WHAT DETERMINES PHENOLOGY AND SYNCHRONY OF UNGULATE BREEDING IN SERENGETI?

A. R. E. Sinclair,[1] Simon A. R. Mduma,[1,3] and Peter Arcese[2,4]

[1]*Centre for Biodiversity Research, 6270 University Boulevard, University of British Columbia, Vancouver, Canada V6T 1Z4*
[2]*Department of Wildlife Ecology, 226 Russell Laboratories, 1630 Linden Drive, University of Wisconsin, Madison, Wisconsin 53706 USA*

Abstract. Birth seasons of ungulates in tropical regions show a complex pattern varying from asynchronous to highly synchronous and at different times of year. We examine the factors determining the phenology and synchrony of birth seasons of 13 species of ungulates in the Serengeti ecosystem, Tanzania. We propose that *phenology* of births (time of year) is determined by food supply, whereas birth *synchrony* (degree of coordination or spread) is an antipredator adaptation that functions in two different ways. High synchrony may occur through ''predator satiation'' in species with precocious newborn (''followers''), whereas asynchrony may occur through ''predator avoidance'' in species with nonprecocial young (''hiders''). We used green biomass of grass or tree shoots and percentage crude protein as measures of food supply. Births were determined from monthly sample counts covering the period 1967–1997. The frequency distribution of births was compared to that predicted by the abundance of green biomass and percentage protein, and by an even (asynchronous) monthly distribution. Wildebeest, topi, warthog, and Grant's gazelle births differed from all predicted distributions. Another group showed birth distributions similar to that of green biomass food (buffalo, oribi) or the distribution of percentage protein (giraffe, waterbuck, kongoni, zebra). Also giraffe, waterbuck, and Thomson's gazelle showed births spread more evenly through the year. For grazing species the lag in months between birth peak and protein peak is a positive function of metabolic body size whereas the lag with biomass is a negative function of body size. We suggest that small grazers produce their young early in the wet season ahead of the high protein peak, whereas large species produce their young in phase with high biomass and after the protein peak consistent with metabolic requirements. In terms of synchrony, large species in large herds with precocial young (wildebeest, topi, buffalo) have highly synchronized birth seasons consistent with the ''predator satiation'' hypothesis. Small species living in small groups with nonprecocial young (impala, Thomson's and Grant's gazelle, waterbuck, oribi) have births less synchronized than the food supply, as predicted by the ''predator avoidance'' hypothesis. In general, food supply determines the phenology of the birth season. Predation appears to shape the synchrony of births through two opposite adaptations. However, no single feature predicts all species' birth distributions. A combination of the phenology of food supply plus antipredator adaptations accounts for most but not all these distributions.

Key words: birth seasons; browser; food supply; grazer; phenology; Serengeti; synchrony; tropical ungulates.

INTRODUCTION

The birth seasons of ungulates in north temperate zones are thought to be adjusted so that young are produced when food is plentiful (Bunnell 1982, Linnell and Andersen 1998). Thus, moose (*Alces alces*) and caribou (*Rangifer tarandus*) have well synchronized birth seasons in early June associated with the onset of new plant growth (Bergerud 1974, Dauphine and McClure 1974, Bronson 1989, van Ballenberg and

Miguelle 1993). However, breeding becomes less synchronous as one approaches the tropics (Bronson 1989). In the widespread genus *Odocoileus,* for example, populations at latitudes >30° have birth periods that are highly synchronized with spring green-up. In the Florida Keys, *Odocoileus* deer give birth in all months of the year with a strong peak in spring. In Venezuela, breeding is asynchronous (Brokx 1972).

In temperate Africa births are also associated with spring and summer (Dasmann and Mossman 1962, Fairall 1968, Spinage 1973, Skinner et al. 1973, 1974, David 1978, Sekulic 1978, Underwood 1978, Anderson 1979, Murray 1982). The pattern is less clear-cut than that in the northern hemisphere, particularly in hotter areas such as Kruger National Park (N. Owen-Smith, *personal communication*). In contrast, in tropical Africa both the timing and synchrony of births differs
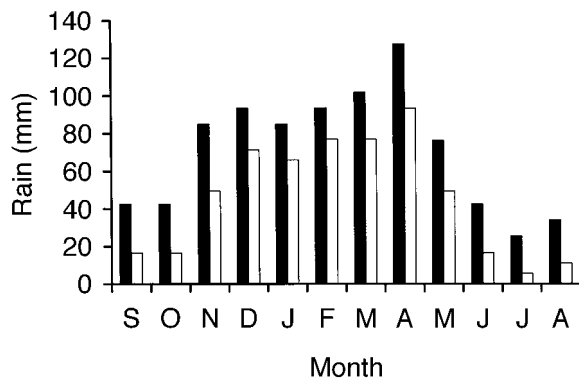
FIG. 1. Monthly rainfall distribution for the wetter north-center of the Serengeti ecosystem (solid bars) compared to the drier Serengeti plains (open bars).

among ungulate species. However, gross habitat, climate, and other factors confound comparisons between species in different regions. Thus, births have been recorded either at different seasons or throughout the year (Spinage 1969, 1973, Bourliere et al. 1976, Sekulic 1978, Wirtz and Kaiser 1988).

As part of a long-term study of ungulate populations in the Serengeti ecosystem of Tanzania, we have accumulated information since 1967 on the timing of births of 13 species of ungulates. The Serengeti ecosystem is a tropical savanna area close to the equator (1–3° S) and has a strong seasonal rainfall pattern (Norton-Griffiths et al. 1975, Sinclair 1979a). Rainfall is the main determinant of vegetation growth and food supply for ungulates (Sinclair 1975, 1977a, McNaughton 1979, 1983).

In this paper we analyze the phenology and synchrony of birth seasons in the context of two major limiting factors, food supply and predation. Phenology and synchrony address different questions. Phenology addresses when in the year births occur, i.e., their seasonality. Synchrony addresses the degree to which births are coordinated or spread over time irrespective of the time of year. We propose first, that the time of year when births occur is related to the timing of growth (phenology) in food supply (Rutberg 1987). Since each ungulate species differs (slightly) in its preferred food, the period in the year when births occur should reflect differences in when food becomes available. Secondly, we propose that the synchrony of births is determined both by the length of time that food is available and by antipredator behavior. If food determines synchrony (as distinct from seasonality) then the distribution of births should be similar to the seasonal distribution of food.

Alternatively, predation may produce extreme synchrony in births as an antipredator adaptation, as proposed for both birds (Kruuk 1964, Findlay and Cooke 1982) and ungulates (Estes 1966, 1976, Sinclair 1977a, b, Estes and Estes 1979, Rutberg 1987, Ims 1990). In essence, if births occur synchronously then predators
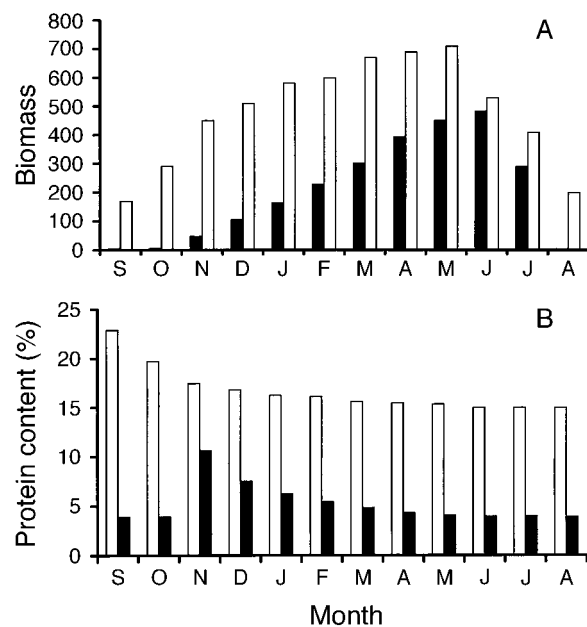

FIG. 2. (A) Monthly dry biomass of green grass and herbs for the woodlands and long grass plains ([kg/ha] $\times 10^{-1}$; solid bars), and young tree shoots (kg/ha; open bars). Note the difference in scales. (B) Monthly protein content of grass for the woodlands and long grass plains (solid bars), and young tree shoots (open bars; data from Pellew 1980).

become satiated and survival of the remaining newborn animals increases. This "predator-satiation" hypothesis should apply only to those species where such synchronized behavior is effective. Jarman (1974) has categorized African ungulates in terms of a suite of co-evolved ecological and behavioral traits. One such category comprises species that are relatively large, eat abundant food such as grass, form large herds, and have precocial young that follow the mother from birth and therefore are visible to predators. These are "follower" species. We predict it is this group that exhibits syn-

TABLE 1. Numbers and distribution of ungulate species in the Serengeti ecosystem considered in this study.

Species	Population (no. inds.)	Body mass (kg)	Distribution
Wildebeest	1 300 000	163	Migratory
Thomson's gazelle	450 000	16	Migratory
Zebra	200 000	220	Migratory
Topi	95 000	110	West, North
Impala	75 000	42	All woods
Buffalo	45 000	450	All woods
Grant's gazelle	26 000	43	Plains, East
Kongoni	14 000	126	East
Giraffe	9 000	800	All woods
Oribi	7 000	19	North
Warthog	6 000	53	Widespread
Waterbuck	1 600	175	Riverine
Dikdik	⋯	5	All woods

Note: Data from Campbell and Borner (1995) and Mduma (1995).

TABLE 2. Total numbers of newborn and adult female Serengeti ungulates (all adults for zebra, warthog) recorded in each month, summed over 1977–1997.

Month	Wildebeest	Topi	Warthog	Impala	Waterbuck†	Giraffe	Zebra	Kongoni
Total numbers of newborn								
1	244	9	254	44	8	9	59	15
2	930	4	936	11	1	3	33	13
3	4143	2	4148	10	3	10	8	10
4	74	1	79	1	15	0	22	10
5	5	0	10	4	12	1	63	26
6	5	0	11	74	5	12	19	40
7	1	1	9	116	2	14	39	47
8	0	12	20	75	7	16	23	44
9	0	270	279	19	9	27	24	63
10	0	866	876	22	7	4	10	23
11	0	436	447	74	9	10	41	19
12	0	515	527	77	6	30	107	63
Total	5402	2116	498	527	84	136	448	373
Total numbers of adult females (or adults of both sexes [warthog, zebra])								
1	8861	1099	503	2156	83	254	3143	239
2	4862	2782	317	2891	104	276	5541	320
3	9518	3189	208	3705	39	230	1083	384
4	4399	1444	144	1145	88	52	3066	268
5	4456	1732	232	3218	135	203	9476	532
6	10514	5295	614	6234	204	378	4437	1077
7	8391	6969	990	7756	113	633	10113	1059
8	3006	2978	767	4330	87	377	6297	442
9	3456	2510	570	3584	52	340	6405	560
10	5925	1840	520	2053	66	200	3126	340
11	3571	2383	686	3935	96	306	4556	389
12	1709	4097	1126	6356	170	520	5990	687
Total	68668	36318	6677	47363	1237	3769	63231	6297

† Data for waterbuck include small calves, back-calculated to month of birth.

chronized births as an adaptation to satiate predators and constrain predation. In Serengeti, follower species include wildebeest (*Connochaetes taurinus*), topi (*Damaliscus korrigum*), buffalo (*Syncerus caffer*), and zebra (*Equus burchelli*). Both kongoni (*Alcelaphus buselaphus*) and warthog (*Phacochoerus aethiopicus*) have precocial young but live in dispersed, small groups (see Plate 1).

Another group of adaptive traits identified by Jarman (1974) is shown by small to medium sized, territorial species that eat dispersed food, live at lower density in small groups, and hide their newborn young (see Plate 2). These are "hider" species. We predict that this group should not synchronize their births. Because they are not sufficiently abundant to satiate predators, synchrony would result in greater rather than lesser predation (Ims 1990). Instead, this group should show the opposite trait of asynchronous births as a "predator

TABLE 3. Percentage of newborn ungulates in each month in the Serengeti study areas.

Month	Wildebeest (%)	Topi (%)	Warthog (%)	Buffalo (%)	Grant's gazelle (%)	Impala (%)
1	4.1	0.9	2.8	6.0	32.0	17.0
2	28.4	0.2	2.4	6.0	26.5	3.2
3	64.7	0.1	0.0	22.5	6.8	2.2
4	2.5	0.1	0.0	34.7	1.2	0.7
5	0.2	0.0	0.0	18.4	5.0	1.0
6	0.1	0.0	0.0	6.0	0.0	9.9
7	0.0	0.0	0.0	4.0	0.4	12.5
8	0.0	0.4	3.0	0.0	5.7	14.4
9	0.0	11.9	30.8	0.0	4.8	4.4
10	0.0	52.2	34.0	0.0	3.4	8.9
11	0.0	20.3	15.7	2.0	3.8	15.7
12	0.0	13.9	11.4	0.0	10.3	10.1
No. newborns	5402	2116	498	49	137	527

Note: Calculated from data in Table 2, buffalo data from Sinclair (1997*a*), Thomson's gazelle data from Bradley (1977), Grant's gazelle data from Walther (1972), dikdik data from Hendricks and Hendricks (1971), and oribi data from Jongejan et al. (1991; P. Arcese, *personal observation*).

PLATE 1. Kongoni (two individuals on left-hand side of photo) and topi are two closely related antelopes in Serengeti that eat very similar food and live in mixed groups. Topi are numerous and have highly synchronized births while kongoni are scarce and spread births through the year. These species illustrate the extremes in birth strategies.

PLATE 2. As an adaptation to spread the risk of predation, the impala antelope has one of the least synchronized birth seasons in Serengeti.

avoidance'' behavior. In Serengeti, this group includes impala (*Aepyceros melampus*), the two gazelles (*Gazella granti, G. thomsoni*), waterbuck (*Kobus defassa*), oribi (*Ourebia ourebi*), and the very small dikdik (*Rynchotragus (Madoqua) kirki*). Giraffe (*Giraffa camelopardalis*) although large and visible, live at low density in small groups and leave their young in the care of a guardian while feeding. Giraffe do not fit easily into either category but are more similar to the latter group in their suite of adaptations. In general, local abundance distinguishes the two groups, with ''followers'' tending to be locally abundant whereas ''hiders'' tend to be locally sparse. Thomson's gazelle are anomalous, at least in the migratory Serengeti population, by being ''hiders'' that are locally abundant, whereas kongoni and warthog are ''followers'' that are locally sparse.

We test these predictions using data collected over 31 yr (1967–1997) on births for the thirteen ungulate

species: unpublished data are presented for wildebeest, zebra, topi, kongoni, impala, waterbuck, warthog, and giraffe while other data are available for African buffalo (Sinclair 1977*a*), Grant's gazelle (Walther 1972), Thomson's gazelle (Bradley 1977), oribi (Jongejan et al. 1991; P. Arcese, *personal observation*), and dikdik (Hendrichs and Hendrichs 1971). Rainfall data, collected by members of the Serengeti Research Institute and its successor, the Serengeti Wildlife Research Centre, cover 34 yr (1961–1994).

METHODS

Data collection

For most species samples of animals were counted from a vehicle and scored according to age and sex. Size, coat color, presence of umbilical remnant, and absence of horns identified newborn animals, the combination depending on species. The sex of the newborn could not be identified. Adult females in most species were identified by size, color, absence of horns, or

TABLE 3. Extended.

Waterbuck (%)	Giraffe (%)	Zebra (%)	Thomson's gazelle (%)	Kongoni (%)	Oribi (%)	Dikdik (%)
10.1	9.3	20.5	11.6	8.7	9.9	44.4
1.3	2.9	6.5	4.1	5.7	4.7	5.6
3.1	11.4	8.1	3.4	3.6	8.5	0.0
18.0	0.0	7.8	3.0	5.2	14.9	6.7
14.7	1.3	7.3	3.0	6.8	15.9	20.0
6.0	8.3	4.7	4.5	5.2	13.2	53.3
2.8	5.8	4.2	9.7	6.2	12.2	20.0
7.8	11.1	4.0	6.0	13.9	7.7	0.0
10.2	20.9	4.1	12.0	15.7	4.1	0.0
8.4	5.3	3.5	8.2	9.4	1.8	0.0
10.3	8.6	9.8	13.1	6.8	4.2	0.0
7.3	15.2	19.5	21.3	12.8	2.8	50.0
84	136	357	87	368	176	33

TABLE 4. Kolmogorov-Smirnov values for monthly birth distribution relative to even distribution (K-S$_{even}$) and relative to that predicted by food-plant biomass (K-S$_{biomass}$) and distributions of protein content (K-S$_{protein}$) for respective areas of the Serengeti.

Species	Area	Comparisons vs. observed birth distributions					
		K-S$_{even}$	P	K-S$_{biomass}$	P	K-S$_{protein}$	P
Wildebeest	Plains	0.72	0.000	0.76	0.000	0.63	0.000
Topi	North	0.65	0.000	0.92	0.000	0.57	0.000
Warthog	Northcenter	0.58	0.000	0.88	0.000	0.50	0.000
Buffalo	West	0.46	0.000	0.22	0.169	0.48	0.000
Grant's gazelle	Plains	0.41	0.000	0.48	0.000	0.32	0.000
Oribi	North	0.21	0.001	0.15	0.044	0.29	0.000
Dikdik	East	0.19	0.738	0.36	0.026	0.23	0.373
Thomson's gazelle	Plains	0.20	0.063	0.59	0.000	0.22	0.000
Impala	Northcenter	0.17	0.000	0.25	0.000	0.16	0.000
Giraffe	Northcenter	0.19	0.016	0.32	0.000	0.15	0.108
Waterbuck	Northcenter	0.11	0.763	0.38	0.000	0.12	0.673
Kongoni	East	0.17	0.000	0.51	0.000	0.10	0.037
Zebra	Plains	0.13	0.002	0.39	0.000	0.05	0.540
Maximum value		0.92		0.92		0.92	

Note: Distributions were different if $P < 0.004$ (Bonferroni correction).

where present, their shape and size, and from the genital organs. In giraffe bony lumps on the forehead differ between the sexes. In zebra and warthog the sexes could not be distinguished reliably so that females and males were scored together as adults.

We collected data using vehicle transects that ran through four main areas of the Serengeti ecosystem: (i) the north (north of the Grumeti River in the northern extension), (ii) center and east (from the Research Institute northeastwards to the Grumeti River), (iii) west (from the Research Institute west along the corridor), and (iv) the Serengeti plains. All animals within a distance where age and sex could be distinguished with binoculars (about 200 m) were counted except in the case of wildebeest and zebra, where large numbers required us to count samples at systematic intervals. The timing of births in buffalo, Grant's gazelle, and Thomson's gazelle was obtained from published data on fetuses and pregnancy rates (Walther 1972, Bradley 1977, Sinclair 1977a) and those of oribi and dikdik from observations of juveniles (Jongejan et al. 1991, Hendrichs and Hendrichs 1971; P. Arcese, *personal observation*).

Rainfall was measured monthly from storage gauges placed in various parts of the ecosystem. Scientists, park wardens, and park rangers read the gauges. The data were stored at the Research Institute. Sometimes a gauge was not read for several months so those records were for the accumulated amount. The data set was purged of all records where the accumulated amount was for >2 mo. For two-monthly records the data were divided evenly.

Births

For each species the age–sex records were summed by month and the mean monthly newborn/adult female ratio (R_{mth}) calculated. For warthog and zebra the equiv-alent newborn/adult ratio was calculated. The ratios were summed over the year to give the annual newborn/adult female ratio ($R_y = \Sigma R_{mth}$). The percentage of annual births occurring in each month (pNB_{mth}) was therefore

$$pNB_{mth} = 100R_{mth}/R_y. \tag{1}$$

This procedure overcame bias from unequal samples of animals counted each month.

Food supply

Rainfall gauges were grouped according to the different areas of the ecosystem. For each area the mean monthly rainfall was calculated, and from this we obtained the proportion of annual rainfall occurring in each month.

Grass biomass in the wet season was calculated from the relationship given in Sinclair (1975, 1977a) and Braun (1973) of accumulated biomass (B_{wet}) as a function of accumulated rainfall (R_a) since the start of the wet season. The relationship differed slightly between the short grass plains (B_{wetp}) and the long grass plains and woodlands (B_{wetw}):

$$B_{wetp} = 0.0496R_a^{1.7888} \text{ (coefficient of variation [cv]} = 0.89) \tag{2}$$

$$B_{wetw} = 3.501R_a^{1.1022} \text{ (cv} = 0.94). \tag{3}$$

The percentage crude protein in the dry grass biomass was calculated from the relationship given in Sinclair (1977a) of percentage crude protein (P_{grass}) and accumulated biomass (B). This did not differ between plains and woodlands so that

$$pP_{grass} = 146B^{-0.4269} \text{ (cv} = 0.78). \tag{4}$$

At the end of the wet season (June or July depending on the area), the grass persists at high biomass and

remains green if rainfall continues. However, the grass senesces if no rain falls. Therefore, green biomass in July was estimated by taking the June biomass and discounting by the degree of senescence. The senescence discount was taken as the ratio of July to June rainfall (for eastern woodlands and plains May and June replace June and July):

$$B_{\text{july}} = B_{\text{june}}(R_{\text{july}}/R_{\text{june}}). \quad (5)$$

By the end of July the grass is dry and senescence is complete. Dry season rain then results in new growth from the roots, and hence a new relationship of biomass to rainfall. For the dry season months (August to start of wet season depending on area) biomass was calculated from monthly growth (B_{drym}) and monthly rainfall (R_{drym}) given in Sinclair (1979b) and Mduma et al. (1998):

$$B_{drym} = 1.25\ R_{drym}. \quad (6)$$

For herbaceous dicots and small woody shrubs we have used the same phenology as that for monocots. However, for trees a different phenology occurs. Pellew (1980) measured monthly production, biomass and protein of available shoots and leaves in *Acacia* trees fed upon by giraffe. We use his values for available biomass and calculate from his data the relationship between protein (pP_{tree}) and biomass (B) as

$$pP_{\text{tree}} = 95.689B^{-0.2787}. \quad (7)$$

To detect the seasonality of births we used the nonparametric two sample Kolmogorov-Smirnov test. With this we examined differences between observed birth distributions and (i) expected even distributions through the year (K-S $_{\text{even}}$) and (ii) expected distributions determined by biomass (K-S$_{\text{biomass}}$) and percentage protein (K-S$_{\text{protein}}$). The observed numbers of births or fetuses were used for the tests.

Synchrony of births

Because births were recorded by month our measure of synchrony was the degree to which births were distributed over the 12 months. This measure was the Index of Evenness J', which for 12 months is given by

$$J' = (\Sigma p_i \log p_I/\log 12) \quad (8)$$

where p_i is the proportion of births of species i occurring in any month. Evenness (J') ranges from zero for maximum synchrony to unity for no synchrony (Krebs 1989:366).

RESULTS

Phenology

Mean annual rainfall in Serengeti varies from 1050 mm in the northwest woodlands to 550 mm on the southeastern plains. Rainfall is highly seasonal with a wet period from about November to June and a dry period from July to October. We illustrate this in Fig.

1 for the northcenter of the system (solid bars). On the plains (Fig. 1, open bars) the wet season starts later (December) and ends earlier (May) but otherwise the seasonality is similar throughout the region.

With the start of the rains grass and herbs begin growth and green biomass accumulates until May or June. This is illustrated for the woodlands (Fig. 2A) from data in Sinclair (1977a) (Eq. 3), and differs only in detail with growth on the plains (Eq. 2). With the drop in rainfall in July, green biomass declines. Dry season storms in the north maintain some green biomass (Eq. 6) but the plains receive too little rain for any growth at this time.

The first growth of grass is high in protein content. As green biomass increases, however, percentage protein declines as illustrated in Fig. 2B (Eq. 4 from data in Sinclair 1977a). Both protein and green biomass were calculated separately for the north, east, west, and plains regions of the ecosystem, based on their respective rainfall regimes.

Available biomass of twig shoots and green leaves of *Acacia* trees measured by Pellew (1980) is shown in Fig. 2a. Biomass increases in the rains and decreases in the dry season. Tree green biomass is about one-tenth that of grasses and is more evenly distributed over the year. Also, these trees differ from grasses in that they anticipate the rains by one or two months with new growth starting in September. Thus crude protein is highest in this month, declining gradually over the rest of the year (Fig. 2B).

Distribution of births

Table 1 summarizes the abundance and distribution of species from data in Campbell and Borner (1995). Table 2 gives the sample sizes of newborn and adult females (or total adults for zebra, warthog) for the eight species counted on road transects over the years 1977–1995. Table 3 gives the monthly proportion of births for all thirteen species. The Kolmogorov-Smirnov values for differences in frequency distributions between observed births and those predicted by even monthly distributions, green biomass, and percentage crude protein for the same sample size are given in Table 4.

For the six grazing species with precocial young (wildebeest, topi, kongoni, warthog, buffalo, zebra), Fig 3. shows the frequency distribution of births. Four of these species show a marked peak of births near the beginning of the wet season. However, buffalo births coincide with the peak rainfall in April, and the kongoni birth peak occurs in the middle of the dry season.

Fig. 4 shows the frequency distribution of births for the less precocial ''hider'' species, and giraffe. Of these the two gazelles produce their young in the early rains, while oribi, of similar size to the gazelles, have a birth peak that coincides with late wet season. Dikdik, the smallest of these antelopes, produces two young per year. Based on the small sample given in Hendrichs and Hendrichs (1971) there are two peaks, one in early
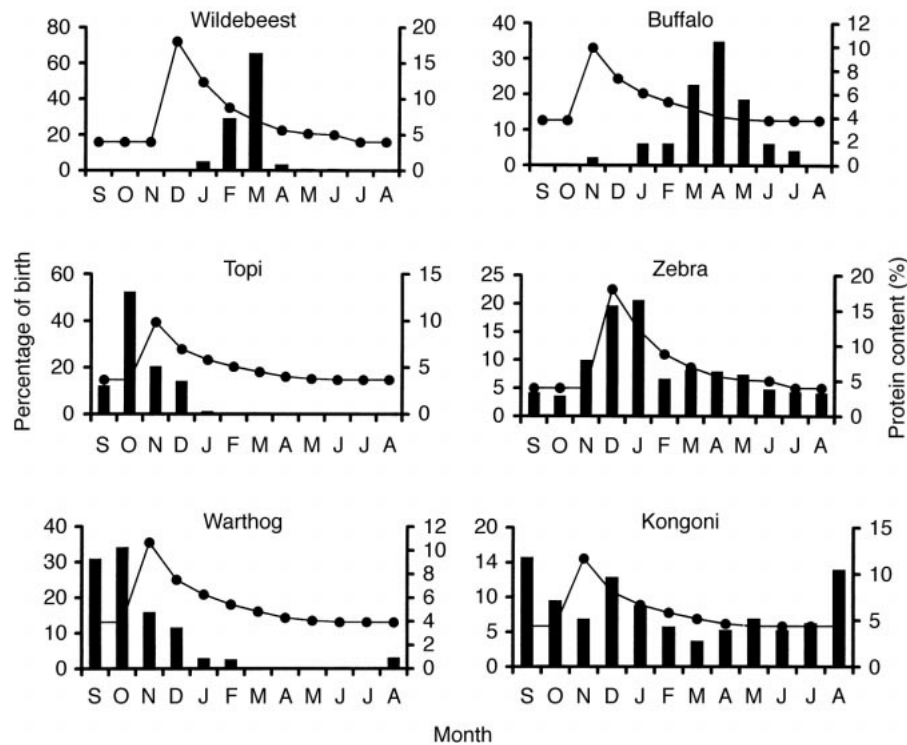
FIG. 3. Monthly distribution of births in grazing ungulates with precocial young (histogram) and the percentage crude protein of grass for their respective regions of the ecosystem (circles).

wet season the other at the end of the rains. Waterbuck distribute their births over the year with a small peak in late wet season. Impala have fewer births in the main wet months and have peaks in dry season and early wet season. Giraffe, the only species feeding on tree shoots, have their peak of births in the dry season al-though births occur frequently all through the year. Flowering, fruiting, and new shoots of *Acacia* trees (a major food of giraffe) occurs in mid dry season when crude protein levels reach $21.0 \pm 1.7\%$ of dry mass [mean $\pm$ 1 SE) compared to $15.3 \pm 0.9\%$ for older shoots later in the year (Pellew 1980).
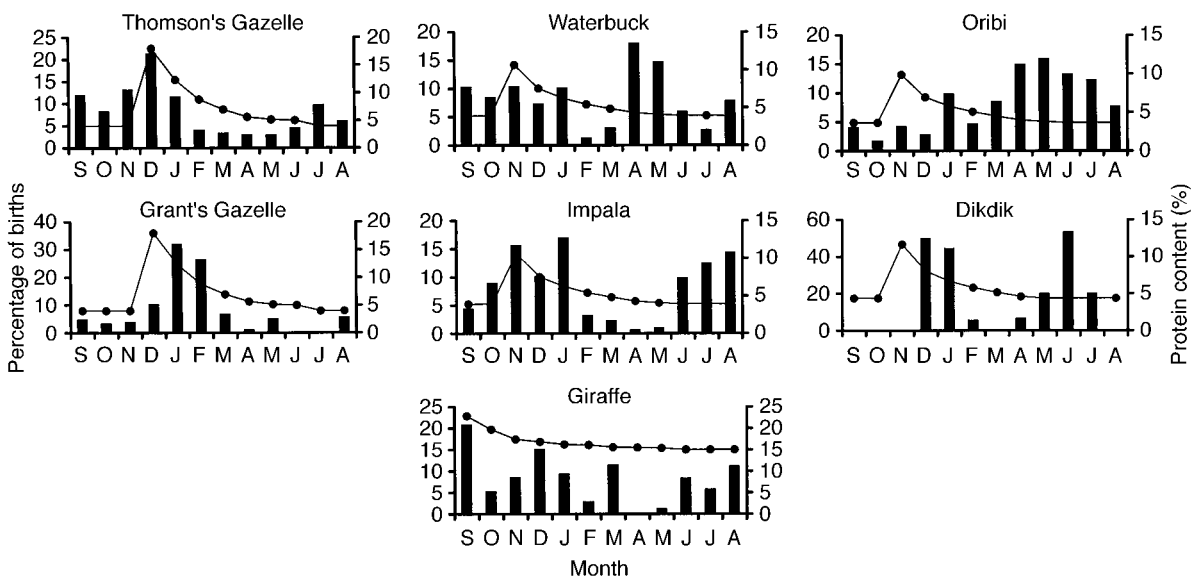

FIG. 4. Monthly distribution of births in grazing and browsing ungulates with nonprecocial young (histogram) and the percentage crude protein of grass for their respective regions of the ecosystem (circles).

TABLE 5. Evenness (J') values for monthly birth distribution of Serengeti ungulate species relative to evenness for rainfall, food biomass, and food percentage protein, and the ratios of birth J' to rain and food J'.

Species	Area	J'_{births}	J'_{rain}	J'_{births}/J'_{rain}	$J'_{biomass}$	$J'_{births}/J'_{biomass}$	$J'_{protein}$	$J'_{births}/J'_{protein}$
Wildebeest	Plains	0.354	0.910	0.389	0.736	0.481	0.938	0.377
Topi	North	0.515	0.965	0.534	0.835	0.617	0.976	0.528
Warthog	Northcenter	0.629	0.961	0.655	0.835	0.753	0.975	0.645
Dikdik	East	0.680	0.951	0.715	0.831	0.818	0.976	0.697
Buffalo	West	0.695	0.935	0.743	0.818	0.850	0.977	0.711
Grant's gazelle	Plains	0.771	0.910	0.847	0.736	1.048	0.938	0.822
Giraffe	Northcenter	0.894	0.961	0.930	0.962	0.929	0.997	0.897
Impala	Northcenter	0.894	0.961	0.930	0.835	1.071	0.975	0.917
Oribi	North	0.933	0.965	0.967	0.835	1.117	0.976	0.956
Waterbuck	Northcenter	0.933	0.961	0.971	0.835	1.117	0.975	0.957
Zebra	Plains	0.924	0.910	1.015	0.736	1.255	0.938	0.985
Thomson's gazelle	Plains	0.924	0.910	1.015	0.736	1.255	0.938	0.985
Kongoni	East	0.962	0.951	1.012	0.831	1.158	0.976	0.986
Maximum value		1.000	1.000					

Food supply

We divided species into grazers, mixed feeders, and browsers. The diet of each species was obtained either from our own observations or from the literature: for wildebeest (Watson 1969, Kreulen 1975), topi (Duncan 1975, Murray 1993, Murray and Brown 1993), buffalo (Sinclair 1977*a*), waterbuck (Field 1972, Spinage 1982), zebra (Klingel 1969), Thomson's gazelle (Gwynne and Bell 1968), kongoni (Stanley-Price 1978, Murray 1993), dikdik (Hendrichs and Hendrichs 1971), giraffe (Pellew 1980), and oribi (Mduma 1991, Mduma and Sinclair 1994).

The Kolmogorov-Smirnov values provide a measure of how different observed birth distributions were from those predicted with the same sample size (number of births corrected for monthly sample size) by food biomass, crude protein content of food, and an even distribution through the year (Table 4). Sample size for dikdik was too small to provide meaningful values and we do not consider this further. All but two species showed birth distributions significantly different from those predicted by food biomass. The two exceptions are buffalo and oribi, whose distributions are very similar to biomass (Figs. 3 and 4). Eight species showed different birth distributions from those predicted by the protein content distribution. In contrast, giraffe, waterbuck, kongoni, and zebra showed birth distributions very similar to that for percentage protein. Nine species showed birth distributions that differed from an even distribution through the year. However, births of giraffe, waterbuck, and Thomson's gazelle did not differ from an even monthly distribution (Fig. 4). Thus, at one extreme there is a group of species that had high Kolmogorov-Smirnov values and that differed from all predicted distributions by having short, synchronized seasons (wildebeest, topi, warthog, and Grant's gazelle). At the other extreme there is a group with birth distributions similar to that of the food supply (buffalo, oribi, kongoni, and zebra), or births distributed evenly

through the year (dikdik, Thomson's gazelle, giraffe, and waterbuck).

There is some indication of a pattern in the timing of the peak of births. The number of months that the birth peak occurred before or after the food-protein peak or green-biomass peak was found by cross-correlating the birth distribution with that predicted by the food protein or biomass distributions. The birth distribution was shifted one month at a time, and the maximum correlation coefficient was used as the indicator of the lag (Table 5). For grazing species the lag between birth peak and protein peak is a positive function of metabolic body size ($W^{0.75}$, in kilograms) (Spearman rank correlation $r_S = 0.73$, $n = 8$ grazing species, $P < 0.05$) whereas the lag with biomass is a negative function of body size ($r_S = -0.76$, $n = 8$, $P < 0.05$) (Fig. 5). Tentatively, small grazers produce their young early in the wet season in anticipation of the high protein peak. These species are out of phase with high green biomass. In contrast, large species tend to produce their young more in phase with high biomass and after the protein peak. This relationship is not evident with the five browsers and mixed feeders (Grant's gazelle, impala, oribi, dikdik, and giraffe). Giraffe births are directly in phase with their protein peak (Pearson correlation $r = 0.57$, $P < 0.05$) and out of phase with biomass ($r = -0.566$, $P < 0.05$).

Synchrony of births

We measured the synchrony of births using the index of evenness (J') and compared that with the evenness of rainfall, green biomass, and percentage food protein through the year (Table 6). Despite the evident seasonality of rainfall and food supply, both rain and protein are fairly evenly distributed over the months with all areas having $J' > 0.9$. Green biomass is slightly less evenly distributed.

In contrast, the evenness of births varies widely with species. The most uneven is wildebeest with $J'_{births} \approx$

0.35 and this species is highly synchronized relative to rainfall and food supply. There is a group of four species (topi, warthog, buffalo, and dikdik) with J'_{births} ~0.5–0.7 and these are also more synchronized than predicted by rainfall and food supply. At the other end of the scale, kongoni has the least synchronized birth season and births are more evenly distributed than rainfall and food biomass. This is also the case for Thomson's gazelle and zebra. The remaining five species show a more even distribution of births than food biomass and only slightly more synchrony than percentage protein and rainfall.

DISCUSSION

Phenology of births

We compare our results with our initial prediction that births should be related to food supply in a way consistent with their known food requirements. As a general pattern birth peaks occur sometime in the wet season when there is more green food. However, even this broad pattern is not universal, for giraffe, impala, and kongoni have their peak of births at the driest time of year. Giraffe births coincide with the flush of tree shoots and their high protein content.

Among grazers, the pattern suggested by Fig. 5 is consistent with known metabolic constraints. Births of small species appear to coincide with the protein peak and those of large species coincide with the green biomass peak. This is consistent with the idea that small ungulates have high specific metabolic rates and require high protein and energy but less bulk relative to large species (Kleiber 1947, Bell 1970, Jarman and Sinclair 1979, Clutton-Brock and Harvey 1983). Thus, grass-feeding ungulates may be adapting their birth seasons to their own specific food peaks, and these differ from species to species. This pattern of births and protein, therefore, is complex. It also does not account for all species, particularly the browsers or mixed feeders such as dikdik and oribi. Dikdik have two births per year 6 months apart. If they are to produce both births in the wet season they are constrained in timing. The first must occur in November–January if the second is to occur in the late wet season May to July.

It is not clear why the oribi, a small species, produces its young at the peak biomass, unless other factors override nutritional intake. Oribi live in habitats of very tall grass in which they hide. They are also subject to high levels of predation (from telemetry studies; P. Arcese, *personal observation*). They may be using the period of maximum grass height in late wet season to hide newborn young. Moreover, oribi are unusual in that they have a gestation of 7–7.5 mo, are capable of an immediate postpartum estrus, and often produce two young within a period of 14–15 mo (Jongejan et al. 1991). Oribi that do give birth more than once per year will have at least one young outside of the primary
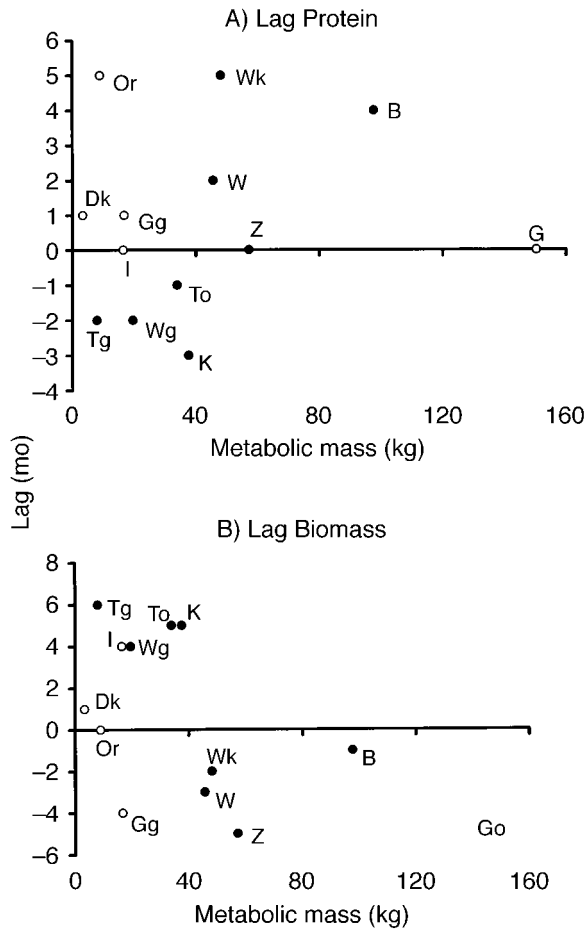

FIG. 5. The time difference in months (lag) of the birth peak before (−) or after (+) the peak of (A) percentage protein or (B) green biomass relative to the metabolic body mass. Grazers (solid circles) show a positive association with percentage protein and a negative association with grass biomass that is not yet evident in browsers and mixed feeders (open circles). B = buffalo, Dk = dikdik, G = giraffe, Gg = Grant's gazelle, I = impala, K = kongoni, Or = oribi, Tg = Thomson's gazelle, To = topi, W = wildebeest, Wg = warthog, Wk = waterbuck, and Z = zebra.

peak in births, which coincides with maximum biomass and cover available for young. Thus, it may be that some oribi trade off an increased number of young over their lifetimes at the cost of having a fraction of their young during suboptimal periods with respect to biomass and cover. Oribi, being highly selective mixed feeders, can also choose herbs and young grass leaves within tall grass stands so that high grass biomass may not be a nutritional impediment to them.

Synchrony of births

We predicted that species with precocial newborn should have synchronized births as an antipredator strategy. Four of the five most synchronized species (wildebeest, topi, warthog, and buffalo) fall into this

TABLE 6. The lag in months of the birth peak before ($-$) or after ($+$) the peak of food biomass and food percentage protein using the Pearson correlation coefficient (r) to identify the lag.

Species	Biomass			Protein content (%)		
	Lag (mo)	r	P	Lag (mo)	r	P
Kongoni	5	0.632	0.02	-3	0.757	0.01
Warthog	4	0.642	0.02	-2	0.920	0.001
Topi	5	0.707	0.01	-1	0.935	0.001
Thomson's gazelle	6	0.846	0.001	-2	0.601	0.05
Zebra	-5	0.791	0.001	0	0.877	0.001
Impala	4	0.614	0.02	0	0.440	NS
Wildebeest	-3	0.772	0.01	2	0.718	0.01
Buffalo	-1	0.864	0.001	4	0.824	0.001
Waterbuck	-2	0.215	NS	5	0.675	0.01
Giraffe	-5	0.516	NS	0	0.570	0.05
Grant's gazelle	-4	0.876	0.001	1	0.883	0.001
Dikdik	1	0.245	NS	1	0.650	0.02
Oribi	0	0.861	0.001	5	0.774	0.01

category. However, dikdik, the other synchronized species, is very much a "hider" species. We also predicted that synchronized births should occur in locally abundant species. Wildebeest, topi, and buffalo are abundant but warthog and dikdik are not. Furthermore, both zebra and Thomson's gazelle are locally abundant and neither show greater synchrony than predicted by their food supply. This is all the more curious since zebra and wildebeest migrate together, have close spatial correlation, and overlap in food preferences by >90% (Maddock 1979, Sinclair 1985). Thus, the predator-satiation hypothesis (Rutberg 1987) is supported by some species but not all of them.

Five of seven species that we predicted from the "predator avoidance" hypothesis (Ims 1990) to show a more even distribution of births than their food supply conformed to this prediction (impala, Thomson's and Grant's gazelle, waterbuck, and oribi). They all had more even birth distributions than that of food biomass and a birth distribution similar to that of food protein content. Waterbuck are a classic example of this category. They live at low density and hide their young. Because this species is closely tied to water and riverine vegetation it may not need to rely on seasonal rainfall for optimal food supplies to give birth. Thus, they can spread their births through the year, a result similar to that found by Spinage (1969) and Wirtz and Kaiser (1988) in Uganda and Kenya. We add the caveat, however, that the data on waterbuck are sparse and dates of birth are the least accurate of all the species.

Giraffe births appear to coincide with food quality and are only slightly more synchronized than this food. This species does not fit easily into the classical groupings of Jarman (1974). Giraffe have a gestation period of 15 months and hence it is difficult for them to produce young at a given time of year without delaying reproduction and reducing fecundity. Dikdik showed more birth synchrony than predicted. Since this is the only species in our sample that could produce two young per year it is possible that they were constrained by their food supply to become synchronized.

The kongoni is perhaps the most anomalous species in our sample. It is a large grazer and has precocial young. It is closely related to topi and wildebeest, both of which show extreme birth synchrony. Yet the kongoni has the most evenly distributed births of all the species. Its main difference in life history from the other two relatives is that it lives at low density in small widely distributed groups. In general, the large difference we observe in birth synchrony among closely related species suggests that ecology rather than phylogeny better explains the differences. A preliminary check on these interspecific comparisons using the method of independent contrasts (Felsenstein 1985) confirms these impressions (J. Brashares, *personal communication*).

It is tempting to conclude, therefore, that birth synchrony has coevolved with living in large groups, until we see that warthog have extreme birth synchrony and they live as isolated individuals or small families. At present, therefore, we can find no single feature that predicts all species birth distributions. A combination of the phenology of food supply plus antipredator adaptations accounts for most but not all these distributions.

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