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The reproductive biology of the Greater kudu, *Tragelaphus strepsiceros*

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Abstract

The reproductive biology of the greater kudu *Tragelaphus strepsiceros* was examined in the Eastern Cape Province of South Africa in relation to season, social organization and the biology of other Tragelaphines. Macroscopic and microscopic methods were employed to examine the reproductive condition of bulls and cows. Kudu bulls attained puberty at eighteen months of age while fifty percent of cows produced their first calf when two years old. Specific conception rates of 100% were realized and maintained. The foetal sex ratio did not differ significantly from parity. It was inferred that kudu cows were seasonally polyoestrous, with no prolonged lactational anoestrus but with a post-partum oestrus. Breeding was strictly seasonal and the incidence of conceptions suggested that kudus are short day breeders. The strict seasonality of reproduction is discussed in relation to that of other Tragelaphines.

Introduction

Although general information exists concerning the reproductive biology of kudus, much of it is anecdotal or non-quantitative. Consequently, it has been difficult to summarise the life history of kudus in relation to that of other Tragelaphines.

Seasonal breeding in mammals has evolved to ensure that conditions are optimal for the survival of both mother and young, and such conditions are referred to as the ultimate cause of the timing of breeding (Sadlier 1969). The most common ultimate factors influencing ungulate reproduction are rainfall and nutrition (Spinage 1973) but are difficult to separate (Sadlier 1969). Lactation, the period when the energetic demands of the mother are greatest (Sadlier 1972), usually occurs when plant growth is significant and the plane of nutrition is high.

Here we report on the reproductive biology of the greater kudu, *Tragelaphus strepsiceros* Pallas, 1776 (Bovidae), from a study population in the eastern Cape Province of South Africa.

The main aims of the study were to (a) quantify the reproductive parameters of kudus, (b) account for the seasonality of breeding, and (c) compare the results with data for other southern African Tragelaphines of different body mass, occupying different habitats, and over a range of latitudes. Information on the reproductive biology of kudus has significance for their conservation and management, and an understanding of their social and spatial organization (Perrin and Allen-Rowlandson 1993, 1994).

Material and methods

Reproductive organs from shot kudus were collected during the hunting seasons (June–August) of 1976 to 1979 on farms adjacent to the Andries Vosloo Kudu Reserve (33 °8′ S, 26°39′ E), eastern Cape Province, R.S.A. The vegetation of the reserve and farms consists of valley bushveld, which Acocks (1975) described as Fish River scrub. The vegetation comprises eight principal communities which range from near desert conditions, through almost pure grassveld, succulent and non-succulent bush, to non-succulent forest.

Paired testes were weighed to the nearest 0.1 g, and Kerr's (1965) smear technique was adopted for the detection of spermatozoa. Foetuses were weighed to the nearest 1.0 g and when possible (>50 g) sexed; ovaries of non-pregnant cows were sectioned sagittally at 2 mm. Each was examined microscopically for corpora lutea or corpora nigra and mean follicle diameter (two diameters at right angles) was recorded. Follicle diameters larger than 5 mm, indicative of ovulation, indicated adulthood. Lactation was recorded in shot cows, and in live cows captured to fit identification collars for behavioural research (Allen-Rowlandson 1980). Young animals (< 3 years) were categorized by horn development, and tooth eruption and replacement criteria (Simpson 1966). Rutting and calving periods were determined during field observations (>1 000 hours; Allen-Rowlandson 1980).

Seasonality of conception and births

Foetal age was determined using the Huggett and Widdas (1951) formula,

$$W = a(t - t_0)$$

where W = foetal mass, a = specific foetal growth velocity, t = foetal age and $t_0 = 0.2\times$ gestation period (for animals with a gestation length of 100–400 days).

Mean birth mass and gestation period were used to calculate a (Anderson 1978). Few records of the mass of kudu neonates have been published (Vice and Olin 1969) and data on the duration of gestation show considerable variation (Dittrich 1972). Consequently, the mean birth mass (15.3 kg) and mean gestation period (251 days) were determined from captive animals (Allen-Rowlandson 1980). When entered into the Hugget and Widdas (1951) equation, these data yielded an a value of 0.0123.

Foetal age was determined, $t = \dfrac{W + a \cdot t_0}{a}$

To determine conception date, foetal age (days) was subtracted from the culling date, while birth (calving) date was predicted by adding the length of gestation (days) to the conception date.

Results

Birth dates

Ninety-seven percent of foetuses (n = 62) had a predicted birth date between December and February, with a peak (52%) in January (Figs. 1, 2). Five pregnant yearlings shot in 1976 had birth dates in February or March. The predicted mean calving date of 22 non-lactating cows was 13 January (±17 days).

Age at attainment of puberty

Bulls: twenty (95%) of the eighteen-month-old bulls examined had spermatozoa in the testes and epididymides, with a mean paired testes mass of 64.9 (±10.0) g. The only prepubertal bull of this age had a combined testes mass of 41.6 g. All bulls less than one-year-old (n = 9) showed no evidence of spermatogenesis. Twenty-eight (96%) of two-year-old bulls examined possessed spermatozoa.

Cows: six (46%) eighteen-month-old cows were pregnant. A further two had large corpora lutea (indicating that ovulation had occurred), and three others had mature Graafian follicles (indicating conception). Therefore only two (15%) were prepubertal.

Material was not available for cows under one year of age. Seventy-six (99%) of cows two or more years old were sexually mature.

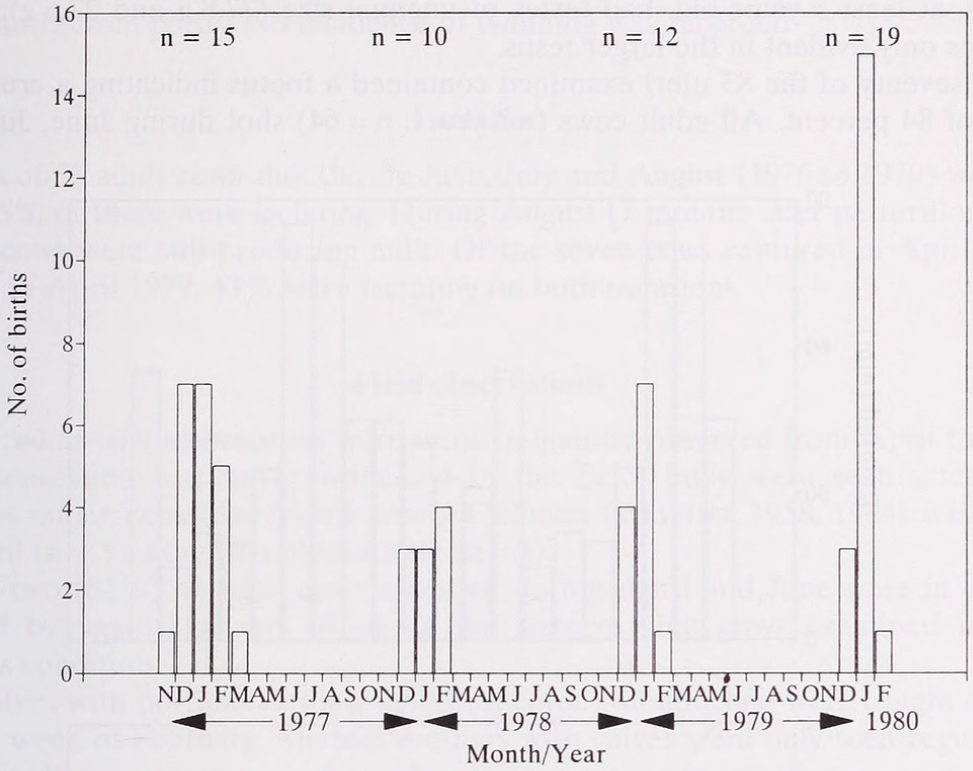

Fig. 1. Parturition dates of kudus in the Fish River Valley area, determined from foetal age.

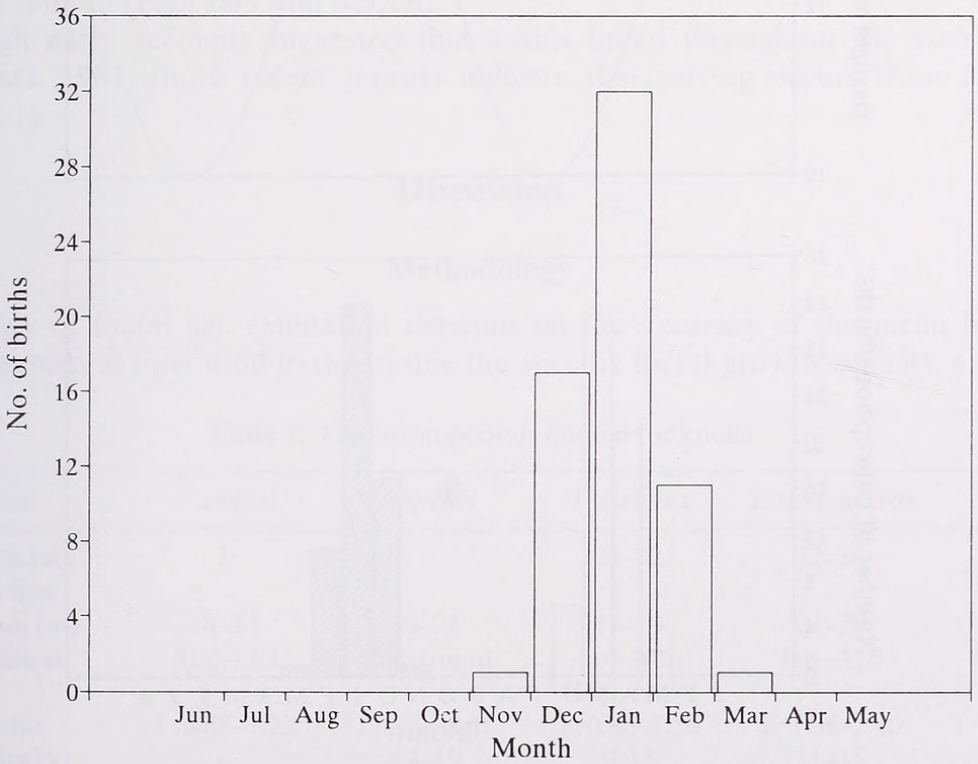

Fig. 2. Accumulated parturition dates of kudus in the Fish River Valley area determined from foetal age. (Data from 1976–1979 summed, n = 62).

Fertility

Bulls: ninety (97%) bulls older than eighteen months possessed spermatozoa (92% of samples were collected between June and August). The three exceptions were two 3.5-year-old bulls (shot in February and August) with paired testes masses of 24.6 g and 62.6 g respectively, and a 2.5-year-old bull (shot in July) with a paired testes mass of 60.5 g. One other bull, at least 5-years-old, had testes of unequal size (77.8 g and 27.6 g); spermatogenesis was only evident in the larger testis.

Cows: seventy of the 83 uteri examined contained a foetus indicating a crude conception rate of 84 percent. All adult cows (>2 years: n = 64) shot during June, July and Au-

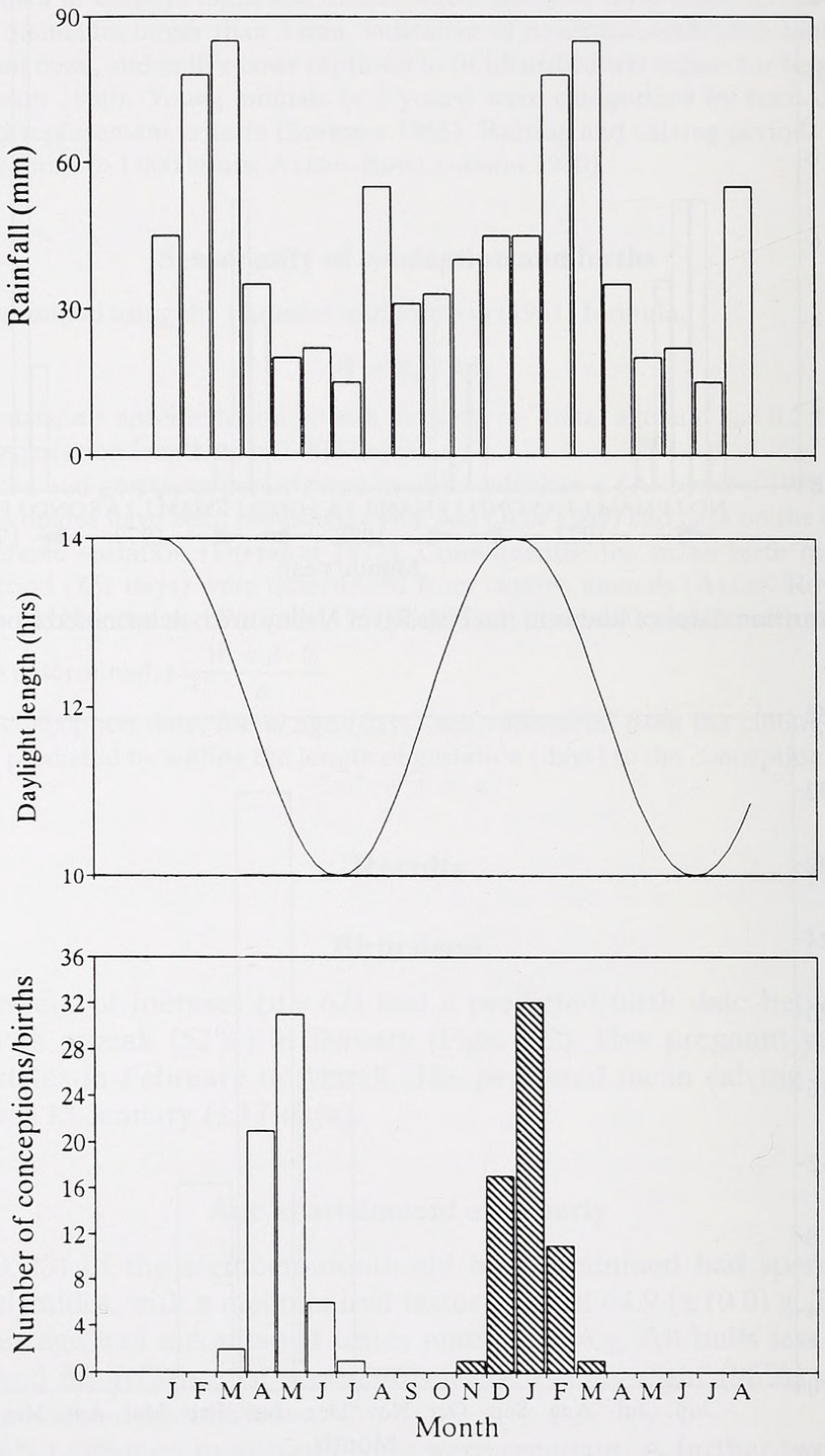

Fig. 3. The distribution of kudu conceptions (open) and births (striped) in the Fish River Valley area in relation to rainfall and photoperiod.

gust were pregnant, as were 46% of the yearlings collected at this time. Thirty-three (91%) lactating cows shot early in the year were pregnant.

Foetal sex ratio

Of the 51 foetuses sexed, 30 were bulls and 21 were cows (1 : 0.7). This ratio does not differ significantly from parity. No incidence of twinning was recorded.

Lactation

The udders of 51 adult cows shot during June, July and August (1976 to 1979) were examined and 65% of these were lactating. During August (7 months after parturition) 62% of (13) adult cows were still producing milk. Of the seven cows captured in April 1978 and recaptured in April 1979, 43% were lactating on both occasions.

Field observations

Adult bull : adult cow associations were most frequently observed from April to July, and although copulation was never witnessed in the field, bulls were seen attempting to mount cows on six occasions (April–June). Flehmen (Walther 1958, 1964) was observed during April (n = 3), May (n = 4) and June (n = 1).

Twenty-two (82%) of adult cows captured during April and June were in oestrus, as determined by vaginal smears. None of the sixteen adult cows examined in January showed this condition.

Four calves with portions of their umbilical cords still attached were caught in January or the first week of February, whereas mothers with calves were only seen regularly from March onwards.

The distributions of kudu births and monthly rainfall in the Fish River Valley area (Fig. 3) show that most calves were born just prior to the months of maximum and most predictable rainfall (February and March).

Although early accounts suggested that kudus breed throughout the year (Ansell 1960; Asdell 1964) more recent reports indicate that calving occurs from January to April (Tab. 1).

Discussion

Methodology

The accuracy of foetal age estimation depends on the accuracy of the mean birth mass and mean gestation time used to determine the specific foetal growth velocity, a. Early re-

Table 1. Gestation periods quoted for kudus

Species	*T. angasi*	*T. spekei*	*T. scriptus*	*T. strepsiceros*	*T. oryx*
Gestation (w)	1	–	26–32	32–36	37–39
Age at first parturition (m)	18–24	18–24	17–19	24–28	38–40
Birth season	Aug–Oct	year round	Apr–May Oct–Nov	Jan–Apr	Jul–Nov
Sex ratio	1 : 0.88–1.22	1 : 1.75–4.18	1 : 0.88–1.50	1 : 1.36–2.40	1 : 3.06–6.10
Longevity (y)	–	14–19	9–13	11–15	12–20

w = weeks, m = months, y = years

ports of gestation cited durations of 210 to 214 days (Stevenson-Hamilton 1912; Jennison 1927; Wilhelm 1933; Asdell 1964) but more recent records suggest 271 days (Allen-Rowlandson 1980). Since, (a) the length of gestation is rarely influenced by environmental conditions (Sadlier 1969), and (b) gestations of 210 to 220 days are known for nyala (Anderson 1978) and captive lesser kudu (Dittrich 1972), both of which are considerably smaller than the greater kudu, and (c) the length of gestation is closely correlated with the mass of the adult (Sadlier 1969, 1972), a longer duration of gestation in the greater kudu is probable. However, known parturition intervals of 259 and 266 days (Allen-Rowlandson 1980) infer that gestation is unlikely to be much longer than the 251 days used here. Entering these values in to the Huggett and Widdas (1951) equation yields a value similar to those determined for other Tragelaphines (Anderson 1978). Field observations corroborate the accuracy of the technique, and adult kudu bulls were most frequently seen associating with cows during May and June (Allen-Rowlandson 1980).

Reproduction in the bull

Kudu bulls achieved puberty (spermatozoa in the epididymides) and were sexually mature by eighteen months of age. Under natural conditions, however, young bulls (< 5 years old) are prevented from mating by older, dominant bulls that have reached sociological as well as sexual maturity, which occurs at 6 years of age (Owen-Smith 1984).

Spermatogenesis likely continued throughout the year, but fluctuated according to season (Skinner and Huntley 1971; Skinner 1971). Sexual senescence was not evident in kudu bulls, but 3% of the bulls examined during this study were infertile.

Reproduction in the cow

Kudu cows reached puberty by eighteen months of age, and 50% of two-years-old produced a calf; similar results have been reported for Zimbabwean populations (Dasmann and Mossman 1962; Simson 1968). At two years of age, specific conception rates of 100% were realized and maintained, so fecundity was not age-specific. Simpson (1968) reported that cows over 30 months of age have a specific birth rate of 80% and that fecundity decreases with age. However, there was no evidence of sexual senescence in the present study.

Results indicated that kudu cows in the Fish River Valley population calved consecutively each year. However, the seasonal changes in the proportion of cows lactating suggested substantial calf mortality.

The high conception rate suggests that the kudus were seasonally polyoestrous, since, like the congeneric nyala, they are receptive for a few hours only (Owen-Smith 1984). The mean interval of 45 days between parturition and conception (Allen-Rowlandson 1980) indicates that kudus have a post-partum oestrus.

Data suggest that primiparous cows came into oestrus slightly later than multiparous cows. A similar trend has been reported in other kudu populations (Simpson 1968), in eland (Underwood 1975), and in red deer (Mitchell and Lincoln 1973).

Foetal sex ratio

The foetal sex ratio recorded here is equivalent to the published ratios of 1 male : 0.7 female (n = 34) and 1 male : 1 female (n = 20) (Simpson 1968). The preponderance of males in each of these ratios is not statistically significant. Kudus born in captivity exhibit a sex ratio closer to unity (1 male : 1.1 female, n = 490) (Allen-Rowlandson 1980).

Kudu bulls experience vastly elevated mortality rates compared with cows, generating a sex ratio of 1 male : 12 females in the Kruger Park (Owen-Smith 1984). The ratio of 1 male : 2.2 females for adult kudus in valley bushveld may be attributable, *inter alia*, to the absence of large predators (Allen-Rowlandson 1980).

Seasonality of reproduction in kudus

Predicted conception and parturition dates clearly demonstrated that breeding in the kudu is strictly seasonal in valley bushveld. The calving season may occur slightly later in the eastern Cape than elsewhere in the subregion, but its duration remains short.

Photoperiod is often the proximate factor initiating seasonal breeding in mammals. Since ninety-eight percent of all kudu conceptions occurred during days with decreasing and short photoperiod, they are short day breeders.

Since seasonal fluctuations in protein and water content are less severe in browse than graze (Leuthold and Leuthold 1975 a), and growing seasons are long in dicotyledonous plants (Jarman 1974), seasonality of breeding is usually more marked in grazers than in browsers (Leuthold and Leuthold 1975 b). The marked seasonality of breeding in kudus, which are almost exclusively browsers, is therefore surprising and remains unexplained.

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Zusammenfassung

Über die Reproduktionsbiologie des Großen Kudu Tragelaphus strepsiceros

An Kudus, die während verschiedener Jagdzeiten in der östlichen Kapprovinz Südafrikas erlegt wurden, konnten Daten über den Reproduktionsstatus erstellt werden.

Kudubullen werden mit 18 Monaten fortpflanzungsreif, während 50% der Kühe in einem Alter von 2 Jahren ihr erstes Kalb zur Welt bringen. Die Geschlechtsverhältnisse der Foeten entsprechen 1 : 1. Kudukühe waren scheinbar jahreszeitlich polyöstrisch und zeigten Postpartumöstrus ohne ausgedehnten Anöstrus während der Laktationsperiode. Wenige Daten lassen vermuten, daß primipare Kühe geringfügig später im Jahr brünstig wurden als diejenigen, die mehrfach geboren hatten. Die Fortpflanzung war streng saisonal und entsprechend dem Zeitpunkt der Konzeption ist zu vermuten, daß sie bei Kudus unter Kurztagbedingungen stattfindet.

Diese Saisonalität der Reproduktion wird in Beziehung zu anderen Vertretern der Tragelaphini diskutiert.

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