

WHY ARE MIGRATORY UNGULATES SO ABUNDANT?

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Many grassland ecosystems around the world supported vast herds of migratory ungulates before the influence of modern man. In retrospect, we can make only educated guesses about the size of these herds. Nevertheless, it seems likely that such populations as the migratory bison on the North American plains, saiga on the Russian steppes, and springbok on the fringes of the Kalahari Desert numbered in the millions (Hornaday 1889; Cronwright-Schreiner 1925; Bannikov et al. 1967). Populations of migratory herbivores still predominate in a number of savanna ecosystems in Africa (table 1). These observations suggest that migratory species tend to dominate the ungulate community in many grassland ecosystems, in some cases by an order of magnitude.

We consider three hypotheses that might explain why migratory ungulates are more abundant than residents. First, migrants could have access to greater food supplies than residents simply because they use a much larger area. Second, migrants could make more-efficient use of resources than residents. Periodic movements may allow migrants to shift to fresh pastures when their own grazing has seriously depleted the supply of food. This would allow vegetation a period free from grazing during which aboveground tissues could be restored. Since growth is often highest at intermediate levels of vegetation abundance (Braun 1973; Noy-Meir 1975), seasonal migration could increase grassland productivity and therefore allow a larger population of consumers. Third, migrants may be less vulnerable to regulation by predators. If predators are unable to follow migratory herds, then they would exert little impact during a large portion of the year. This would reduce the total number of deaths from predation and decrease the possibility of predator regulation of migratory prey. For the purposes of this paper, we define *regulation* as any density-dependent process that tends to stabilize population numbers over time.

These hypotheses may be addressed by considering the dynamics of intact ecosystems comprising migratory herbivores and grasslands. Perhaps the best-known example is the migratory population of wildebeest in the Serengeti-Mara region of East Africa. The dynamics of this ecosystem are relatively well under-

TABLE 1
RELATIVE ABUNDANCE OF MIGRATORY AND SEDENTARY UNGULATES IN THREE SAVANNA
ECOSYSTEMS IN AFRICA

LOCATION*	MOST ABUNDANT SPECIES		ABUNDANCE RATIO
	Migratory	Sedentary	
Serengeti, Tanzania ^a	wildebeest	buffalo	11.0 (750,000/68,000)
Jonglei, Sudan ^b	tiang	Nile lechwe	11.3 (360,000/32,000)
Boma, Sudan ^c	white-eared kob	lelwel hartebeest	16.8 (840,000/50,000)

* SOURCES.—*a*, Sinclair 1977*b*; *b*, Howell et al. 1988; *c*, Fryxell 1987, unpubl. data.

stood, as a result of several complementary studies over the past 25 years (Sinclair and Norton-Griffiths 1979).

In general terms, the Serengeti ecosystem may be divided into two components: (1) open grasslands with low annual rainfall (ca. 600 mm) that support an extensive cover of shortgrasses; and (2) wooded grasslands in areas with higher rainfall (ca. 1000 mm) that support tall, highly lignified grasses (Braun 1973; McNaughton 1979, 1985). Rainfall is the most important factor influencing primary productivity of both grassland types (Braun 1973; Sinclair 1975; McNaughton 1979, 1985). Most rainfall occurs from November to May, with occasional dry periods in January and February (Norton-Griffiths et al. 1975). As a result, grass growth shows pronounced spatial and seasonal variation (McNaughton 1985).

Wildebeest exhibit seasonal shifts in habitat use, migrating from open grasslands that are used during the wet season to wooded grasslands in higher-rainfall areas that are used during the dry season (Pennycuik 1975; Maddock 1979). A number of factors may influence the apparent preference by wildebeest for shortgrasses during the wet season. Shortgrasses on the Serengeti plains are more digestible, have higher concentrations of calcium and protein, and have a higher ratio of leaf to stem tissue than taller grasses in other areas (Braun 1973; Kreulen 1975). However, wildebeest cannot remain in the open grasslands year-round because water holes on the plains evaporate during the dry season. Like most grazing ungulates, wildebeest cannot extract sufficient moisture from forage to meet their metabolic requirements (Western 1975). Hence, the availability of nearby water is a primary determinant of habitat suitability.

Current evidence indicates that migratory wildebeest in the Serengeti region are regulated by the amount of green grass available during the dry season (Sinclair et al. 1985). Food abundance influences the survival of calves and adults more strongly than it influences fecundity (Sinclair 1979). In contrast, nonmigratory populations of wildebeest that also occur in savanna grasslands of the Serengeti and nearby Ngorongoro regions may be regulated by predation by lions and hyenas (Sinclair 1979). Approximately 10% of the Ngorongoro population of wildebeest is killed each year by predators, compared with 1% of the migratory population in the Serengeti (Kruuk 1972; Schaller 1972; Elliot and Cowan 1978).

For several years during the 1970s, dry-season rainfalls were above average, leading to higher grassland productivity, which resulted in a substantial increase in the numbers of migratory wildebeest; nonmigratory species such as kongoni, topi, and impala were apparently unaffected (Sinclair 1979). These empirical observations suggest that migratory wildebeest in the Serengeti ecosystem are regulated by food abundance, whereas nonmigratory populations are regulated by predators.

We examined the resource-use and predator-regulation hypotheses further by constructing a simulation model of the dynamics of the interactions between the wildebeest and the grassland. This model incorporates seasonal changes in both grassland productivity and patterns of habitat use by migratory or sedentary populations of herbivores. Although parameter values of our model were derived from the Serengeti ecosystem, the model structure is sufficiently general to apply to other grazing ecosystems populated by migratory herbivores. The conclusions that emerge from our simulations suggest an answer to the question raised earlier: why are migratory ungulates an order of magnitude more numerous than residents in some grassland ecosystems?

THE MODEL

Dynamics of Vegetation

To simulate the effects of seasonal use by herbivores, we partitioned vegetation into discrete populations influenced by herbivores for only part of each annual cycle. In our model, we consider two vegetation components: open grasslands occupied by wildebeest during the wet season, and wooded grasslands occupied during the dry season. Seasonal changes in the distribution of wildebeest have been well documented from aerial surveys conducted at monthly intervals from 1969 to 1972 (Pennycuik 1975). These data suggest that roughly 3000 km² of each grassland type are used repeatedly by wildebeest.

The general structure of our model is modified from Caughley (1976), using difference-equation approximations to differential equations. The net change in grass biomass for each daily time step is calculated as the sum of growth minus the consumption by herbivores. Daily growth during the wet season of each grass type is calculated as

$$\text{growth} = r(V + d)[1 - (V + d)/(k + d)],$$

where r is the intrinsic rate of increase, V is vegetation biomass, d is a constant that shifts the productivity curve toward the origin, and k is the peak vegetation abundance in the absence of grazing. This equation assumes that the relative rate of grass growth is linearly density-dependent, producing a logistic trajectory of abundance over time. As in the usual logistic formulation, incremental growth is parabolic, being highest at intermediate levels of abundance (ca. $k/2$) and declining as V approaches k . Perennial grasses that predominate in the Serengeti maintain low levels of productivity following denudation by grazers or grass fires, presumably by translocating labile carbohydrates from root and crown reserves (Trlica

1977). We therefore include a constant (d) in the above formulation that leads to continued grass production when the standing crop declines to 0. Parameter values for r , d , and k were estimated from data found in Braun (1973), Sinclair (1975), and McNaughton (1985). During the dry season, a small amount of production occurs in wooded grasslands as a result of infrequent rain showers (Sinclair 1975; McNaughton 1985). Given the low levels of dry-season productivity (less than 3 kg/ha/day), we assumed that density-dependent effects on grass growth never come into play during the dry season.

We assume that the daily rate of forage consumption by individual wildebeest is related to vegetation abundance by a type-II functional response (Holling 1959). This form is consistent with the rates of forage intake exhibited by domesticated livestock and other large herbivores whose grazing behavior is similar to that of wildebeest (Wickstrom et al. 1984; Short 1985; Renecker and Hudson 1986). In our model, we use a modified form of the Ivlev (1961) formula:

$$\text{forage eaten per day} = g(aA + aC/2)(1 - e^{-bV}),$$

where a is the maximum rate of food intake per adult, b is a constant that determines how rapidly intake approaches a with increasing forage availability, V is the biomass (kg/ha) of the type of grass consumed in a given season, g is a constant to convert total numbers of herbivores to density per hectare, and A and C are population numbers of adults and calves. This formula indicates that forage intake per herbivore rises initially with increasing vegetation biomass but levels off at high biomass because of the restricting effect of fixed handling time (feeding plus digestion). Given the structural similarities between semiarid grasslands in Australia and East Africa, we used Short's (1985) estimate of b for sheep and kangaroos in our simulation model. The maximum rate of intake by calves is presumed to be only one-half that of adults.

Similar approaches have been used in previous plant-herbivore models (Noy-Meir 1975; Caughley 1976). Our grazing model differs from most in (1) distinguishing discrete vegetation types that are fed upon for only part of each annual cycle, and (2) varying the maximum rate of vegetation growth according to season. The cost of including even this minimal realism in our model is the necessity of keeping track of calendar time, since several key processes (growth phenology of grasses and foraging on given grass types) are time-dependent. Parameter values of the grassland components of the model are summarized in the Appendix.

Herbivore Dynamics

At daily intervals, wildebeest population numbers increase by increments of the difference between recruitment (which occurs only during the wet season) and losses from malnutrition and predation. Serengeti wildebeest produce calves mainly during a 4-wk period in the middle of the wet season (Estes 1976; Sinclair 1977a). Observations over a wide range of population sizes suggest that natality rates and early survival rates of calves are largely independent of population density (Sinclair 1979). Accordingly, we calculate recruitment of calves by multiplying the total number of calves born (equal to one-half the number of adults) by

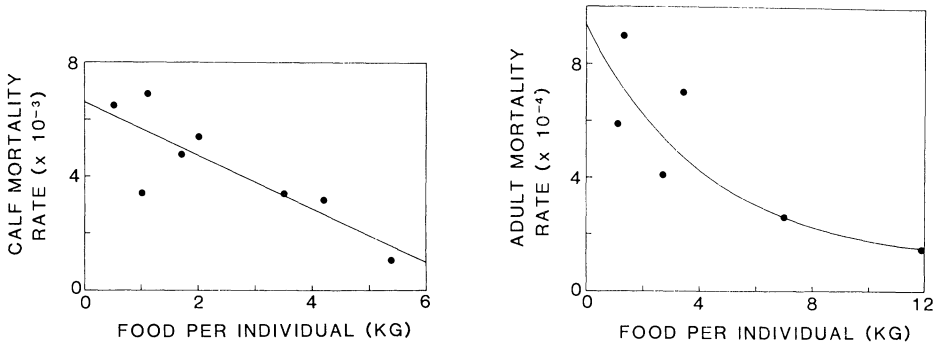


FIG. 1 (left).—Daily rates of mortality of wildebeest calves (m) in relation to per capita food availability (F) (replotted from data in Hilborn and Sinclair 1979: $m = 0.0066 - 0.00093F$; $r^2 = 0.70$, $F_{1,6} = 13.9$, $P < 0.05$).

FIG. 2 (right).—Daily rates of mortality of adult wildebeest (n) in relation to per capita food availability (F) (replotted from data in Sinclair et al. 1985: $n = 0.0001 + 0.00083e^{-0.232F}$; $r^2 = 0.91$, $F_{1,4} = 40.1$, $P < 0.05$).

early survival rates (57%; Sinclair 1979). Subsequent survival during the dry season depends on per capita food availability (fig. 1):

$$\text{calf mortality rate} = u - vF,$$

where F is per capita food availability. At the end of their first year, all calves that have survived are added to the adult population.

Long-term studies (Sinclair 1979; Sinclair et al. 1985) suggest a curvilinear relationship between adult mortality and per capita food availability (fig. 2). A small amount of mortality (ca. 0.01% per day) occurs at higher levels of food availability, presumably as a result of senescence, disease, or accidents. With decreasing food availability, mortality rates increase sharply. Using least-squares regression, we fitted a negative-exponential curve to these estimates:

$$\text{adult mortality rate} = x + ye^{-zF}.$$

In our analysis of demographic data for wildebeest, we found no significant relationships between either calf or adult mortality and absolute food abundance. As pointed out by Caughley (pers. comm.), the correlation between mortality and per capita food abundance suggests that additional density-dependent processes are at work, such as spacing behavior or feeding interference between grazers. Whatever the underlying cause, the available evidence suggests that per capita food availability is a more useful demographic predictor than absolute food abundance.

An additional complication in modeling seasonal grassland ecosystems is that grasses typically decline in quality as they mature. For example, the protein content of Serengeti grasses declines from over 20% early in the growing season to 4% in the dry season (Braun 1973; Sinclair 1975). Since wildebeest require forage containing at least 5%–6% crude protein to maintain adequate rates of digestion (Sinclair 1975), much of the standing crop that is present at the end of the growing

season may be simply unsuitable as food. Field studies conducted in the dry season indicate that wildebeest feed on senescent grasses only when little green growth is available (McNaughton 1985).

We have dealt with this problem by constructing alternative forms of the model. In the first case, we assume that grasses do not change in quality as they mature; thus, the entire standing crop remains potentially edible during the dry season. In the second case, we assume that none of the standing crop remaining at the end of the wet season is edible and that wildebeest forage only on new growth. Although it is clear that the true situation probably falls somewhere between these two extremes, we feel that the second form of the model is perhaps more realistic than the first.

A wide variety of predators lives in the Serengeti ecosystem, but only lions and hyenas occur in numbers large enough to have a significant impact on wildebeest numbers. Population densities of these predators are probably limited by the abundance of resident prey, since few lions or hyenas are able to follow migratory herds because of the need to feed immobile young during the long period of dependence (Schaller 1972; Hanby and Bygott 1979). Since few prey occur year-round on the plains, predators are largely restricted to the wooded grasslands. Our model maintains a constant population of 1000 predators (based on Schaller's [1972] estimates of lion density in areas with abundant wildebeest) that feed on wildebeest when they are present in the wooded grasslands.

We assume that Serengeti predators have a sigmoid or type-III functional response (Holling 1959) for two reasons. First, if predators are limited by resident prey rather than by migrants, then some alternative prey must be available throughout the year. Second, field estimates of changes in the diet composition of lions during a decline in wildebeest numbers in Nairobi National Park suggest that lions tend to exploit selectively the species of prey that is most abundant in their territories. When wildebeest were the most abundant prey species in the park (>20% of total numbers averaged over the entire year), they provided more than 70% of the lion's diet (Foster and Kearney 1967). However, as wildebeest numbers declined (<10% of the population total), their proportion in the lion's diet decreased to 14% (Rudnai 1974). These figures are crude, since they are based on population totals averaged over the entire year, and temporary influxes of migrants caused considerable monthly fluctuations in numbers. Nonetheless, they suggest that the normal preference of lions for wildebeest changed drastically as their proportion in the population declined. We have modeled this response with the following equation:

$$\text{number killed per day} = qpN^6/(N^6 + s^6),$$

where q is the daily ration of wildebeest required per predator and p , N , and s are population numbers of predators, wildebeest, and alternative prey. This formulation results in predators' taking wildebeest only when the herds are present in the wooded grasslands and when the biomass of wildebeest exceeds that of alternative prey. We estimated q to be 0.053 wildebeest per day, based on Schaller's (1972) calculations of annual food requirements of Serengeti lions. We calculated s from the population estimates of Grimsdell (1979); each prey species (topi, kon-

goni, and impala) was converted by weight to an equivalent number of wildebeest (e.g., 1 impala = 0.33 wildebeest).

A summary of our model and a complete list of parameter values used in the simulations is given in the Appendix.

RESULTS

Food Regulation

The simulated dynamics of wildebeest-grassland interactions depend on whether or not seasonal changes in forage quality are assumed. We first consider the case in which grasses decline in quality as they mature, and old growth is unavailable as forage during the dry season. Under this condition, populations of either migrant or resident wildebeest exhibit logistic trajectories that approach a food-regulated equilibrium of approximately 1.6 million animals (fig. 3).

The model predicts that a migratory population near equilibrium should maintain the standing crop of shortgrasses at a small fraction of the levels attained in the absence of grazing. It is interesting to note the abrupt change in the peak biomass of shortgrasses as wildebeest approach equilibrium. This is indicative of a sudden switch to a lower stable state of vegetation abundance, as suggested by previous models of plant-herbivore interactions (Noy-Meir 1975; May 1977). Tallgrasses show little change over time because wildebeest are absent throughout most of the growing season. Despite the strong impact of migratory wildebeest on the dynamics of shortgrasses, wildebeest are regulated by per capita food availability during the dry season. A resident population of wildebeest causes an analogous shift in the abundance of tallgrasses to a lower stable state as herbivores approach equilibrium (fig. 3b).

If we assume that grasses do not decline in quality as they mature, then equilibrium densities of wildebeest reach higher levels, but the numerical trends over time remain qualitatively similar to the previous case. In the migratory scenario, wildebeest numbers temporarily exceed 5 million before settling at a food-regulated equilibrium of 3.2 million animals (fig. 4a). A resident population shows similar temporal changes, stabilizing at 1.7 million animals (fig. 4b). Our model predicts a twofold difference between the abundance of migratory and resident herds under equilibrium conditions. As in the previous case, migratory herds can maintain shortgrasses at low levels, and residents do the same to tallgrasses. Although it was not true for the previous case, migratory wildebeest in this case are regulated by food availability during the wet season. Even when feeding at maximum rates, the wildebeest require most of the dry season to consume the standing crop accumulated during the preceding growing season. As a result, food is in shortest supply during the wet season, when most mortality from malnutrition takes place.

This emphasizes the importance of seasonality in our trophic model. If resource levels vary considerably during the year, then the population abundance of consumers is determined by food availability during the period of relative scarcity. In the first form of our model, food is most scarce during the dry season because old

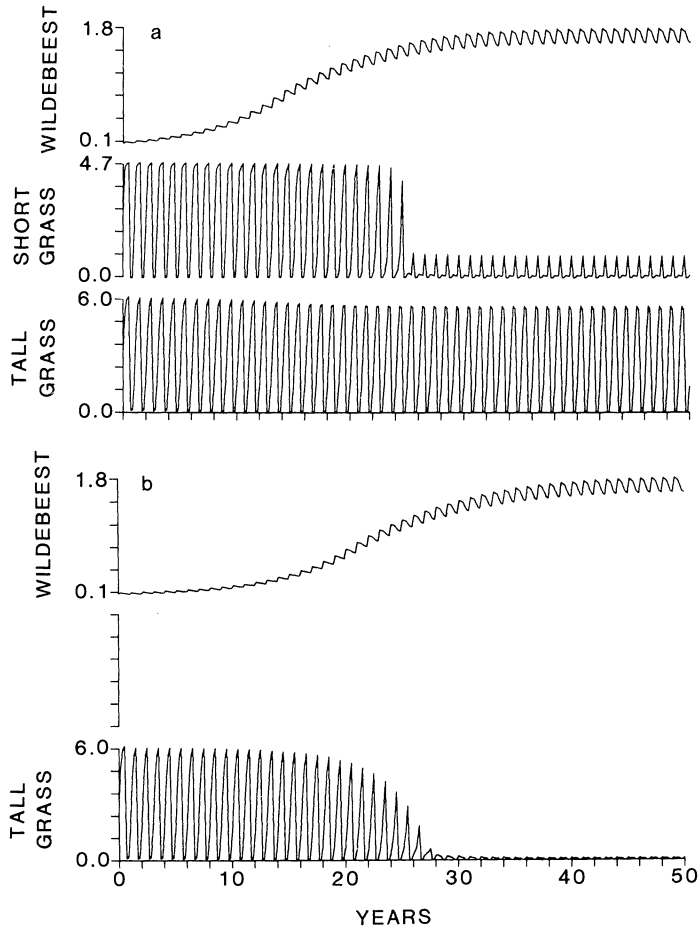


FIG. 3.—Simulated trends over time in the abundance of wildebeest ($\times 10^6$), shortgrasses, and tallgrasses ($\text{kg/ha} \times 10^3$), assuming that forage quality declines with maturation: *a*, migratory scenario; *b*, resident scenario.

growth is unsuitable as food. As a result, an increase in food supplies during the wet season obtained by migrating elsewhere in the ecosystem does not lead to higher herbivore numbers. In the second form of our model, migration to the open grasslands during the growing season allows the accumulation of a massive reservoir of food in the wooded grasslands. This removes the dry-season food constraint, and the wet season becomes the period of greatest scarcity. Consequently, migrants reach higher densities before food regulation (imposed by food supplies in the wet-season range) comes into play.

The dynamics of the first form of our model, incorporating seasonal changes in grass quality, are most consistent with empirical observations from the Serengeti ecosystem. First, the equilibrium population size of 1.6 million is close to the current (apparently stable) population of 1.4 million wildebeest (Sinclair et al.

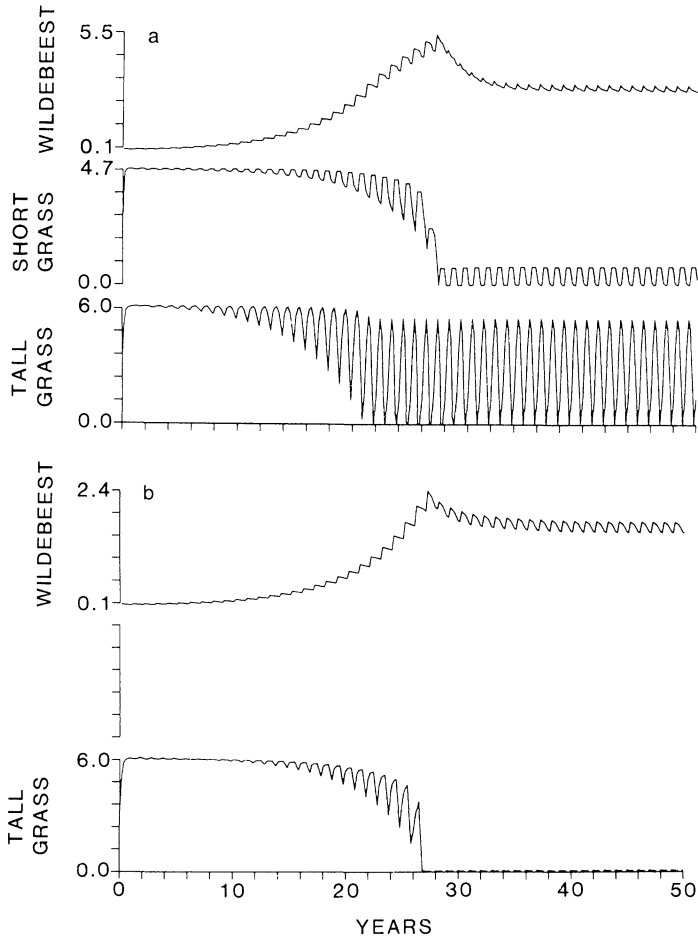


FIG. 4.—Simulated trends over time in the abundance of wildebeest ($\times 10^6$), shortgrasses, and tallgrasses ($\text{kg/ha} \times 10^3$), assuming that forage quality does not decline with maturation: *a*, migratory scenario; *b*, resident scenario.

1985). It is encouraging that our model mimics observed population trends without fine-tuning the parameters. Second, our model predicts a long-term decline in the peak standing crop of shortgrasses consistent with anecdotal observations. Grass fires were once a common occurrence on the Serengeti plains, but the total area burned has declined considerably following the increase in wildebeest numbers since the late 1960s (Norton-Griffiths 1979). This could be explained by a decline in the amount of fuel that accumulates during the growing season. Third, our model predicts that mortality from malnutrition should be most severe during the dry season, in agreement with long-term studies in the region (Sinclair et al. 1985). In sum, we feel that our first migration model mimics the salient features of wildebeest-grassland dynamics in the Serengeti ecosystem.

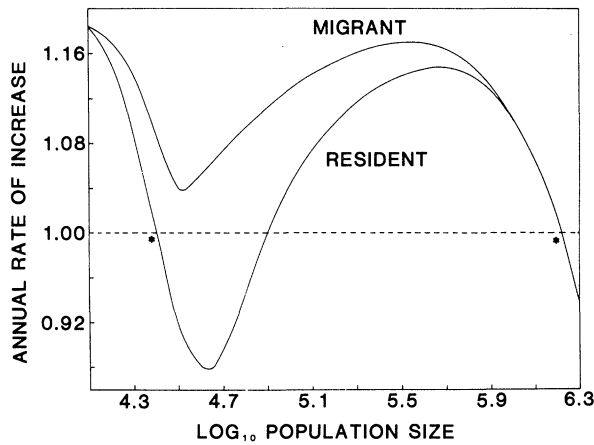


FIG. 5.—Annual rate of population increase of migratory or resident herds of wildebeest in relation to population size. Stable equilibria indicated by asterisks.

Predator Regulation

Our simulations suggest that 1000 predators in the Serengeti could regulate a resident population of wildebeest below 85,000 animals (fig. 5). In contrast, this number of predators could not regulate a migratory herd. The lower equilibrium for a resident herd is stable because of the sigmoid functional response assumed for predators, such that predators switch to resident prey when wildebeest become less numerous. We emphasize that wildebeest could be regulated by predation even in the absence of a predator numerical response, since predator numbers were held constant in our simplistic model.

The population density of alternative prey has a strong influence on whether regulation by predators can occur (fig. 6). In our model, we assume that the density of predators in Serengeti woodlands is approximately 0.33 per square kilometer. At this density, predators could not regulate a resident herd if the density of alternative prey exceeded 15 per square kilometer, because our model assumes that predators ignore wildebeest as long as they are less abundant than alternative prey. If predators did not switch until wildebeest exceeded 15 per square kilometer, then the total number of wildebeest killed over the entire year would not compensate for recruitment, and wildebeest numbers would increase.

Model with Both Residents and Migrants

The simulations we have described thus far depict interactions among vegetation, predators, and a population of herbivores that either migrates seasonally or else remains in one location year-round. Of course, many savanna ecosystems have both migratory and resident populations whose ranges overlap during at least part of the year. Competition for food supplies, particularly during seasonal periods of scarcity, could influence the dynamics of both behavioral morphs.

We considered this problem by modifying our basic Serengeti model to include both a migratory and a resident population of wildebeest. In our modified model,

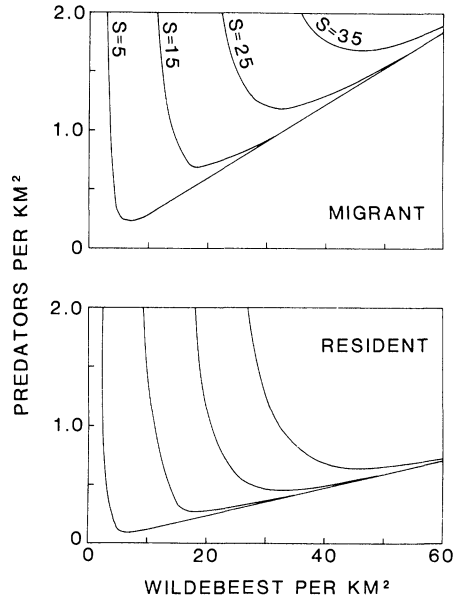


FIG. 6.—Zero isocline ($N_{\text{year1}} = N_{\text{year2}}$) of migratory and resident populations of wildebeest for various densities of predators and alternative prey. Wildebeest are potentially regulated by predators when the isocline appropriate to a given density of alternative prey (s) intersects the observed predator density.

tallgrasses are subject to herbivory by a resident herd throughout the year and by migrants during the dry season. As before, shortgrasses are fed upon only during the wet season. Resident herbivores are subject to predation year-round, whereas migrants are only affected during the dry season. Since we assume that predators do not discriminate between migrants and residents when both are present, the numbers of each morph killed by predators are proportional to their relative abundance. As before, we assume that predators ignore wildebeest when alternative prey are more numerous.

Under these conditions, a single stable equilibrium is possible, with high numbers of migrants (ca. 1.6 million) and low numbers of residents (ca. 17,000). Population trajectories and the amount of time taken for equilibration depend on the initial numbers of each morph. If the initial ratio of migrants to residents is large, then population levels stabilize quickly. When equal numbers of migrants and residents are assumed initially, both morphs increase rapidly in abundance until vegetative carrying capacity is reached; then residents slowly decline while migrants increase. Equilibration often takes as long as 100 simulated years.

Residents never stabilize at high densities because they always experience higher mortality rates than migrants. When the total number of migrants plus residents is large, both morphs are subject to identical rates of mortality from malnutrition, because food availability in the dry-season range is limiting. However, residents always experience marginally higher predation rates because they alone are preyed upon during the wet season, whereas both morphs have similar

predation rates during the dry season. Consequently, migrants increase slowly and residents decline over time. These results suggest that residents are always driven to a low stable equilibrium when they compete with migrants for the same limiting resources.

DISCUSSION

Our simulation of the wildebeest population in the Serengeti illustrates three principles that may apply to other migratory herbivores. First, the larger area often used by migrants does not lead inevitably to higher numbers of migrants. If resource levels vary considerably throughout the year, then herbivore abundance is determined by food availability during periods of resource scarcity. Even though migrants may have access to greater food supplies during the rest of the year, they do not outnumber residents if both morphs have similar food supplies during the dry season.

Second, in a migration system, vegetation has a period free from grazing during which tissues removed by herbivores may be restored. If this regrowth is used by migrants when they return, then carrying capacity is enhanced and consumer populations may be maintained at higher levels than would otherwise occur.

Conceivably, this process could lead to pronounced disparities in the abundances of migrants and residents. However, we think it is unlikely in African ecosystems for a number of reasons. First, there is little evidence that migratory ungulates in Africa feed extensively on old growth when they return to the dry-season range (McNaughton 1985; Fryxell and Sinclair 1988), probably because tropical grasses decline rapidly in quality as they mature (Braun 1973; Sinclair 1975). Second, demographic studies of migratory wildebeest and white-eared kob suggest that most mortality from malnutrition takes place during the dry season, which would not be expected if old growth was an important source of food (Sinclair et al. 1985; Fryxell 1987). Third, pronounced disparities in abundance would be expected only if the area used by migrants during the wet season was much larger than that used during the dry season. There is little indication that wet-season ranges of migrants are appreciably larger than those in the dry season (Maddock 1979; Fryxell and Sinclair 1988). Even if old-grass growth was used by migrants, our simulations suggest that in the Serengeti this process would at most produce a twofold difference between migrants and residents. The increased efficiency in resource use resulting from rotational grazing is unlikely to explain the order-of-magnitude disparities in abundance observed in some communities of African ungulates.

A third consequence of seasonal movements is that migrants may be less vulnerable to regulation by sedentary predators, simply because prey are unavailable during part of the year. Predator regulation would usually result in low densities of resident herbivores. Differences in regulating factors could therefore explain the pronounced disparity in the abundances of migrants and residents. Populations of migratory herbivores regulated by food availability would readily outnumber predator-regulated residents by an order of magnitude.

The predictions of our model should apply, in principle, to other herbivores

with predictable migration patterns that are synchronized with seasonal changes in vegetation growth. However, our model is inappropriate for truly nomadic species, whose movements are unpredictable in space and time. For example, dorcas gazelle living on the arid fringes of the Sahara Desert obtain food and water from ephemeral patches of green growth that occur as a result of localized rain showers (Carlisle and Ghobrial 1968; Ghobrial 1974). A transient life-style may be obligatory for survival in such a harsh environment, because the availability of critical resources is unpredictable in any given location from year to year.

Our model is also inappropriate for migratory herbivores whose predators can follow migrants over their annual circuit. Short-distance migrations, such as the seasonal altitudinal migrations of many montane ungulates (McCullough 1985), may not take migrants outside the range of their predators. As a consequence, we would not expect such short-distance migrants to be necessarily less vulnerable than residents to regulation by predators.

Data on the relative densities of wildebeest, predators, and alternative prey are available for a limited number of savanna ecosystems (table 2). We used our model to predict the range of densities in each of these areas at which wildebeest could be regulated by predators. Our calculations suggest that all of the sedentary populations are regulated by predation, whereas two of the three migratory populations are regulated by food abundance. The Etosha population of migratory wildebeest may provide an interesting exception. Predator regulation should be impossible at the current densities of predators and alternative prey, according to our model. The question then arises why wildebeest numbers in Etosha are so low. One possible explanation is that this herd suffered an outbreak of anthrax in the 1970s that apparently caused a severe reduction in numbers (Berry 1981a,b).

TABLE 2
OBSERVED DENSITIES OF WILDEBEEST, PREDATORS, AND ALTERNATIVE PREY IN FIVE
SAVANNA ECOSYSTEMS AND THE PREDICTED DENSITY OF WILDEBEEST UNDER THE
PREDATOR-REGULATION HYPOTHESIS (PER km²)

LOCATION*	MIGRATORY?	OBSERVED POPULATION DENSITIES†			PREDICTED DENSITY OF WILDEBEEST
		Predators‡	Other Prey	Wildebeest	
Serengeti main herd ^a	yes	0.33	11	467	—
Nairobi ^b	yes	0.26	16	130	—
Etosha ^c	yes	0.32§	21	2	—
Serengeti corridor herd ^d	no	0.33	11	15	<28
Ngorongoro ^e	no	0.99	41	64	<83
Kruger ^f	no	0.25	5	3	<21

* SOURCES.—*a*, Schaller 1972; Hilborn and Sinclair 1979; Sinclair et al. 1985. *b*, Foster and Kearney 1967; Rudnai 1974; Hillman and Hillman 1977. *c*, Berry 1981a,b. *d*, Sinclair, unpubl. data. *e*, Kruuk 1972; Elliot and Cowan 1978. *f*, Pienaar 1969; Smuts 1978.

† Individuals per km².

‡ Lions + hyenas (assume 1 hyena = 0.4 lion).

§ Hyenas were not counted, but since they are considered abundant (Berry 1981a,b), we assume that the ratio of hyenas to lions is similar to that of nearby Kruger (1800:700).

This presents a useful opportunity for testing our model. If anthrax can be eliminated, then this population should increase to the upper equilibrium determined by food abundance, rather than remaining low because of predator regulation.

A second field test of the model may have been initiated inadvertently in the Kalahari/Gemsbok National Park. Wildebeest usually migrate outside the reserve during the dry season to use permanent water supplies. Fences have been erected in recent years to prevent the transmission of hoof-and-mouth disease from wildebeest to cattle. As a result, wildebeest are now excluded from most of their normal dry-season range. Recent studies suggest that restricted migration has led to rapid decline in wildebeest numbers from malnutrition (Williamson and Williamson 1984), as would be predicted by our model.

Recent studies on niche partitioning among Serengeti grazers suggest that predation causes greater overlap in habitat and food selection than would be expected from competition theory (Sinclair 1985). Various resident species form mixed herds, apparently to avoid predation. These data support our hypothesis that resident herds in the Serengeti are regulated by predation, and demographic studies are currently under way to test this.

SUMMARY

Migratory ungulates outnumber residents by an order of magnitude in several savanna ecosystems in Africa, as was apparently the case in other grasslands around the world before the intervention of modern man. Migrants may be more numerous than residents because (1) they use a much larger area, (2) they make more-efficient use of resources, or (3) they are less vulnerable to regulation by predators. These hypotheses were examined using simulation models of migratory and sedentary wildebeest in the Serengeti ecosystem.

The larger area used by migrants would not lead inevitably to higher numbers. In seasonal environments, herbivore abundance is probably determined by food availability during periods of resource scarcity. Even though migrants may have access to greater food supplies for most of the year, this would not lead to increased abundance if both morphs have similar food supplies during the leanest period of the year.

Rotational grazing could lead to increased numbers of migrants relative to residents only if migrants are able to use mature vegetation that has accumulated while they are foraging elsewhere. This is unlikely for savanna ecosystems in Africa because tropical grasses decline rapidly in quality as they mature. Moreover, our simulations suggest that in the Serengeti such a process would at most produce a twofold difference in abundances of migrants and residents. We conclude that increased efficiency in resource use by migrants is insufficient to explain the order-of-magnitude disparities in abundance seen in some African ecosystems.

Our simulations suggest that realistic numbers of predators could regulate resident herbivores at low population densities, whereas such regulation is probably rare for migratory herds. When residents and migrants have overlapping

ranges, migrants should always outcompete residents, reducing them to low numbers. These results suggest that differences in the modes of regulation explain the predominance of migratory herbivores in some grassland ecosystems.

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APPENDIX

SUMMARY OF THE SERENGETI GRAZING MODEL

The grazing system is modeled by four sets of equations: two relate to daily changes in the biomasses of shortgrasses and tallgrasses, and two relate to changes in the abundance of wildebeest calves and adults. Changes in the biomass of grass type i (short or tall) during each daily time step are calculated as

$$\Delta V_{i,t} = \gamma_{i,t} - \beta_{i,t},$$

where $\gamma_{i,t}$ is the daily growth of grass i on day t , and $\beta_{i,t}$ is the amount of grass i consumed by herbivores on day t . Daily growth is calculated as

$$\gamma_{i,t} = \begin{cases} r_i(V_i + d_i)[1 - (V_i + d_i)/(k_i + d_i)] & \text{for Nov. } 1 \leq t < \text{July } 1 \\ c_i & \text{for July } 1 \leq t < \text{Nov. } 1 \end{cases}$$

Daily consumption of grass i is calculated as

$$\beta_{\text{short},t} = \begin{cases} g(aA + aC/2)[1 - \exp(-bV_{\text{short}})] & \text{for Nov. } 1 \leq t < \text{June } 1 \\ 0 & \text{for June } 1 \leq t < \text{Nov. } 1 \end{cases}$$

$$\beta_{\text{tall},t} = \begin{cases} 0 & \text{for Nov. } 1 \leq t < \text{June } 1 \\ g(aA + aC/2)[1 - \exp(-bV_{\text{tall}})] & \text{for June } 1 \leq t < \text{Nov. } 1 \end{cases}$$

Of the 10 parameters used in these equations, 5 have a reasonable empirical basis (k_{tall} , k_{short} , c , g , and a), and 5 are simply educated guesses (r_{tall} , r_{short} , d_{tall} , d_{short} , and b). Parameter values are listed below.

Changes in the numbers of wildebeest adults (A) and calves (C) are calculated as

$$\Delta A_t = \begin{cases} -A(x + ye^{-zF}) & \text{for Nov. } 1 \leq t < \text{June } 1 \\ -A(x + ye^{-zF}) - qpN^6/(N^6 + s^6) & \text{for June } 1 \leq t < \text{Nov. } 1 \end{cases}$$

$$\Delta C_t = \begin{cases} uA - C(v - wF) & \text{for } t = \text{Feb. } 1 \\ -C(v - wF) & \text{for Feb. } 1 < t < \text{Feb. } 1 \end{cases}$$

Surviving members of the previous year's cohort of calves are added to the adult population on February 1. Total population abundance (N) is calculated as the sum of adults (A) plus calves (C). All seven parameters in the herbivore equations have a reasonable empirical basis. The predator functional response, though not known, is qualitatively consistent with limited data for lions in Nairobi National Park (data in Foster and Kearney 1967; Rudnai 1974).

State Variables

- V_i biomass of grass type i (kg/ha)
 A number of wildebeest adults
 C number of wildebeest calves
 N total number of wildebeest ($A + C$)
 F per capita food availability (V_i/gN)

Parameters

r_i	intrinsic rate of increase of grass i during the wet season	tall 0.26 short 0.057
c_i	daily growth of grass i during the dry season (kg/ha)	tall 2.3 short 0
d_i	parameter to shift the incremental growth curve of grass i toward the origin	tall 539 short 179
k_i	peak biomass of grass i (kg/ha)	tall 6000 short 4700
g	constant to convert total wildebeest abundance to density per ha	3.33×10^{-6}
a	maximum rate of forage consumption (kg/day)	4.0
b	grazing-efficiency parameter	0.01
x	adult mortality rate per day when food is abundant	0.0001
y	increase in adult mortality rate when there is no food	0.00083
z	slope of \ln adult mortality vs. F	0.232
u	maximum rate of calf recruitment	0.285
v	intercept of calf mortality vs. F	0.00658
w	slope of calf mortality vs. F	0.00093
q	number of wildebeest required per predator per day	0.053
s	number of alternative prey in wooded grasslands	32,100
p	number of predators in wooded grasslands	1000

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