



Adaptive activity patterns of a blue wildebeest population to environmental variability in fragmented, semi-arid Kalahari, Botswana



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ABSTRACT

The blue wildebeest (*Connochaetes taurinus*) population in semi-arid savannah regions face intense spatial and temporal environmental variability over the annual cycle. The population in the Kalahari has lost critical seasonal ranges outside the protected areas due to human induced landscape changes. The population is faced with sparse and patchy forage availability, seasonally very high day temperatures, high predation pressure and limited availability and variable quality of water. We investigated the adaptive strategies of wildebeest in the Central Kalahari Game Reserve with a focus on how daily activity patterns respond to environmental variability in semi-arid Kalahari. The population coped with heat stress by maximising their activity in the cool hours of the day. They avoided predation pressure and loss of body condition by minimising activity at night and in dry seasons, respectively. We conclude that seasonal variations in temperature and light play a critical role in the timing of foraging activity.

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1. Introduction

African herbivore populations in semi-arid savannah regions have to contend with large spatial and temporal variability of forage quantity and quality over the annual cycle (Illius and O'Connor, 1999). The regions are characterised by high diurnal temperatures and low rainfall (Williamson and Williamson, 1985). These conditions lead to heat stress and dehydration in animals and plants (Shrestha et al., 2014), which is expected to worsen with increasing aridity associated with reduced rainfall combined with increased temperature (New et al., 2006). Adaptive behavioural characteristics such as timing their activity schedule (Green and Bear, 1990), and feeding strategies (Lima, 1998; Valeix et al., 2009) have helped animals cope with scarce water, forage variability, heat stress, and high predation risk.

In the Central Kalahari Game Reserve (CKGR), Botswana, the blue wildebeest (*Connochaetes taurinus*) has lost seasonal ranges beyond reserve boundaries due to human induced landscape changes (Williamson and Williamson, 1985; Conservation

International, 2010). Preferred habitats are limited, and forage is highly variable between seasons (Selebatso et al., in review). The blue wildebeest is water dependent (Knight, 1991) and its dark colour makes it vulnerable to heat loads and as a consequence depends on shade seeking which limits the times of the day they can forage in (Lease et al., 2014). The CKGR, including Khutse Game Reserve (KGR) has no permanent natural surface water and ungulates depend upon moisture from grasses or thirteen artificial waterholes with saline water dispersed over a vast region (54,695 km²). Availability of water in the waterholes is inconsistent (*pers. obs.*). Consequently, the CKGR has a low density and declining population of large ungulates (Conservation International, 2010), which presents a high probability of wildebeest predation by carnivores (Smuts, 1978). Large carnivore population spoor surveys estimates for the CKGR and KGR are brown hyaena (874), lion (552), wilddog (383), leopard (328), spotted hyaena (213), and cheetah (137) (Maude and Selebatso, 2014; unpublished). Thus, wildebeest face sparse and patchy forage availability, seasonally very high day temperatures, high predation pressure and limited, unreliable and poor quality of water.

Maximising energy gains under these various constraints, demands that wildebeest make substantial calculated risks with regards to heat stress during the day and predation at night. The

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trade-offs associated with maximising energy intake, water demands and antipredator strategies may compromise the survival of the population (Sinclair and Arcese, 1995; Lima, 1998). Wildebeest are expected to take greater risks of predation while foraging when their body condition is low (Sinclair and Arcese, 1995; Lima, 1998). This is likely to occur during the hot, late dry season when individuals have been subjected to 4–5 months of low quality, dry grass since the end to the wet season. In addition, conservation of moisture becomes a key survival priority during the hot, late dry season, when heat stress and moisture loss are greatest and moisture content of forage is lowest. Under the predation-sensitive foraging hypothesis (Sinclair and Arcese, 1995) we predicted that during the moisture-limited, hot, late dry season when body stores are declining and moisture constraints greatest, wildebeest would take greater risks by foraging more at night in cooler conditions but when visibility is worst and predators most active (Sinclair and Arcese, 1995). The alternate hypothesis is that wildebeest would simply reduce activity in the late dry season to conserve body stores while avoiding taking excessive risks by extending foraging bouts into the night. Our objective was to investigate the adaptive strategies of the isolated blue wildebeest population of the CKGR, with a focus on daily activity schedule in response to seasonal environmental variability and predation risk in semi-arid Kalahari ecosystems.

2. Materials and methods

2.1. Study area

The Central Kalahari Game Reserve (52,145 km²) and the Khutse Game Reserve (2550 km²) formed the study area. The area falls within 21°00'–23°00' S and 22°47.5'–25°25' E. The area is hot and dry, with extreme temperatures ranging from –6 °C to 43 °C in winter and summer, respectively (DHV, 1980; Williamson and Williamson, 1985). Mean annual rainfall ranges from 350 to 400 mm (DHV, 1980). There is no permanent surface water in the reserves, however, there are 13 artificial waterholes developed for wildlife. The CKGR contains four main habitats; (1) pans/valleys with open, high-quality short grassland on the higher clay soils of lacustrine origin, (2) dunes and (3) interdunes both with open to dense savanna/scrub and taller coarse grasses and (4) plains with open and mixed savanna (Williamson and Williamson, 1985). Larger ungulates are Giraffe (*Giraffa camelopardalis*), eland (*Taurotragus oryx*), blue wildebeest, gemsbok (*Oryx gazella*), kudu (*Tragelaphus strepsiceros*) and springbok (*Antidorcus marsupialis*) while larger carnivores include lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*) and brown hyaena (*Hyaena brunnea*) (Williamson and Williamson, 1985).

3. Method

Ten female wildebeest from different herds were immobilised and fitted with a Vectronic Aerospace's GPS Plus satellite collars between August 2011 and July 2014. High mortality and the low population of study herds led to less than 5 study animals surviving in any one season; we therefore used cumulative data from 2011 to 2014. We divided each year into wet (January–February), cold, early dry (June–July) and hot, late dry (September–October) seasons. Due to high inter-annual variability at the onset of the rains and associated effects on forage quality the other months were not included in the analysis. Sometimes rains start any time from November to December–March and April can be wet or dry season depending on the timing of rainfall during the wet season. We therefore focused comparison between months of the seasons that

have minimal annual variations. We had eight animals in each season.

The collars were equipped with 3-axis acceleration sensors that measured relative forward/backward, sideways and up/down movements of the wildebeest four times every second and averaged every 5 min (Krop-Benesch et al., 2012). We used the forward/backward movements as they are known to represent activity rhythms of animals (Krop-Benesch et al., 2012; 2013). We developed an activity chart (Actogram) using Vectronic Activity Pattern (software 1.2.3) program (Krop-Benesch et al., 2012; pg 41–43) to display mean hourly activity intensity. We also divided each day into four distinct two-hourly periods (dawn, midday, dusk and night) that we believed represent functionally different periods with regards to adaptive and predator-sensitive foraging strategies. Dawn and dusk have low temperature and enough light for foraging and visibility, while midday temperatures are too high and night has high predation risk. We used www.sunrise-and-sunset.com to estimate dawn and dusk. We extracted mean hourly activity data for these periods and used these data for relative activity analysis. Due to variations between individual collars associated with the circumference of the animal neck and the circumference of the collar (Krop-Benesch et al., 2013) we standardised the activity data for each sensor as a percentage of the maximum activity recorded by respective sensor (Hetem et al., 2012). Repeated measures ANOVA and Tukey's post-hoc tests in R (R Core Team, 2014) was used to test for differences in the seasonal and time of the day activity patterns. A two way ANOVA with repeated measure in R (R Core Team, 2014) was used to test for difference in night activity between seasons. To test for increase in the night activity, only data set for 8pm–11pm was used.

4. Results

Wildebeest activities peaked during the cooler periods of daylight hours (sunrise and sunset) but contrary to our first hypothesis, wildebeest did not display greater activity at night during the hot, late dry season compared to the wet season (Figs. 1 and 2) ($F_{6, 16} = 0.654, p > 0.05$). There was a little increase in their activity from 8pm until midnight in all the seasons.

The peak activity levels differed significantly between seasons ($F_{2, 13} = 11.93, p < 0.01$) and between different times of the day ($F_{3, 24} = 210, p < 0.001$). All seasons were different from each other, with greatest activity during the wet season then the cold, early dry and hot, late dry seasons (Fig. 1). There was no difference in activity between mid-day ($p = 0.727$) and mid-night ($p = 0.866$) during dry seasons; between mid-day and mid-night ($p = 0.854$) during the wet season; and between mid-day and dawn ($p = 0.638$) during the cold early dry season. The hour with the relatively lowest activity at night was 4am–5 am in both wet and hot late dry seasons and from 4.30 am to 5.30 am in the cold, early dry season.

5. Discussion and conclusion

During the hot, late dry season forage abundance and moisture content are lowest although moisture content increases in Kalahari grasses to some extent at night (Williamson and Williamson, 1985). Owing to the extreme heat during the day, wildebeest foraging activity is strictly limited to cooler periods in the early morning and late afternoon. During the hot, late dry season, when body stores of wildebeest are declining, they would likely not get enough intake of energy and protein as forage quality is at its lowest (Selebatso et al., in review) and diurnal foraging greatly restricted. We therefore predicted that wildebeest would risk predation by foraging at night to increase daily intake (the predator sensitive foraging hypothesis), as well as take advantage of increased grass moisture content.

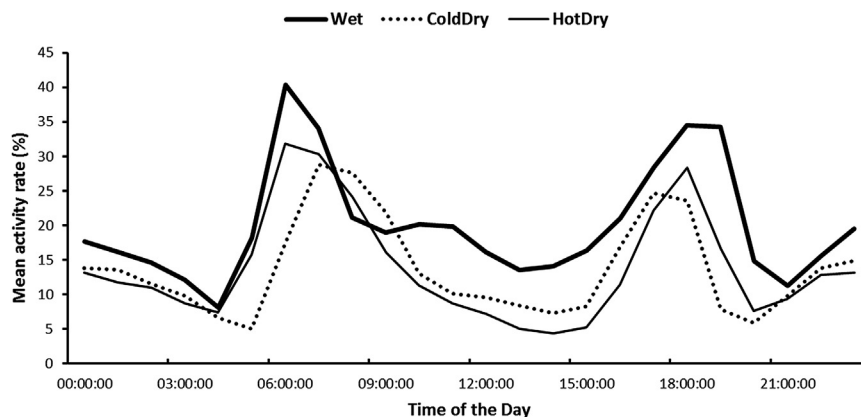


Fig. 1. Seasonal patterns in mean activity levels of 10 blue wildebeest in a 24 h cycle, in the Central Kalahari Game Reserve, Botswana between 2011 and 2014.

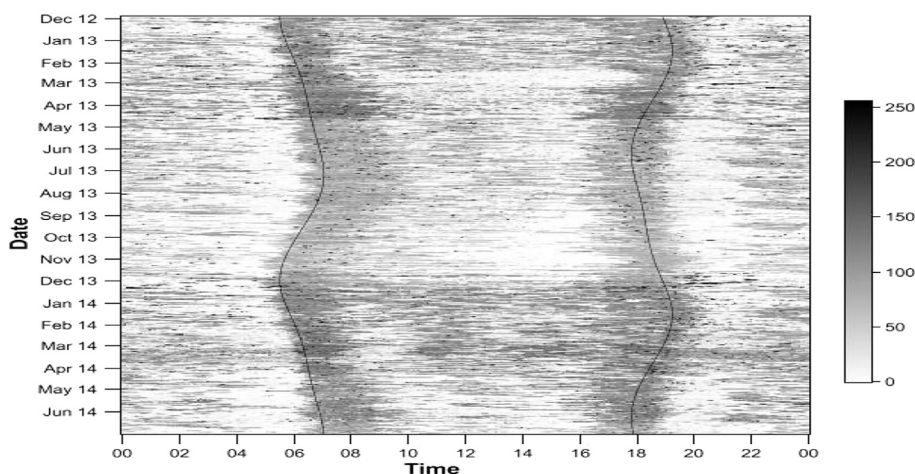


Fig. 2. Actogram showing an example of one blue wildebeest activity pattern against the sunrise and sunset (vertical curves on the graph), between 2012 and 2014. The activity rates is represented by the intensity of darkness on the graph, ranging from white to dark black, as represented on the bar on the right.

However, our results did not support the predator-sensitive foraging hypothesis. Our collared wildebeest did not display greater activity at night during the hot, late dry season compared to the wet season; instead wet season activity was highest at this time suggesting that their strategy was to conserve body stores over the dry season (Fig. 1). Unlike the Arabian Oryx (Hetem et al., 2012), which has low predation risk, the wildebeest avoided predation risks and chose to conserve energy by reducing activity in forage limited dry seasons. While food is abundant during the wet season, temperatures are generally high and thus we had expected wildebeest to rest longer in the wet season when they could eat plentiful high-quality food in early morning and late afternoon. However wildebeest chose to maximise foraging in the wet season, probably to accumulate enough body reserves to take them through the dry season (e.g. Parker et al., 2009). Forage quality is very high in the wet season (Selebatso et al. in review) and so it makes sense to maximise intake before the quality declines. The wet season is expected to have some cloudy and so cooler days, enabling wildebeest to continue grazing into the midday. The cold, early dry season activity was even lower, with minimal activity in the morning because temperatures are low at this time (Williamson and Williamson, 1985) and the sun rises a little later than in the hot, late dry season. Wildebeest, minimised activity in the dry season when conditions are bad, and only become active in the not too cold and not too hot times of the day, with evident

avoidance of night activity. Our results suggest that the wildebeest obtain enough forage in the dry season or acquire enough fat reserves in the wet season, and so could afford to avoid predation by not foraging during risky periods. This adaptive strategy is expected to sustain the population as long as forage quality and quantity is sufficient to maintain the population. Periods of drought or persistence of below-average rainfall and occasional heat waves associated with climate change would probably push wildebeest to either predation or heat risk.

Contrary to findings by Knight (1991), wildebeest in the CKGR did not increase their activity during midday in any season. The CKGR wildebeest population showed reasonably high activity between the morning peak and noon in the wet season compared to other seasons. In the Kalahari Transfrontier Park (KTP), Knight (1991) reasoned that the wildebeest population had an optimal water supply and so could afford to graze longer on hot days and later dissipate the heat. The scenario at KTP suggests that the population did not get enough daily food intake during cool hours, such that they even when it was hot to maximise foraging. The CKGR wildebeest population chose to be active during the cool hours of the day to avoid heat stress but only when sufficient light enables them to detect predators.

To conclude, the foraging activities of the CKGR blue wildebeest population was constrained by high day temperatures and predation risk at night suggesting that avoidance of immediate threats

(heat stress and predation) dominates the hierarchy of foraging decisions. Our findings support our alternate hypothesis that the strategy of wildebeest in the CKGR is to build body stores during the wet season and then to conserve those body stores during the dry season, while avoiding heat stress in both seasons. The persistence of this adaptive strategy may be compromised by inconsistency climatic conditions resulting from climate change and increased variability.

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