Seasonal variation in reproductive behaviour of bushbuck (*Tragelaphus scriptus* Pallas, 1766) in an equatorial savannah ecosystem

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Abstract

While several authors suggest that bushbuck (*Tragelaphus scriptus* Pallas) from tropical areas with an approximately bimodal rainfall pattern breed throughout the year, there is also a report of seasonal breeding in this species. In this study, we provide indirect evidence of seasonality in reproduction by analysing behavioural data (e.g. rates of mixed-sex sightings) in a population of bushbuck inhabiting an equatorial savannah ecosystem in western Uganda. Observation rates of mixed-sex sightings were correlated with rainfall patterns. We suggest that peaks in reproductive behaviour following the wet season may be advantageous if calves are born during the next wet season, when fresh vegetation is available.

Key words: antelopes, mating behaviour, seasonality, Uganda

Résumé

Alors que plusieurs auteurs suggèrent que le bushbuck (*Tragelaphus scriptus* Pallas) des régions tropicales qui ont un régime de pluies à peu près bimodal se reproduisent tout au long de l'année, il y a aussi un rapport signalant une reproduction saisonnière chez cette espèce. Dans la présente étude, nous apportons des preuves indirectes d'une saisonnalité de la reproduction par l'analyse des données comportementales (e.g. taux d'observations de sexes mélangés) dans une population de bushbucks habitant dans un écosystème de savane équatoriale, dans l'ouest de l'Ouganda. Les taux d'observations de groupes mélangés étaient liés aux chutes de pluies. Nous suggérons que les pics observés dans le comportement reproducteur en fonction de la saison des pluies peuvent être bénéfiques si les jeunes naissent durant la saison des pluies suivante, lorsque la végétation fraîche est abondante.

Introduction

In some populations of African ungulates, seasonal variation in the social organization and reproductive behaviour can be observed (Skinner, Van Zyl & Oates, 1974; Leuthold, 1977; Skinner, 1991). Most of this behavioural variation in the course of the year is ultimately related to seasonal fluctuations in water and food supply and thus, typically corresponds with rainfall patterns. For example, in subtropical South Africa, a mono-modal rainfall pattern leads to a pronounced annual cycle in reproductive behaviour in several ungulate species, which is characterized by a short lambing season in early summer and a corresponding rutting season in autumn (e.g. eland, *Taurotragus oryx* (Pallas); gemsbok, *Oryx gazella* (Linnaeus); springbok, *Antidorcas marsupialis* (Zimmermann); blesbok, *Damaliscus pygargus phillipsi* (Harper); red hartebeest, *Alcelaphus buselaphus caama* (Geoffroy Saint-Hilaire); black wildebeest, *Connochaetes gnou* (Zimmermann), Skinner, Van Zyl & Van Heerden, 1973; Skinner *et al.*, 1974). In arid ecosystems like the Arabian Peninsula or the Sahelo-saharan region, reproduction of Arabian oryx

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[*Oryx leucoryx* (Pallas)] or Scimitar-horned oryx [*Oryx dammah* (Cretzschmar)] is strongly linked with annual rainfall and temperature (Malbrant, 1952; Stanley Price, 1989; Grettenberger & Newby, 1990). In contrast, in equatorial, central African forest ecosystems [e.g. Maxwell's duiker, *Philantomba maxwell* (S.H. Smith); Wilson, 2001], or in the tropical climate of eastern Africa, little or no support for seasonality in the reproductive behaviour of ungulates is found [e.g. waterbuck, *Kobus ellipsiprymnus* (Ogilby); Spinage, 1982; impala, *Aepyceros melampus* (Lichtenstein); Jarman & Jarman, 1973, 1974].

Several authors (e.g. Ansell, 1960; Asdell, 1964; Wilson & Child, 1964) suggest that bushbuck from tropical areas with an approximately bimodal rainfall pattern (e.g. Zimbabwe) breed throughout the year. Consequently, bushbuck from equatorial areas are also expected to show no pronounced seasonal reproduction (compare Wronski, Apio & Plath, 2006c). However, when Allsopp (1971) investigated foetal development in bushbuck from Nairobi National Park in Kenya and inferred the date of conceptions and parturition, evidence for seasonal breeding was found. In that area, peaks of conceptions occur 1–2 months prior to major peaks of rainfall, and parturition are most frequent at the same time (1–2 months before peaks of rain), subsequent to a gestation period of 6 months. Allsopp (1971) also reanalysed the data provided by Wilson & Child (1964) on the foetal weights of bushbuck from Zimbabwe and inferred that parturition occurs most frequently in December, and to a far lesser extent in April. These findings suggest that seasonal fluctuations in rainfall may have an effect on the reproductive behaviour in bushbuck even in tropical areas.

In this study, we used behavioural data as an indirect indication of seasonality in reproduction in a bushbuck population from an equatorial savannah ecosystem in Uganda. We tested for variation in reproductive behaviour in relation to monthly precipitation. Using longitudinal behavioural observations, we analysed seasonal variation in male–female associative behaviour ('mixed sightings') as well as variation in male–male aggressive behaviour. Territorial bushbuck males aggressively defend females against younger males, which employ a nonterritorial (sneaky) mating tactic (Apio *et al.*, 2007), and aggressive behaviour should be more frequent during peak reproductive periods (Leuthold, 1977). Because the gestation period of bushbuck is *c.* 6 months (Dittrich, 1972, 1974; Mentis, 1973) and peak rainfall also occurs every 6 months, it can be predicted that reproductive behaviour peaks during the wet season, such that calves are born during the next wet season.

Methods

Data were collected from a free-ranging bushbuck population on the Mweya peninsula and the adjacent mainland area in Queen Elizabeth National Park (QENP) in western Uganda (0°10′S to 0°12′S, 29°52′E to 29°54′E). The altitude of our study area is 910 m above sea level. The study area covers approximately 8.7 km^2 and comprises *Sporobolus pyramidalis* grassland with scattered *Capparis tomentosa/Euphorbia candelabrum* thicket clumps (Lock, 1977; Zandri & Viskanic, 1992). Seasonal variation in QENP is evident only for rainfall patterns, while there is little or no seasonal variation in temperature (maximum temperature: mean ± SE = 30.67 ± 0.27°C, range: 27.90–34.52°C; minimum temperature: 19.95 ± 0.08°C, range: 18.78–20.69°C). Also the time of daylight is constant throughout the year, lasting from approximately 07.00–19.00 hours. The rainy seasons last from March to May and from September to December, with a monthly mean of more than 50 mm rainfall (daily precipitation, wet season: 3.2 ± 7.1 mm; dry season: 0.5 ± 2.4 mm). Mean annual rainfall in the study period was 680 mm (Deutsch, 1992; Apio, Plath & Wronski, 2006).

Bushbuck were continuously observed from April 1999 to February 2002. Individual bushbuck were identified by external characteristics, aided by the use of a photo identification catalogue. In total, we identified 52 male and 46 female bushbuck in the study area, which were observed during 3654 random sightings. During daily patrols throughout the study area (at least twice a day), we collected behavioural data from a vehicle. Also off-road areas were patrolled by car wherever possible. Patrols were carried out equally throughout the dry and wet season, during day- and night-time and in all habitats accessible by car. Sloping areas, gullies and thickets were patrolled on foot, but less frequently.

The exact date of parturition of the calves born during the study period could not be determined with accuracy, because juveniles cannot be observed directly after parturition during a prolonged lying-out phase (8–10 weeks after parturition; Reif, 1989; Wronski *et al.*, 2006a). On the basis of this, we chose to analyse behavioural data instead. We noted all incidences of aggressive male–male interactions (Wronski & Plath, 2006; Wronski *et al.*, 2006a,b) and male–female associations ('mixed sightings';

Apio *et al.*, 2007). In our previous studies, we demonstrated that some (adult) males are territorial, while other (younger) males are nonterritorial and form bachelor pools (Wronski, 2005; Wronski *et al.*, 2006b; Apio *et al.*, 2007). The territorial males perform herding and various premating behaviours, probably to monopolize oestrous females (Wronski *et al.*, 2006a; Apio *et al.*, 2007). However, also young-adult males achieved mating success, such that we considered any association between a male (adult or young-adult) and a female an indication of a male's interest to mate. Hence, adult (territorial) and young adult males were included, but subadult males were not included in the analysis.

Data on precipitation were collected on a daily basis using a rain gauge, and monthly precipitation was calculated. We tested for correlations between the monthly rainfall and (i) the monthly number of sightings of aggressive male–male interactions and (ii) female–male associations using nonparametric Spearman rank correlations (SIGMASTAT 2.0). We used nonparametric tests here, because data deviated from the assumptions of normal distribution (Kolmogorov–Smirnof-test). Data are based on the observation of male–female association between 27 males and 41 females, and aggressive interactions between 29 males. Shifts in behaviour patterns because of rainfall might occur with a certain delay; for example, peaks in agonistic behaviour might be found some time after peak rainfall. To account for this, we calculated Spearman rank correlation coefficients not only for immediate behavioural responses and precipitation (zero-point on *x*-axis in Fig. 1), but also calculated the correlations between the observed behaviour patterns and rainfall 1, 2 and 3 months before and after the respective monthly behaviour observation (i.e. before and after the zero point).

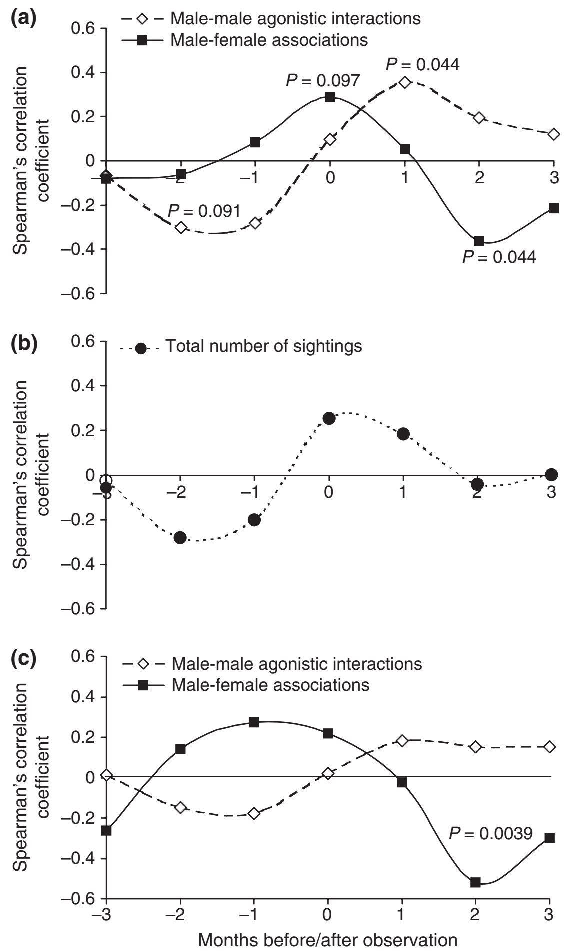

Fig 1 Spearman's correlation coefficient for the relationships between rainfall (1, 2 and 3 months before and after the behavioural observation) and frequencies of behaviour observations: (a) number of male–male agonistic interactions and male–female associations, (b) total number of sightings and (c) rates of male–male agonistic interactions and male–female associations (# behavioural observations/total # of sightings). *P*-values are only shown for significant correlations

Results

Our analysis revealed seasonal variation in the number of male agonistic interactions (sum of observations per month) as well as in the monthly frequency of male–female associations ('mixed sightings'). As an immediate response to rainfall (zero-point on the *x*-axis in Fig. 1a), there was a nonsignificant positive relationship between the number of mixed sightings and monthly precipitation (Fig. 1a).

As a delayed response, the frequency of male–male agonistic interactions was positively correlated with the amount of rainfall with a delay of 1 month (+1 on *x*-axis in Fig. 1a). Hence, 1 month after heavy rainfall, males were fighting most frequently, whereas 1 month after a dry period, frequency of aggressive interactions were reduced.

Likewise, the number of mixed sightings was significantly negatively correlated with the monthly amount of rainfall with a delay of 2 months (Fig. 1a). There was also a nonsignificant (negative) correlation between the frequency of male–male agonistic interactions and monthly rainfall 2 months before the observation (−2 on *x*-axis in Fig. 1a).

We checked whether seasonal variation in male–male agonistic interactions and the number of mixed sightings was influenced by seasonal variation in the total number of sightings of bushbuck in the study area. Indeed, seasonal variation in the total number of sightings was observed, and a positive correlation coefficient was detected as an immediate response to rainfall (zero-point on *x*-axis in Fig. 1b). However, in no case was the correlation between rainfall and the total number of sightings significant (Fig. 1b).

Nevertheless, we conducted another analysis after correcting the data for variation in the overall number of sightings, i.e. after we had calculated rates of agonistic male–male interactions and male–female associations. We still detected a negative correlation between the rate of mixed sightings and the amount of rainfall with a delay of 2 months (+2 on *x*-axis in Fig. 1c). Thus, it seems that this 'long-term effect' of rainfall on the frequency of male–female interactions is independent of any variation in the overall number of sightings of bushbuck in the study area.

Discussion

Our data suggest that there is seasonal variation in reproductive behaviour of bushbuck in Queen Elizabeth National Park. Even when the behavioural data were corrected for variation with the overall number of sightings in relation to rainfall, the observation rate of mixed sightings was still negatively correlated with the amount of rainfall 2 months before the observation. This means that 2 months after heavy rainfall, males and females associate less frequently, whereas 2 months after a dry period, associations between males and females are more frequent. Hence, there seems to be some degree of seasonal reproduction, even though at least some fawns were observed throughout the year during the study period. The fact that some fawns were seen throughout the year, however, demonstrates that reproduction in bushbuck is not completely dependent on rainfall patterns. Further reports of seasonal breeding in Ugandan ungulates confirm our findings (waterbuck: Spinage, 1969; impala: Kayanja, 1969).

Our study highlights the importance of correcting behavioural field data like numbers of male–female associations or aggressive male–male interactions for seasonal variation in the overall number of sightings. Indeed, when the data were not corrected, several apparent correlations with precipitation were found (Fig. 1a), which disappeared after correcting for seasonal variation in the overall number of sightings (Fig. 1c).

A potential drawback of this study could be that analysing actual mating behaviour would have been more appropriate. However, observation rates of mating behaviours are generally very low in this cryptic bush-dwelling species (Apio *et al.*, 2007), such that an analysis of the temporal dynamics of mating behaviour was not feasible. It was also not possible to exactly determine the time of parturition. In no case could parturition or newborn calves be observed directly, because bushbuck calves perform lying-out behaviour for approximately 2 months after parturition (Reif, 1989). Because of differing extents of habituation of individual mothers, the exact date of parturition could not be calculated with accuracy from the estimated age at which the calf was first seen together with its mother. Hence, we analysed male–female associations as an indication of reproductive behaviour instead.

The gestation period of bushbuck is roughly 6 months (Allsopp, 1971; 178–182 days: Dittrich, 1972, 1974; Mentis, 1973), and parturition peaks are therefore likely to occur close to the beginning of the next rainy season. A possible explanation for seasonal variation in mating behaviour might be the synchronization of parturition with the time when fresh vegetation shoots are available to the weaned calf or the lactating mother (Duncan, 1975; Estes, 1976). Bushbuck are browsers and prefer leaves of shrubs and herbs (Smits, 1986; Apio & Wronski, 2005). Fresh herbs and shoots are considerably more abundant after rainfall. Indeed, our data show that 2 months after peak rainfall (during the mid-dry season) mixed sightings were significantly less frequent. In other words, 2 months after the driest month, which usually represents the onset of the rainy season, bushbuck show increased rates of reproductive behaviour.

Another benefit of synchronizing parturition could also be reduced predation (Daan & Tinbergen, 1979). The main predators of bushbuck in the study area are leopard (*Panthera pardus* Linneus), lion (*Panthera leo* Linneus) and python [*Python sebae* (Gmelin); A. Apio and T. Wronski, pers. obs.; see also Estes, 1992], but newborn bushbuck may also be prone to predation by martial eagles [*Polemaetus bellicosus* (Daudin)] and other large birds of prey (Kingdon, 1982). It must be mentioned though, that benefits because of the dilution effect are probably especially pronounced in gregarious species, in which fawns are born within the herd. By contrast, bushbuck are more or less solitary, and females hide their young, such that benefits because of the dilution effect probably play a subordinate role.

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