Endocrine patterns of the estrous cycle and pregnancy of wildebeest in the Serengeti ecosystem

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ABSTRACT

Despite the importance of the western white-bearded wildebeest (Connochaetes taurinus mearnsi) to the Serengeti–Mara ecosystem, surprisingly little is known about the reproductive physiology of this keystone species. A longitudinal, non-invasive endocrine study was conducted on female wildebeest captured from the Serengeti–Mara migration and maintained for \(-16\) months in large fenced enclosures within the species’ natural range. An intact bull was introduced to a female subgroup \(n = 5\), while remaining females \(n = 10\) were unexposed to a male. Fecal progestagen patterns reflected ovarian activity and pregnancy. In non-pregnant animals, luteal and inter-luteal baseline progestagen values differed \((p < 0.001)\) over time, thereby allowing identification of recurrent estrous cycles. The average durations of the luteal phase, estrous cycle, gestation, and post-partum anestrus were \(14.3 \pm 0.5\), \(22.6 \pm 1.0\), \(240.8 \pm 11.7\), and \(104.1 \pm 15.6\) days, respectively. Annual reproductive patterns indicated a distinctive period of ovarian activity that extended from 13 May through 3 December \((203.5 \pm 29.9)\) days with all unmated females displaying from one to 14 estrous cycles. Progestagens were higher \((p < 0.001)\) in pregnant \(n = 4\) than non-pregnant \(n = 10\) cows. These data (1) reveal the value of fecal hormone monitoring for establishing the first ever endocrine profiles of female wildebeest in semi-free-living conditions in their native range, and (2) indicate that the species is a seasonal breeder that is polyestrous and a spontaneous ovulator.

1. Introduction

The Serengeti ecosystem encompassing the great plains of southern Kenya and northern Tanzania is comprised of the world’s largest aggregation of large land mammals. This includes \(\sim 1.25\) million western white-bearded wildebeest \((Connochaetes taurinus mearnsi)\), the smallest race of common wildebeest \((Estes, 1991)\). The species is water dependent, with both mating and calving highly synchronized over a 2–3 weeks period. The rut occurs from May to July, at the end of the wet season, and parturition then typically occurs from January to March, at the beginning of the long rainy period \((Talbot and Talbot, 1963; Watson, 1967; Sinclair, 1977a; Tanzania Wildlife Conservation Monitoring, 2000)\). Predation on neonates is limited by birth synchrony as well as excellent mobility displayed by precocious ‘follower’ calves \((Estes, 1991)\).

Despite the highly synchronous rutting and birthing peaks, it is unknown if female wildebeest are truly seasonal breeders, monoreproductive endocrine patterns for the species. Based upon estimations of population mating and calving peaks, gestation has been estimated to range from 8 to 9 months \((Talbot and Talbot, 1963; Estes, 1991)\). The duration of gestation has been calculated in several other Alcelaphinae species including: black wildebeest \((Connochaetes gnou, 9 months, Skinner et al., 1973)\); blesbok \((Damaliscus dorcas phillipsi, 8 months, Marais and Skinner, 1993)\); and red hartebeest \((Alcelaphus buselaphus, 8 months, Skinner et al., 1973)\). Other than this information, there is a lack of fundamental data on reproductive physiology of Alcelaphinae with the exception of blesbok, which have been shown to be seasonally polyestrous \((Marais and Skinner, 1993)\). Substantially greater basic knowledge has been generated for other wildlife species comprising the Bovidae subfamilies, including Antilopinae \((Lsukuto et al., 1990; Skinner et al., 2001; Penfold et al., 2005)\), Bovinae \((Fogwell, 1999)\), Caprinae \((Goodrow et al., 1996)\), and Hippotraginae \((Asa et al., 1996; Sempé et al., 1996; Thompson et al., 1998; Morrow et al., 1999)\). The common feature within these taxa is the significant variation in physiological function between species, thereby reinforcing the need to characterize each species of interest because ungulates have evolved substantially different reproductive mechanisms.

Non-invasive assessments of hormonal metabolites in excreta have allowed understanding of the physiology of reproduction...
for many wildlife species that never could have been studied otherwise (Monfort, 2003; Schwartz and Monfort, 2008). A major advantage of fecal monitoring is the ability to collect repeated samples to study animal endocrine patterns longitudinally without disturbance or stress (Monfort, 2003; Adkins-Regan, 2005; Schwartz and Monfort, 2008). Among the Bovidae family, longitudinal fecal progestagen profiles have been characterized in the scimitar-horned oryx (Oryx dammah, Morrow and Monfort, 1998), sable antelope (Hipotragus niger, Thompson and Monfort, 1999), bison (Bison bison, Kirkpatrick et al., 1996) and moose (Alces alces, Monfort et al., 1993). In the only study utilizing endocrine monitoring in wildebeest, Mduma (1996) analyzed fecal progestagens to ascertain pregnancy rates in the wild population. Single fecal samples from pregnant females were obtained from culled females during months 4 to 8 of gestation, whereas single fecal samples from non-pregnant animals were obtained from females found in proximity to newborn calves ~3 weeks following the birth peak. He found that fecal progestagen concentrations in non-pregnant females were one-half that observed in pregnant females.

The present study applied non-invasive endocrine techniques to characterize ovarian function in wildebeest maintained in captivity within their natural range. This design allowed for repeated sampling from known individuals to follow longitudinal patterns over the course of a year in both mated and unmated females. This is the first study designed to validate the use of non-invasive progestagen monitoring for establishing normative reproductive-endocrine parameters in wildebeest.

2. Experimental methods

2.1. Study area

The study area was located within the Grumeti Game Reserve, in the Western part of the Serengeti ecosystem (33° 30' to 34° E and 1° 30' to 2° 30' S). The Grumeti Game Reserve adjoins the Western corridor of Serengeti National Park north of the Grumeti River, and is leased from the Tanzanian government as a hunting concession by the Singita Grumeti Reserves. The Reserve is within the natural range of the western white-bearded wildebeest. The ecosystem has been well-described (see McNaughton, 1985) and is characterized by a wet season that occurs from November through June with short, dry periods in January and February, but rainfall patterns are highly variable. The dry season runs from approximately June through October (Norton-Griffiths et al., 1975).

Habitat types include closed-canopy woodland, deciduous and semi-deciduous thorn tree savanna, and plains of short and medium grasslands (McNaughton, 1985).

2.2. Animals, captures, husbandry, and habituation

Eighteen female wildebeest were captured from the main, migratory population as it passed through the Grumeti Game Reserve in early November. Fifteen pregnant females without calves and 3 juvenile, non-pregnant females (~2 years of age) were captured. Animals were darted from a vehicle using capture darts containing etorphine hydrochloride (Immobilon, 2-3 mg/animal; Novartis, South Africa) combined with xylazine hydrochloride (Rompun, 50-70 mg; Bayer HealthCare, USA) administered i.m., according to successful anesthetic protocols developed by Serengeti National Park veterinarians. The capture team was led by the Tanzanian Wildlife Research Institute (TAWIRI) veterinarian. Anesthetized animals were fitted with plastic ear tags for individual identification, and transported by truck (~0.5 to 2 h) to the study site.

During an initial habituation period of ~5 weeks, the cows were held in a 30 × 60 m boma divided into two units (approximately 30 × 30 m each) connected by a sliding door that could be operated from outside the enclosure. The animals were limited to one side of the boma at a time to allow for the contralateral side to be cleaned and for fresh feed to be supplied daily. An observation platform outside the boma allowed the wildebeest to be readily observed without disturbance. All animals were exposed to natural fluctuations in climate and photoperiod and allowed to graze on native grasses. Grazing was supplemented as needed with grasses cut from neighboring habitat as well as a feed mix of maize meal, cottonseed cake, and salt. Water, mineral licks, and supplemental feed were available ad libitum throughout the course of study.

Wildebeest were gradually exposed to the presence of researchers, initially by approaching from upwind without direct visual contact, but by exposing them to consistent vocalizations from the researchers to facilitate recognition. As the animals became habituated, as evidenced by no behavioral disruptions, exposure to the researchers became progressively more direct, culminating with an ability to remain within 10 m of the animals while collecting behavioral data, without any apparent changes in animal behavior.

The boma was contained within a large 500 × 500 m (25 hectare) fenced enclosure designed to accommodate the dietary needs (4.54 kg daily dry matter intake; Kreulen, 1975; Murray, 1995) of more than 17 lactating cows. Habituation was judged successful ~5 weeks after capture, and animals were released from the boma into the larger enclosure. All cows were left in the 25-hectare enclosure throughout the calving season and until the youngest calf was 2 weeks of age and the Serengeti veterinarian deemed it safe to dart and transport the animals. At the end of March 2003, all wildebeest were anesthetized and transported to one of three newly constructed enclosures, each 100 × 100 m. This move was necessitated by a concurrent long-term study on reproductive synchrony. Calves remained with dams, and adults and juveniles were randomly distributed amongst the three groups (n = 5, 5, 5). At the beginning of May 2003, a territorial bull from a resident population was introduced to one of the three groups, using the same capture protocol described for females.

Throughout the 1 year study interval (March 2003 through February 2004), the Serengeti veterinarian was consulted on any potential health issues of the study animals. Members of the local community were employed as guards to protect the wildebeest from predation by leopards and lions. Of the 18 cows initially captured, three died during the course of study. Because death occurred early in the study for two cows, data from these individuals were excluded. The remaining cow died ~8 months after study onset, and data collected while this animal was healthy was included in the analysis. Another female maintained with a bull also was excluded as she was estimated (from oral examination, overall poor body condition, lack of appetite, and lethargy) to be >11 years of age at capture. At the conclusion of the study, all wildebeest were released into surrounding native habitat in accordance with the veterinarian’s recommendations.

2.3. Fecal sample collection and hormone extraction

Fecal samples were collected from each cow at least once every 3 days by following movements of the herd within the enclosures, for a total of 3907 samples (range, 118–158 samples per individual). Each fresh fecal sample from a known wildebeest (based on ear tag and horn shape/size) was collected immediately after defecation and placed in a plastic zip bag. Each bag was marked with animal number, identity of the collector, date, and time of collection. Samples were stored in a thermos on ice (<3 h) and then stored in a propane-powered freezer (−20 °C) until extraction.

Fecal extractions were conducted on site in a field laboratory with a diesel generator powering necessary equipment. Each sam-
ple was thawed, homogenized, and 0.25 g of feces (wet weight) was weighed in a glass test tube (16 x 125 mm) and briefly vortexed with ~5 ml of 100% ethanol. Samples then were boiled for 30 min in a water bath, any evaporated ethanol replenished, and each tube centrifuged for 30 min at 2500 rpm. Resulting supernatant was poured into a clean glass test tube, dried completely under compressed air, rehydrated with 1 ml ethanol and then vortexed for 60 s. Finally, 0.85 ml of each extract was pipetted into a labeled 12 x 75 mm plastic test tube, dried completely, capped, and stored at room temperature for up to 6 months until analysis (Monfort et al., 1993).

2.4. Hormone assay

Fecal progestagen metabolites were analyzed using a broad spectrum pregnane enzyme immunoassay with antisera [monoclonal pregnane CL425 1:10,000 dilution] provided by Coralie Munro (Univ. of California, Davis, CA, USA). Parallel displacement curves were obtained by comparing serial dilutions of pooled wildebeest extracts with standard preparations. Fecal extracts were diluted in dilution buffer (1:50–1:300) and assayed in duplicate. The antisera cross-react with 4-pregnene-3,20-dione (100%), 4-pregnene-3α-ol-20-one (188%), 4-pregnene-3β-ol-20-one (172%), 4-pregnene-11α-ol-3,20-dione (147%), 5α-pregnane-3β-ol-20-one (94%), 5α-pregnane-3α,20-dione (64%), 5α-pregnane-3,20-dione (55%), 5β-pregnane-3β-ol-20-one (12.5%), 5α-pregnane-3,20-dione (8%), 4-pregnene-11β-ol-3,20-dione (2.7%), and 5β-pregnane-3α-ol-20-one (2.5%) (Graham et al., 2001). Sensitivity of the assay at maximum binding was 0.78 pg/well. Reverse-phase high-performance liquid chromatography (HPLC) as described by Monfort et al. (1991) revealed four immunoreactive fecal metabolites; one co-eluted with progesterone, whereas the other three were unknown immunoreactive progesteragens.

2.5. Recording of mating and parturition

As part of a parallel study, all wildebeest were observed within their respective bomas for a minimum of 2.5 h per cow per week for a total of ~43 h of behavioral monitoring per week. Mating (defined as successful mounting and copulation), parturitions and suckling behavior were recorded ad libitum.

2.6. Statistical analysis

For each female, a 3 days running average progestagen value was calculated and used for the following analyses, unless otherwise stated. One day was subtracted from the date of each sample to compensate for the lag time between steroid hormone production and excretion, which is ~12 to 24 h for ruminants (Morrow and Monfort, 1998). All statistical analyses were performed using SigmaStat (2004, v. 3.11, Systat Software, Inc.), and graphs generated using SigmaPlot (2004, v. 9.0, Systat Software, Inc.).

For non-pregnant females, luteal phase and baseline progestagen values were differentiated using an iterative process (Graham et al., 1995; Brown et al., 1996). Baseline values were determined by calculating the mean plus 1.5 standard deviations (Graham et al., 1995; Morrow et al., 1999). Any value exceeding this criterion was considered elevated and removed from the set of nadir values. The process then was repeated until no values exceeded the criterion. Progestagen concentrations that were elevated for three or more data points (i.e., 9 days) were classified as 'luteal.' To compensate for apparent seasonal shifts in baseline values, any progestagen elevations in non-pregnant animals lasting for nine or more data points (i.e., 27 days; based on the mean cycle length of the raw data, which was ~26 days) were re-evaluated using the described iterative process, this time with a cut-off criterion of 0.75 standard deviations. Data points not classified as luteal using the above criteria were considered baseline. Differences between baseline and luteal values were analyzed by two-way analysis of variance with Holm–Sidak method of pair-wise comparison.

Estrous cycle duration was calculated as the number of days from the first elevated progestagen value in one cycle to the first elevated progestagen value in the subsequent cycle, and the durations for all cycling individuals were averaged. Average luteal phase duration was calculated using all luteal phases of all animals. The duration of post-partum anestrus in females that gave birth was calculated as the average number of days from parturition until the first luteal rise. Any additional periods when progestagen values remained at baseline for 7 or more data points (i.e., 21 days) were considered anestrus. Average duration of gestation was calculated from observed mating and parturitions, and confirmed by sustained elevations in fecal progestagen concentrations.

To compare longitudinal progestagen excetration patterns during gestation, values throughout pregnancy were compared among pregnant females using Pearson product moment correlation. To compare average progestagen concentrations among pregnant individuals, samples collected during gestation were compared using Kruskal–Wallis one-way analysis of variance on ranks. Subsequent pair-wise multiple comparisons used Dunn’s method. Progestagen concentrations in pregnant versus non-pregnant cows were compared using a Student’s t-test. A range of progestagen concentrations also was established for each category (pregnant and non-pregnant) utilizing all samples (rather than 3 days averages) collected during gestation and the same time period in non-pregnant cows.

3. Results

3.1. Estrous cycle and gestational traits

Fecal progestagen profiles in non-pregnant females unexposed to a bull revealed cyclical patterns over time (Fig. 1), including clear differences (p < 0.001) in average baseline (267.6 ± 4.5 ng/g) and luteal (522.6 ± 9.1 ng/g) phase concentrations (Fig. 2). However, in 45 pair-wise comparisons, overall, baseline and luteal phase progestagen concentrations differed significantly in 44, 42, and 44% pairs of females (p < 0.05). Of the 10 study females...
The average gestation (n = 4) was 240.8 ± 11.7 d. Fifteen of the study participants copulated in mid-July, producing a calf after the conclusion of estrous cycling. The last observed copulation in a third cow, which apparently failed to resume estrous cycling, occurred on 5 June. A fourth cow was observed mating with the male after the loss of her calf. The sexual behavior of these cows was not resumed until the male was introduced.

### 3.2. Mating, parturition and suckling behavior

All five of the cows housed with the bull became pregnant during the study (Table 2). One of these was observed mating with the bull once, on the 2nd consecutive day, and no pregnancy was observed in a third cow that nonetheless produced a calf. A fourth cow, which cycled in mid-July, produced a calf after the conclusion of the study.

### Table 1

<table>
<thead>
<tr>
<th>Event</th>
<th>Mean ± SEM</th>
<th>Date (*days)</th>
<th>No. of occurrences</th>
</tr>
</thead>
<tbody>
<tr>
<td>Post-partum anestrus</td>
<td>102.4 ± 17.7</td>
<td></td>
<td>11</td>
</tr>
<tr>
<td>Resumption of estrous</td>
<td></td>
<td>5/13/03 ± 15.2</td>
<td>14</td>
</tr>
<tr>
<td>cycling</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Last estrous cycle</td>
<td></td>
<td>12/3/03 ± 13.7</td>
<td>10</td>
</tr>
<tr>
<td>Consecutive estrous</td>
<td>203.5 ± 29.9</td>
<td></td>
<td>10</td>
</tr>
<tr>
<td>cycling</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual estrous</td>
<td>22.6 ± 1.0</td>
<td></td>
<td>51</td>
</tr>
<tr>
<td>cycling</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Luteal phase</td>
<td>14.3 ± 0.5</td>
<td></td>
<td>76</td>
</tr>
<tr>
<td>Gestation</td>
<td>240.8 ± 11.7</td>
<td></td>
<td>4</td>
</tr>
</tbody>
</table>

Non-invasive fecal progestagen monitoring was useful for establishing reproductive-endocrine traits in the western white-bearded wildebeest. Our study design was novel in that a fractional subset of the Serengeti wildebeest population was removed from the wild and maintained in a natural environment adjacent to their free-living conspecific counterparts. This strategy ensured that resulting data were normative and uncompromised by traditional ecological variability while still allowing controlled observation and frequent fecal sampling. This study details, for the first time, longitudinal assessment of estrous cyclicity in western white-bearded wildebeest. Although there was substantial individual variation in average progestogen concentrations, baseline and luteal concentrations were readily distinguished. Results revealed that wildebeest are seasonal, polyestrous, spontaneous ovulators. Although only a few cows were exposed directly to a bull, these females all became pregnant within weeks of each other, consistent with the high fecundity and reproductive synchrony noted in this species, and allowing quantification of gestational parameters.

The average estrous cycle duration (~ 23 days) was similar to estrous cycle lengths reported for other Bovidae, including Antilopinae (gerenuk, *Litocranius walleri* walleri, 19 days, Penfold et al., 2005; suni, *Neotragus moschatus* zuluenensis, 21 days, Loskutoff et al., 1990), Bovinae (water buffalo, *Bubalus bubalis*, 20 days, Kenai and Shimizu, 1986; domestic cattle, 21 days, Thatcher, 1999; African buffalo, 23 days, Sinclair, 1977b); Hippotraginae (sable antelope, 24 days, Thompson et al., 1998; Arabian oryx, 24 days, Sempere et al., 1996; scimitar-horned oryx, 25 days, Morrow et al., 1999) and Caprinae (*Ovis moschatus*, 20 days, et al., 1990) and Caprinae (*Ovis moschatus*, 20 days, et al., 1990).

### 3.3. Progestagen levels in pregnant versus non-pregnant wildebeest

Progestagen excretion profiles indicated that two of the four pregnancies were preceded by a non-conceptive cycles (Fig. 3B). For concepitive cycles, fecal progestagen concentrations rose (from ~300 to >700 ng/g) shortly following the last observed copulation and declined (to ~400 ng/g) the day before or day of parturition (Table 2). Average fecal progestogen concentrations for individual pregnant cows ranged from 734.4 ± 19.8 to 1066.5 ± 40.8 ng/g (Table 3). While all females excreted elevated fecal progestogen concentrations throughout gestation, some animals experienced more marked fluctuations between 3 days average data points, leading to a lack of correlation (p > 0.05) among individuals in longitudinal excretion profiles (Fig. 3A and B). Nonetheless, in pair-wise comparisons average gestational fecal progestagen concentrations were similar (p > 0.05) in three of four cows (Table 3). The range in fecal progestogen concentrations for pregnant and non-pregnant cows during the sampling interval was 74.1–1718.4 and 74.7–1248.3 ng/g, respectively. Despite this overlap, fecal progestagens in pregnant cows (903.3 ± 69.8 ng/g) were elevated (p < 0.001) compared to non-pregnant cows (374.8 ± 30.6 ng/g) sampled across the same time interval (Fig. 4).
Table 3
Observed mating and parturition in four western white-bearded wildebeest held ex situ within the native Serengeti ecosystem range.

<table>
<thead>
<tr>
<th>Animal</th>
<th>Date of observed mating</th>
<th>Rise in fecal progestagens following observed copulation (ng/g)</th>
<th>Date of parturition</th>
<th>Fecal progestagens 1 day pre-partum (ng/g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NT</td>
<td>May 29, 2003</td>
<td>245.1 - 1344.3</td>
<td>February 4, 2004</td>
<td>372.9</td>
</tr>
<tr>
<td>16</td>
<td>June 5, 2003</td>
<td>526.2 - 729.9</td>
<td>February 4, 2004</td>
<td>Not available</td>
</tr>
<tr>
<td>18</td>
<td>June 5, 2003</td>
<td>364.5 - 1305.0</td>
<td>February 5, 2004</td>
<td>390.8</td>
</tr>
</tbody>
</table>

Fig. 3. Longitudinal fecal progestagen profiles of two representative, pregnant western white-bearded wildebeest.

Table 3
Average gestational fecal progestagen concentrations in four western white-bearded wildebeest held ex situ within the native Serengeti ecosystem range.

<table>
<thead>
<tr>
<th>Animal</th>
<th>Median gestational fecal progestagens (ng/g)</th>
<th>Mean gestational fecal progestagens (ng/g) ± SEM</th>
<th>No. of samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>NT</td>
<td>731.1</td>
<td>734.4 ± 19.8</td>
<td>80</td>
</tr>
<tr>
<td>15</td>
<td>986.5</td>
<td>923.0 ± 40.2</td>
<td>74</td>
</tr>
<tr>
<td>16</td>
<td>1,133.4</td>
<td>1,666.5 ± 40.8</td>
<td>63</td>
</tr>
<tr>
<td>18</td>
<td>1,031.2</td>
<td>1,003.2 ± 38.9</td>
<td>71</td>
</tr>
</tbody>
</table>

* Cow NT had different median and mean gestational progestagen (p < 0.05) from counterparts.

* Values did not differ from each other (p > 0.05).

Fig. 4. Fecal progestagen concentrations (mean ± SEM) in pregnant (n = 4) versus non-pregnant (n = 10) western white-bearded wildebeest (p < 0.001).

The occurrence of recurring cyclic ovarian activity in cows—even while completely isolated from males—suggests that environmental cues are sufficient for annually up-regulating ovarian activity in wildebeest cows. This concurs with findings in other Bovidae (Sempéré et al., 1996; Goodrowe et al., 1996; Thompson et al., 1998; Morrow et al., 1999; Skinner et al., 2001), but differs from the closest related species studied to date, the blesbok. Marais and Skinner (1993) found that female blesbok held in the presence of a male were polyoestrous, whereas those in isolation remained anestrous until the introduction of a male. Although male presence has been shown in a number of ungulates (Brooks and Cole, 1970; Knight and Lynch, 1980; Iason and Guinness, 1985; Verme et al., 1987; Signoret, 1990; Sempéré et al., 1996; Hosack et al., 1999) to have an effect on female reproductive function—ranging from advancement of the date of first estrus to ovulation-induction—the difference between wildebeest and blesbok is surprising, given that the species have similar social systems. Like the Serengeti-Mara wildebeest population, blesbok were formerly migratory, forming mobile aggregations with territorial males who courted females as they crossed their territories (Estes, 1991). However, over-hunting and fencing has resulted in a forced change in blesbok life history from migratory to mostly sedentary, and this may partially explain the differences observed between the two species. It is important to note that although we have demonstrated that seasonal up-regulation of the hypothalamic-pituitary–gonadal axis occurs in cows—female reproduction.

Wildebeest cows are not only seasonal, but appear to display tighter reproductive synchrony than would be expected based upon environmental seasonality alone. The evolutionary benefit of this approach has been attributed to the species having a ‘follower’ calf strategy that increases neonate survival through predator swamping and predator confusion (Estes, 1976; Rutberg, 1987). It is unlikely that synchronous reproduction in wildebeest evolved from an aseasonal breeding pattern, but rather a seasonal reproductive pattern that optimized resource availability was likely adjusted to yield a high degree of reproductive synchrony. The most likely explanation is that an ancestral ‘hider’ calf strategy exemplified in the ‘follower’ strategy implied in the wildebeest today (Estes, 1991).

Understanding the proximate causes of seasonal reproductive onset have been the subject of numerous studies, with a primary emphasis on photoperiod (see review, Bronson, 1985). Indeed daylength has been identified as the major factor in the timing of seasonal breeding in black wildebeest and red hartebeest in South Africa (Skinner et al., 1973). However, in the latitudinal range of the western white-bearded wildebeest, daylight duration varies by only 20 min annually, which suggests that photoperiod alone is unlikely to modulate seasonal gonadal activity in Serengeti wildebeest (Sinclair, 1977a). Skinner and Skinner (2001) identify daylength as the most likely cue in mesic adapted seasonal breed-
ers, but acknowledge that this effect may be negated near the equator. Rubberg (1987) suggests that changes in rainfall and available nutrition are likely involved in modulating ovarian activity in equatorial species. In the wildebeest's native range the wet season typically occurs from November through May, with optimal quality grazing coinciding with energetically demanding lactation (Watson, 1967; Norton-Griffiths et al., 1975; Estes, 1991). Resumption of ovarian activity may require that a female achieve a threshold of nutritional quality and/or body condition, or it is possible that there are qualitative differences in certain compounds in newly growing vegetations (e.g., as suggested for rodents after seasonal rains; Leirs et al., 1994). For our wildebeest study, grazing was supplemented in order to assure the health of the study animals. Although we cannot be certain that this did not affect reproductive fitness, local grasses were utilized to reflect normal, seasonal vegetative quality. Thus, the onset of ovarian function towards the end of the rainy season (May), with cessation after the dry season (December), suggests that nutrition may have an important role in regulating ovarian cyclicity, although the influence of daylength was not addressed in this study and cannot be dismissed.

Copulations observed in the present study occurred during baseline troughs in progestagen excretion (i.e., the presumptive follicular phase) and were followed by a rise in progestagen excretion that reflected the onset of the luteal phase (Edqvist and Staab, 1989). These results are typical of other ungulate species for which female receptivity has been observed to coincide with troughs in fecal progestagen excretion, including moose (Monfort et al., 1993), scimitar-horned oryx (Morrow and Monfort, 1998), sable antelope (Thompson and Monfort, 1999) and gerenuk (Penfold et al., 2005).

One of the mated cows—a young nulliparous female—experienced two non-conceptive cycles. The second cycle occurred following the introduction of the bull and was preceded by observed mating behavior. The impact of female age and experience on reproductive success would be interesting to explore, given a larger sample of mated females. It is important to note, however, that wildebeest in the wild have a reported three week calving peak and 80–100% conception rate (Estes, 1991; Mduma, 1996; Mduma et al., 1999). Although our findings confirm that unmated wildebeest are polyestrous, it is unlikely that wild females experience consecutive non-conceptive estrous cycling in the range reported here (i.e., 13 cycles).

The average duration of gestation (approximately 241 days) was slightly shorter than previously published estimates (range, 213–290 days, Mduma, 1996; Fogwell, 1999). Although we cannot be certain that this did not affect reproductive fitness, local grasses were utilized to reflect normal, seasonal vegetative quality. Thus, the onset of ovarian function towards the end of the rainy season (May), with cessation after the dry season (December), suggests that nutrition may have an important role in regulating ovarian cyclicity, although the influence of daylength was not addressed in this study and cannot be dismissed.

Copulations observed in the present study occurred during baseline troughs in progestagen excretion (i.e., the presumptive follicular phase) and were followed by a rise in progestagen excretion that reflected the onset of the luteal phase (Edqvist and Staab, 1989). These results are typical of other ungulate species for which female receptivity has been observed to coincide with troughs in fecal progestagen excretion, including moose (Monfort et al., 1993), scimitar-horned oryx (Morrow and Monfort, 1998), sable antelope (Thompson and Monfort, 1999) and gerenuk (Penfold et al., 2005).

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In conclusion, we found substantial value in characterizing the fundamental biology of the wildebeest by creating an ‘ex situ, controlled’ environment within the species’ natural range. This allowed precise characterizations of temporal seasonality, the reproductive cycle, type of ovulation, duration of gestation, post-partum anestrus and resumption of ovarian activity. Such measurements would have been logistically challenging, if not impossible, in a purely free-living situation, especially because serial tracking of marked individuals for protracted time intervals is not feasible. Likewise, traditional zoos do not maintain significant herds of this species and, even if available, results may have been confounded due to public disturbance, limited animal enclosure space, and an inability to replicate normal environmental cues that are likely essential for modulating reproductive function in this species. In summary, the fundamental knowledge derived from this study provides a sound foundation for future studies designed to understand the physiological basis of reproductive control and synchrony in one of the largest aggregations of large land mammals on earth—the Western white-bearded wildebeest of the Serengeti–Mara ecosystem.

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