4). Average Ca:P ratios for all grassland habitats varied from 0.99:1 to 2.06:1 (tables 11.3 and 11.4).

Serum and Urine Electrolytes and Proteins
Total protein in sera of the Serengeti wildebeest was high by comparison with wildebeest kept at Whipsnade Zoo, U.K., and by comparison with normal values of cattle (table 11.5). The high level of total protein was associated with a high level of serum globulin, possibly reflecting high levels of immunoglobulins. Animals on the dry season and transitional ranges may have been dehydrated, since both the concentration of creatinine in their serum samples and the specific gravity of their urine were elevated.

Serum phosphate levels were generally low, in keeping with the trend noted for savanna-dwelling artiodactyls (S. Gascoyne, pers. comm.) but

Table 11.5   Protein concentrations in sera of adult female wildebeest in the Serengeti.

Range	Total protein (g/l)	Creatinine (mol/l)	Albumin (g/l)	Globulin (g/l)	n
Reference values (1)	78	—	35	43	
(2)	68.0–71.0	124–154	38.0–40.0	30.0–31.0	
Wet season	79.0 (4.5)	108.6 (12.9)	30.8 (2.4)	48.2 (3.2)	17
Transitional	79.1 (5.3)	165.7 (22.6)	30.0 (3.8)	49.1 (5.2)	9
Dry season	82.0 (3.7)	175.8 (9.8)	30.6 (3.0)	51.4 (3.8)	5
	NS	***	NS	NS	

Note: Mean values and standard deviations (in parentheses) are given. The locality of animals sampled is given by reference to the seasonal movements of the migratory population. Reference values are (1) means for cattle (Topps and Thompson 1984) and (2) those obtained from two healthy adult wildebeest kept at Whipsnade Zoo, U.K. (S. Gascoyne, pers. comm.). Significance of variation in concentrations between different ranges is indicated (see text).
***$P < .001$; NS, not significant.

Table 11.6   Electrolyte concentrations in sera of adult female wildebeest in the Serengeti.

Range	Sodium (mmol/l)	Potassium (mmol/l)	Calcium (mmol/l)	Inorganic phosphate (mmol/l)	Chloride (mmol/l)	n
Reference values (1)	141	5.6	2.48	1.94	—	
(2)	141–143	4.0–4.3	2.23–2.29	1.00–1.13	96.0–98.0	
(3)	—	—	2.0	1.45	—	
Wet season	133.0	4.75	1.91	1.02	98.7	17
	(3.3)	(0.41)	(0.14)	(0.26)	(2.2)	
Transitional	131.4	4.58	1.95	1.05	101.2	9
	(2.7)	(0.46)	(0.13)	(0.18)	(3.4)	
Dry season	132.2	4.72	1.96	0.60	101.8	5
	(1.5)	(0.26)	(0.06)	(0.18)	(1.5)	
	NS	NS	NS	**	NS	

Note: Mean values with standard deviations (in parentheses) are given. The locality of animals sampled is given by reference to the seasonal movements of the migratory population. Reference values are (1) means for cattle (Topps and Thompson 1984), (2) those obtained from two healthy adult wildebeest kept at Whipsnade Zoo, U.K. (S. Gascoyne, pers. comm.), and (3) critical minimum levels for cattle (McDowell 1985). Significance of variation in concentration between different ranges is indicated (see text).
**$P < .01$; NS, not significant.

levels were very low in animals on the dry season range (table 11.6). No phosphate was detected in urine. Serum calcium was low relative to the reference animals at Whipsnade Zoo, but not significantly lower than the critical minimum value for cattle (table 11.6). Lower albumin levels may have reduced the level of bound calcium. Sodium in sera was also low relative to the Whipsnade animals, but the absence of variation in serum sodium among samples collected from the different ranges of wildebeest, in association with a 30-fold variation in sodium clearance (table 11.7), signifies effective homeostatic control. Potassium clearances were particularly high on the wet season range of migratory wildebeest, suggesting a greater effort by these animals to conserve sodium. Conversely, the lower clearance of potassium on the dry season range suggests less need for

Table 11.7 Creatinine clearances (% Cr) of adult female wildebeest in the Serengeti.

Range	Sodium	Potassium	Chloride	n
Wet season	0.037 (0.023)	105.3 (36.3)	1.26 (0.54)	14
Transitional	1.135 (0.972)	52.0 (31.1)	1.26 (0.42)	9
Dry season	0.039 (0.038)	50.9 (9.4)	1.32 (0.42)	5
	**	***	NS	

Note: Mean values with standard deviations (in parentheses) are given. The locality of animals sampled is given by reference to the seasonal movements of the migratory population. Significance of variation in clearances between different ranges is indicated (see text).
**$P < .01$; ***$P < .001$; NS, not significant.

sodium retention, which indicates a higher sodium content in the diet relative to requirements. Chloride in serum was normal.

The concentration of phosphate in serum and the clearances of sodium and potassium were strongly influenced by the location of wildebeest at the time of sampling (tables 11.5–11.7), but were not significantly associated with the calf's age or the mother's body condition.

DISCUSSION

In a pioneering study, Weir (1972) demonstrated that localized sources of sodium strongly affected the distribution of elephant in western Zimbabwe. Likewise, in the Serengeti, resident herbivores are found to concentrate on pastures with a high mineral content (McNaughton 1988, 1989), and it has been suggested that migratory herbivores select habitats on the basis of mineral availabilities (Kreulen 1975; McNaughton 1990). In reviewing the evidence presented here, I am aware of the uncertainty in extrapolating from a narrow database (8 months of data collection from four sites for vegetation; two time periods and three locations for animal sampling). Bearing this caveat in mind, several conclusions concerning the causation of wet season habitat selection in wildebeest emerge from a comparison of the results with the six hypotheses set out above.

Availability of Energy and Protein
The standing crop of grass and of green leaf was higher in the dry season range than in the wet season range of migratory wildebeest, but the clipped plots produced similar quantities of grass and of green leaf in the two areas, suggesting that grassland productivity contained a component related to grass biomass. In a similar comparison between the long and short grasslands of the wet season range (clipped every 2 weeks), Braun (1973) found higher production in the long grasslands and, as with this study, observed a similar proportion of leaf to stem in the two grassland types. Both sets of results are inconsistent with hypothesis 1. There is some evidence that the long grasslands cannot withstand continuing grazing pressure over several years. Plots that were clipped repeatedly for four

consecutive growing seasons showed a steady decline in production (Sinclair 1977). Nevertheless, the results presented here, as well as those of Braun (1973), reveal that tall grasses of the dry season range are capable of withstanding heavy grazing pressure for at least one season, and that wildebeest do not migrate at the start of the wet season because of differences in the availability of green leaf. Fryxell (chap. 12) suggests that rotational grazing by migratory species may result in a mosaic of pastures of different biomass, with the result being a higher production overall than in ungrazed areas. While this scenario was not specifically investigated, it seems unlikely given the high intensity of grazing throughout the short-grass plains.

Metabolizable energy concentration within green leaf was similar in different localities, providing no basis of support for hypothesis 2. Protein was more concentrated in leaf from the wet season range of migratory wildebeest than from the dry season range, but the difference was not great. In fact, CP on the dry season range of migratory wildebeest was as high as that on the wet season range of resident wildebeest. A similar result was obtained by Braun (1973) from experiments on the long grasslands of the wet season range. He found that crude protein in clipped leaf "remains constant at a remarkably high level," a finding that prompted Kreulen (1975) to reject crude protein availability as an explanation for wildebeest habitat selection.

Even small differences in crude protein content could be important if they affected the rate of rumen fermentation. The availability of protein for fermentation was lower on the dry season range of migratory wildebeest, dropping below 1.34 g N/MJ metabolizable energy, the level recommended as sufficient for the rumen microflora to make full use of fermentable carbohydrate (ARC 1984). Values as low as 0.2 g N/MJ ME in the standing crop suggest the potential for a severe constraint on food intake by livestock standards, but in the clipped plots the value remained above 1.0 g N/MJ ME, indicating the possibility of a mild constraint on intake by livestock standards (E. L. Miller, pers. comm.).

Thus, these data do not provide sufficient grounds for rejection of hypothesis 3. They suggest a possible advantage for wildebeest moving onto the wet season range on the basis of an increased protein intake.

Evidence for Mineral Deficiencies

Sodium-conserving mechanisms in the ruminant are so effective that incidents of deficiency on natural forages, even those low in sodium, are uncommon. Given a low intake of dietary sodium, clinical deficiency is most likely in rapidly growing animals, in dairy cattle, which have large losses of sodium in milk, and in any animals that have large losses of sodium in sweat (Underwood 1981; McDowell 1985). Unlike McNaughton (1990),

who found low levels of sodium in the dry season range of the migratory population, this survey found few forage samples that were deficient in sodium relative to the minimum requirements of lactating wildebeest. In fact, the most active retention of sodium was observed in lactating females on the wet season range of the migratory population, but these animals maintained normal levels of serum sodium. The evidence from this study suggests that wildebeest can cope with a low sodium intake by minimizing losses and by selecting sodium-rich habitats within the dry season range. The data do not implicate sodium deficiency in long-distance movements of wildebeest, contrary to hypothesis 4.

Calcium deficiency is rare in ruminant livestock except in high-yielding dairy cows and in other livestock when feeding on quick-growing grasses in humid areas, which can contain very low concentrations of Ca (< 0.2%; Underwood 1981). In the Serengeti, average concentrations of calcium were highest in the wet season range of the migratory wildebeest and lower elsewhere (this study; McNaughton 1990); but even the lower values were usually above the estimate for the minimum requirements of wildebeest at peak lactation. Serum calcium was low relative to the Whipsnade Zoo animals, but this difference may simply reflect lower levels of bound calcium associated with the lower albumin levels. The absence of phosphate in urine samples (indicating that calcium was not being mobilized from bone reserves) and the presence of calcium carbonate crystals in urine also point to a sufficient dietary intake of calcium in all areas sampled. Thus, these data are not consistent with hypothesis 5.

On the strength of more precise livestock models and new information on the calcium concentration of milk from Serengeti wildebeest, Kreulen's (1975) estimate of the minimum requirements for dietary calcium of lactating wildebeest was downwardly revised. Most of the grasses sampled by Kreulen had higher concentrations than this revised minimum standard, which brings into question his explanation of habitat selection within the wet season range on the basis of calcium availability. Wildebeest may risk calcium deficiency in the wet season because of low Ca:P ratios in some habitats. Kreulen (1975) found that the habitat with the lowest Ca in grass leaf (open plains with long grassland) also had a low Ca:P ratio, noting that high concentrations of P may interfere with absorption of Ca in the digestive tract. Recent research has revealed a wider tolerance to the Ca:P ratio than previously suspected (AFRC 1991); nevertheless, ratios as low as those recorded by Kreulen may still be significant (Underwood 1981). The Ca:P ratios recorded in the dry season range of migratory wildebeest were above 1 (this study; McNaughton 1990), and so the problem of Ca absorption does not appear to explain the occurrence of long-distance migratory movements (hypothesis 5).

Natural pastures with a deficiency in phosphorus for cattle or sheep

occur extensively throughout the world, including areas in eastern and southern Africa (Underwood 1981; McDowell 1985). Phosphorus deficiency causes severe clinical and pathological change in grazing livestock, with impairment of fertility, appetite, milk yield, and growth, as well as abnormalities of bones and teeth and an increased mortality rate (Underwood 1981; Read, Engels, and Smith 1986b). Short-term deficiency need not cause harmful effects, as ruminants withstand marginal and even moderately severe dietary deficiencies by drawing upon skeletal reserves (Read, Engels, and Smith 1986a; Brodison et al. 1989). Nonetheless, phosphorus is given as a supplement to grazing livestock more often than any other nutrient, excepting salt.

In the Serengeti, phosphorus concentration on the wet season range of migratory wildebeest was well above the minimum requirements for lactating wildebeest (hypothesis 6), but on the dry season range it remained below lactation requirements throughout the growing season, declining as the season progressed. In the last of the clipped samples, it approached the minimum concentration required for maintenance. In the standing crop, it dropped below this level early on in the wet season, declining to 0.12% by June. A low concentration of phosphorus in the dry season range of wildebeest was also recorded by McNaughton (1990). These data suggest that pregnant wildebeest on the dry season range could fail to maintain phosphorus balance while foraging on mature swards. Were the same animals to remain on the dry season range while lactating, they would fail to meet their phosphorus requirements even on growing swards in the wet season. The animals would therefore have difficulty in replenishing skeletal reserves of phosphorus. It is interesting that the level of serum phosphate in the five animals sampled on the dry season range averaged 0.6 mmol/l, the same level that induced a strong appetite for naturally occurring sources of available phosphate (bone and bird feces) in experiments with phosphorus-deficient cattle (Denton 1984). Thus both sets of data are consistent with hypothesis 6.

Causation of Migratory Movements

Geographic variation in the availability of dietary phosphorus within the Serengeti grasslands, combined with a reproductive cycle in requirements for phosphorus in female wildebeest, can provide an underlying explanation for long-distance migratory movements. Four of the five alternative hypotheses are rejected, but the third hypothesis—that female wildebeest select wet season habitats with higher concentrations of protein in green leaf—is not ruled out. Phosphorus and protein concentrations were only weakly correlated in this study ($r = .23$, $N = 116$), so more intensive sampling of protein and minerals among different pasture blocks, combined with analyses of fecal phosphorus levels (Belonje 1978; Belonje and

van den Berg 1983), might discriminate between the two extant hypotheses.

The return movement of migratory wildebeest to their dry season range occurs with the advent of dry weather. Grass growth on the wet season range stops after a few days without rain, and there remains almost no standing crop as a food reservoir (McNaughton 1985). Free-standing water is also largely absent from this area. The wildebeest are thus forced to return to their dry season range, which maintains green leaf for a longer period and retains a substantial reservoir of grass swards with high biomass due to light grazing pressure in the wet season. Free-standing water is also available there in pools along major river systems. Lactating females may take advantage of swards in the transitional range (see fig. 11.1), which have higher concentrations of phosphorus and other minerals than those in the dry season range (McNaughton 1990).

Resident Ungulates

A requirement of any hypothesis seeking to explain wildebeest migrations is that it should also account for the nonmigratory habits of resident ungulates. If it is hypothesized that wildebeest migrate in order to avoid predators, why do not resident ungulates also migrate? Given the argument forwarded here that wildebeest migration is a behavioral strategy to avoid phosphorus deficiency, how is it that resident ungulates can remain year-round in the long grasslands, which are deficient in minerals? The answer to the latter question may be found in the mineral composition of certain localized pastures favored by resident grazers during the wet season. McNaughton (1988; McNaughton and Banyikwa, chap. 3) has shown that the magnesium, sodium, and phosphorus content of green leaf is substantially higher in these "hot spots" than in surrounding areas. Although any one of the preferred locations could support only a fraction of the migratory wildebeest population, why do so few wildebeest remain on hot spots in the long grasslands during the wet season?

Resident species could be better adapted to diets that are marginal in phosphorus content. One such possible adaptation is in reproductive strategy. Wildebeest breeding is highly synchronized, and the majority of adult females calve each year during the wet season. By contrast, some resident grazers (such as kongoni and waterbuck) breed throughout the year, which would provide postpartum females with the opportunity to replenish reserves of phosphorus by extending the anestrous period. Another way to supplement reserves of dietary phosphorus is by selective consumption of browse species (Pellew 1984). However, neither strategy is easily extended to topi, a resident grazer that rarely feeds on dicotyledons and in which the majority of females breed annually in a well-defined calving season. Possibly, the more selective grazing strategy of topi

(Murray and Brown 1993) provides the opportunity for sustained-yield grazing in mineral-rich hot spots (McNaughton and Banyikwa, chap. 3). Wildebeest graze swards down to a lower biomass than do topi, and this could reduce the productivity of pastures, forcing wildebeest to forage over wider areas.

Implications for Management

In the last century, game migrations in Africa were probably widespread (Houston 1979), but today, only three large-scale migrations remain relatively intact: those of tiang and white-eared kob in southern Sudan (Howell, Lock, and Cobb 1989; Fryxell and Sinclair 1988) and that of wildebeest in the Serengeti-Mara ecosystem. Until recently, migrations of wildebeest also occurred in Botswana (Williamson, Williamson, and Ngwamotsoko 1988), Namibia (Berry 1980), and South Africa (Whyte and Joubert 1988), but each of these populations has declined after the erection of game-control fences that severed traditional routes of migration. Smaller numbers of ungulates still move over long distances in parts of southern, central, and eastern Africa, but these populations are also under an increasing threat (e.g., Borner 1985; Prins 1987; Howell, Lock, and Cobb 1989). The findings reported here and elsewhere (Kreulen 1975; McNaughton 1989, 1990; McNaughton and Banyikwa, chap. 3), that African ungulates move seasonally between pastures to find specific nutrients, provide a new opportunity in the development of land units for conservation purposes. Identification of widespread mineral deficiencies in grasslands at the ecosystem level, and of mineral-rich pastures within the ecosystem, would be an important early step in formulating plans for protection or expansion of migratory herds. As recently burned areas can also be a direct source of minerals for alcelaphines (Messana 1993), there is also a potential for management of fire to provide mineral supplements.

ACKNOWLEDGMENTS

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Serengeti II

*Dynamics, Management, and
Conservation of an Ecosystem*

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