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Short communication

Comparing daily, circalunar and seasonal activity patterns of cheetah *Acinonyx jubatus* in response to livestock presence in Botswana

Michelle J. C. Kral[1,2], Pablo Rios Tubio[2], Femke Broekhuis[2], Ignas M. A. Heitkönig[2], Christopher Mbisana[1], Lucas Motlhabane[1], Rebecca Klein[1] and Frank van Langevelde[2]

[1]Cheetah Conservation Botswana, Gaborone, Botswana
[2]Department of Environmental Sciences, Wildlife Ecology and Conservation Group, Wageningen University and Research, Wageningen, the Netherlands

Correspondence: Michelle J. C. Kral (michellekral1993@gmail.com)

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Animal activity patterns vary on a daily, circalunar and seasonal scale in response to abiotic (e.g. light availability and temperature) and biotic factors (e.g. predation and competition). In the presence of humans and their livestock, carnivores, for example, have been found to become more nocturnal. The aim of this paper is to compare daily, circalunar and seasonal activity patterns of cheetah *Acinonyx jubatus* in the western Kalahari of Botswana between areas where there is no livestock present (i.e. game farms with a relatively low risk of cheetah mortality) and areas where livestock is present (i.e. cattle farms with a higher risk of cheetah mortality). Using two years of camera trap data, we recorded 88% of cheetah observations on game farms and 12% on cattle farms. Our results showed that cheetahs were more nocturnal in the absence of cattle and more crepuscular on cattle farms compared to game farms. Overall, cheetah activity on cattle farms showed a peak in activity after inferred cattle activity and before human activity during the day, specifically during the dry season. We recommend management strategies on a local scale such as temporal zoning of grazing activities during the different seasons or keeping cattle in an enclosure at night. This study sheds new light on our understanding of the impact of land use on free-ranging carnivores in the face of livestock expansion on the African continent.

Keywords: *Acinonyx jubatus*, activity patterns, livestock, mixed-use landscapes, temporal partitioning

Introduction

Wildlife activity can vary at daily, circalunar and seasonal scales in response to anthropogenic factors (Gaynor et al. 2018) as well as abiotic and biotic factors (Mistelberger 2011, Partch et al. 2014) such as changes in light, temperature,

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resources and competition (Aschoff 1960). Activity patterns play a key role in a wide range of ecological, evolutionary and physiological processes such as foraging, mating and thermoregulation (Helm et al. 2017). Changes in activity patterns in response to human activities, including livestock presence, may have consequences for inter- and intra-specific interactions, reproduction, survival and consequently population persistence (Gaynor et al. 2018). This is especially key for large carnivores that reside in predominantly human-transformed landscapes (Broekhuis et al. 2022, Van der Weyde et al. 2022). Therefore, understanding the activity patterns of large carnivores in human-transformed land is particularly important in areas where livestock production and human–wildlife conflict over livestock predation are increasing.

Cheetahs *Acinonyx jubatus* are predominantly diurnal and crepuscular, being active largely during the day but also during twilight and occasionally at night, when sufficient lunar light is available (Cozzi et al. 2012, Broekhuis et al. 2014). During the hottest hours of the day, cheetahs are thought to rest to avoid heat stress (Hetem et al. 2019, Mills and Mills 2022). To date, most research has focused on cheetah activity in protected areas with no livestock presence (Hayward and Slotow 2009, Cozzi et al. 2012, Broekhuis et al. 2014, Swanson et al. 2016, Broekhuis et al. 2019). As a result, the daily, circalunar and seasonal variations in cheetah activity in relation to livestock presence and associated risk of human persecution is still understudied. To address this, we compare cheetah activity patterns in areas with and without livestock where cheetahs face different mortality risks. The study was conducted on commercial, freehold farmlands in the western Kalahari of Botswana which provides a mixture of farms used either for game or cattle production. On these farmlands, 35% of farmers report losses due to cheetah predation annually (Selebatso et al. 2008). As a result, human-induced mortality risk for cheetahs on cattle farms is nearly five times higher than on game farms (Boast 2014). The main competitors of cheetah, namely lion *Panthera leo* and spotted hyena *Crocuta crocuta* are largely locally extirpated in the study area (Cheetah Conservation Botswana unpubl.). Using two years of camera trap data, we investigated whether cheetah daily, circalunar and seasonal activity differs between cattle and game farms. On cattle farms, we expected cheetahs to be more active during the night to minimize interactions with humans and livestock (Oriol-Cotterill et al. 2015a, Gaynor et al. 2018). Furthermore, we expected cheetahs to be more active on cattle farms compared to game farms during full moon nights, as the presence of livestock has shown to increase nocturnality, and carnivores can increase their nocturnality if sufficient moonlight is available (Cozzi et al. 2012, Broekhuis et al. 2014, Gaynor et al. 2018). Lastly, we expected that in the cool, dry season cheetahs will be less active during the night on cattle farms compared to the hot, wet season, as cooler temperatures during the day allow for diurnal cheetah activity (Hetem et al. 2019), and during the cool, dry winter season cattle may graze at night (Ayantunde et al. 2000).

Material and methods

Study site

We conducted this study on commercial game and cattle farms within the Ghanzi Agricultural Block, in the central west of Botswana (Fig. 1). The Kalahari desert landscape on both cattle and game farms is largely flat, sandy, semi-arid shrubland (Houser et al. 2009). The average annual rainfall in the district is 400 mm and mostly falls during the hot, wet season spanning from November to March, with little to no rain falling during the cold, dry season (Statistics Botswana 2013). The hottest month of the year is October, with an average maximum temperature of 33°C and the coldest month of the year is July, with an average maximum temperature of 23°C during the day but below 0°C at night (Statistics Botswana 2013). The total area of the Ghanzi commercial farm block is more than 13 000 km^2 and includes more than 200 farms owned by approximately 50 families, making it the largest commercial farming block in Botswana (Boast et al. 2016, Van der Weyde et al. 2020). Approximately two-thirds of farms are cattle farms with an average cattle density of ~ 4.50 cattle km^{-2} (Statistics Botswana 2015). Cattle often roam freely within farms and are not kept in overnight enclosures. Although the farms have fences, they are permeable to most wildlife. On the game farms, where game animals are kept for eco-tourism, photography and hunting purposes, common species include giraffe *Giraffa camelopardalis*, plains zebra *Equus quagga*, springbok *Antidorcas marsupialis*, impala *Aepyceros melampus*, gemsbok *Oryx gazella*, common eland *Taurotragus oryx* and blue wildebeest *Connochaetes taurinus*. Free-roaming herbivores, including greater kudu *Tragelaphus strepsiceros*, steenbok *Raphicerus campestris* and common duiker *Sylvicapra grimmia* are also present on both cattle and game farms (Van der Weyde et al. 2021). Larger carnivore species in the Ghanzi Agricultural Block also roam across cattle and game farms, and include leopard *Panthera pardus*, cheetah and brown hyena (*Hyaena brunnea*). Human activity levels are similar on game and cattle farms which have small homesteads and a network of sand roads that are regularly driven to track game or to check on cattle, respectively (M. J. C. Kral pers. obs., Van der Weyde et al. 2017).

Camera traps

We used camera traps to record cheetah activity patterns on cattle and game farms. We placed the camera traps at trees known to be used for scent marking by cheetahs in the study area. Cheetahs scent mark prominent landscape features, such as trees, to communicate with conspecifics, for mating purposes or to defend their territory from other males (Melzheimer et al. 2018, Kusler et al. 2019). Marking trees can be visited by many individual cheetahs, and up to nine individuals have been previously recorded at one tree in a two-week period, so these locations provide an opportunity to collect behavioural data in areas where direct observations are rare (Melzheimer et al. 2018, Kusler et al. 2019, M. J. C.

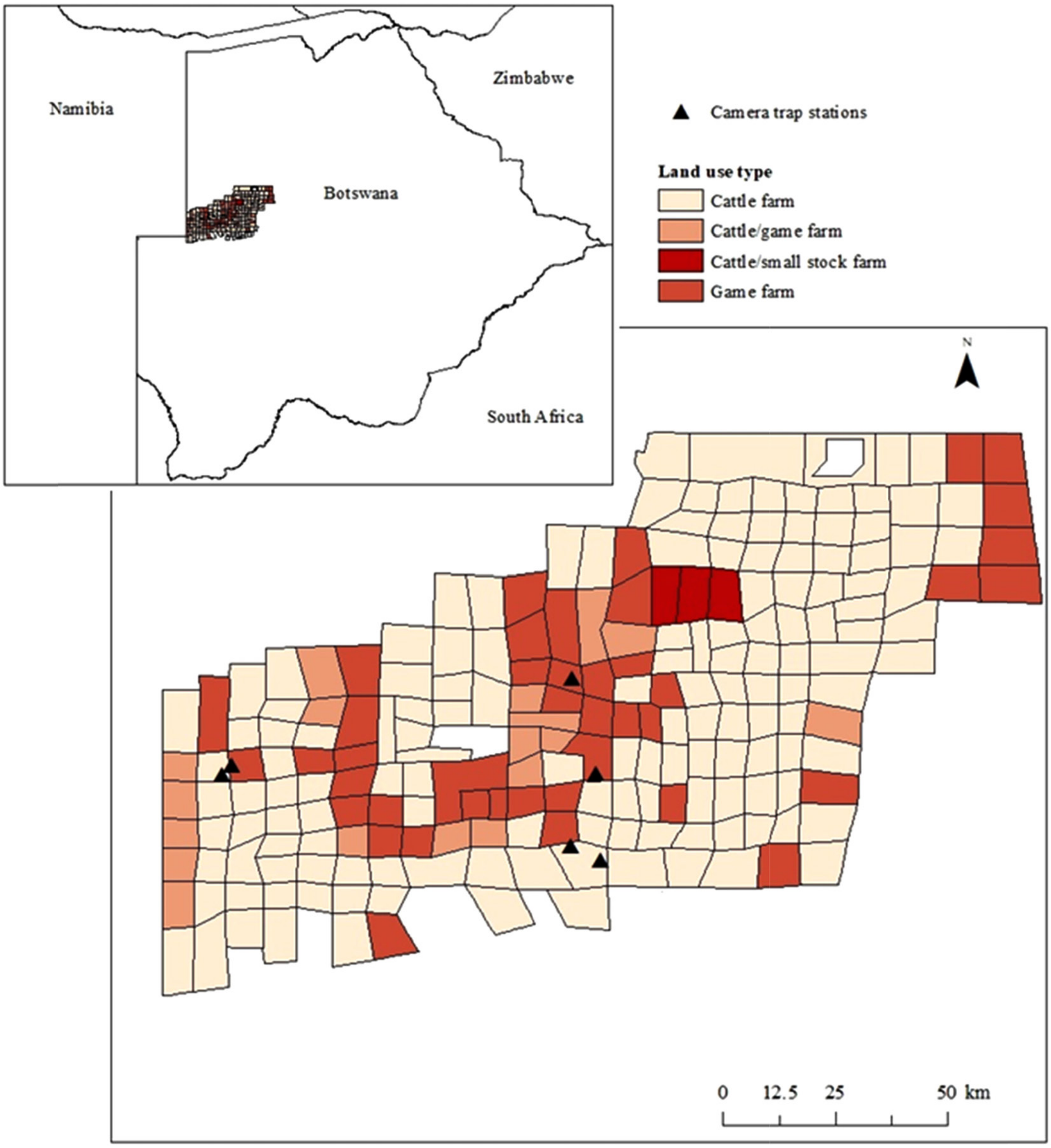

Figure 1. Camera trap stations at marking trees (n = 6) in the Ghanzi Agricultural Block in western Botswana, comprising 13 000 km^2 of cattle and game farms. Small blocks represent individual farms.

KralK pers. obs.). We monitored six cheetah marking trees, three on cattle farms and three on game farms with Bushnell Trophy HD Aggressor cameras between October 2019 and November 2021 (Fig. 1). At each tree we had a camera station consisting of two cameras placed at cheetah shoulder height (75 cm; Boast et al. 2013) and facing each other to capture both sides of the tree. Cameras were active for 24 h a day and the time between photos was set at 15 s. Every two weeks cameras were checked, batteries were changed and imagery was downloaded. All the images were uploaded into Agouti, an online program developed to store, organize and process camera trap imagery (Casaer et al. 2019).

Data analyses

Camera trap data were filtered for cheetah only. We defined cheetah detections as independent using the standard cut-off time of a 30 min interval between a series of cheetah photos (Ridout and Linkie 2009). Series were automatically created by Agouti based on the time stamp on each photo. Photos were labelled into a sequence when the time between subsequent photos was less than 120 s (Y. Liefting pers. obs.). We transformed the time stamps from hours (decimals) into radians (0–2π) for the analyses of circular data. We calculated the number of observations during the day, night and twilight based on the sunrise and sunset data of nearby Ghanzi town (21°41'52.26''S, 21°38'44.916''E) using the packages 'Suncalc' and 'Circstats' of R ver. 3.6.1 (Lund and Agostinelli 2001, Thieurmel and Elmarhraoui 2022, www.r-project.org). Twilight was defined as nautical twilight, when the geometric centre of the sun is between 6 and 12 degrees below the horizon, comprising a period of approximately 52–60 minutes per day for both sunrise and sunset. We determined the lunar phases (i.e. new moon, first quarter (Q1), full moon and last

Table 1. The number of independent cheetah observations recorded per individual marking tree and their farm type between October 2019 and November 2021.

Camera trap station	Number of independent cheetah observations	Farm type
MT3	157	Game
MT7	626	Game
MT17	154	Game
MT22	16	Cattle
MT23	45	Cattle
MT30	68	Cattle

quarter (Q2)) using continuous moon illumination data for the location of Ghanzi town and dates of the nocturnal cheetah observations. To test whether cheetah nocturnal activity patterns were influenced by the lunar cycle, we used the package 'Suncalc' to calculate the fraction, phase and angle of the moon for each given date (Thieurmel and Elmarhraoui 2022). We defined the wet season as spanning from 1 November to 31 March and the dry season from 1 April to 31 October (Statistics Botswana 2013). The packages 'Overlap' (Meredith and Ridout 2021) and 'Lubridate' (Spinu 2023) were used to determine daily, circalunar and seasonal activity patterns of photographed cheetah to compare the patterns between game and cattle farms, lunar phase and season (Ridout and Linkie 2009). The coefficient of activity overlap (Δ) ranges from no estimated overlap ($\Delta = 0$) to total overlap ($\Delta = 1$). The coefficient Δ_4 was used as all investigated data frames had over 50 records (Ridout and Linkie 2009). We then calculated overlap coefficients with a 95% confidence interval and 10 000 smoothed bootstraps for daily, circalunar and seasonal cheetah activity patterns. To test for similarities in daily, circalunar and seasonal activity patterns between cattle and game farms, we conducted three Watson's tests, respectively, using the package 'CircStats' (Lund and Agostinelli 2001). To test if the circalunar activity patterns of cheetahs differed from random, we conducted a Hermans–Rasson test for both farm types (Landler et al. 2019).

Results

Daily activity patterns

A total of 1066 independent cheetah detections were recorded at the six cheetah marking trees between October 2019 and November 2021. Approximately half (46%) of these detections were at night, 24% at twilight and 30% during the day. Of the total of 1066 independent detections, 88% ($n = 937$) were recorded at game farms and 12% ($n = 129$) at cattle farms. Nearly half of the data were from one camera trap station located at a game farm (Table 1).

We found a significant difference in daily cheetah activity patterns between game and cattle farms (Watson's test, Test statistic = 0.409, Critical value = 0.187) even though the overlap coefficient was high ($\Delta_4 = 0.832$; 95% CI 0.762–0.887). On both farm types, daily cheetah activity peaked during the morning twilight and decreased just after sunrise and then remained low during the day and increased again after the evening twilight. Whereas cheetah activity on cattle farms was centred around twilight and decreased significantly at night, cheetah on game farms remained active throughout the night and no steep decrease in activity was observed (Fig. 2).

Circalunar activity patterns

Cheetah activity in response to changes in moon illumination was similar between farm types ($\Delta_4 = 0.861$, ± 95% CI 0.814–0.980). Cheetah activity on game farms remained relatively uniform in relation to moon illumination, whereas on cattle farms cheetah activity varied across the four lunar phases. On cattle farms, cheetah activity peaked between the first quarter towards the full moon, followed by a decrease of activity after full moon into the second quarter (Fig. 3). Despite this peak, there was no significant difference detected in circalunar cheetah activity between cattle and game farms in response to changes in moon illumination. On both cattle farms (Hermans–Rasson test, $T = 3.830$, $p = 0.321$) and game farms (Hermans–Rasson test, $T = 3.176$, $p = 0.469$) cheetah circalunar activity patterns did not differ significantly from random.

Seasonal activity patterns

Cheetah daily activity peaked for both seasons during dusk and dawn, and decreased during the day (Fig. 4). In both seasons cheetah activity on cattle farms centred around twilight and decreased at night, whereas on game farms cheetah activity was detected throughout the night and no such decrease was observed during both seasons. During the dry season, a high overlap between the two farm types ($\Delta_4 = 0.751$, ± 95% CI 0.660–0.853) was recorded, but cheetah activity differed significantly between cattle and game farms (Watson's test, Test statistic = 0.317, Critical value = 0.187). During the dry season, there was less nocturnal cheetah activity than during the wet season (Fig. 4). There was no significant difference in cheetah activity during the wet season between cattle and game farms (Watson's test, Test statistic = 0.182, Critical value = 0.187) with a high overlap between the two land use types ($\Delta_4 = 0.828$, ± 95% CI 0.739–0.901).

Discussion

Overall, we hypothesized that activity patterns of cheetahs would differ between areas where livestock are present and mortality risk is high and areas where there are no livestock present and mortality risk is low. In terms of daily activity patterns, we expected cheetahs on cattle farms to be active during twilight and during the night, as livestock presence and fear of humans can increase wildlife nocturnality (Oriol-Cotterill et al. 2015a, b, Gaynor et al. 2018). However, contrary to our expectations, cheetahs were not more nocturnal

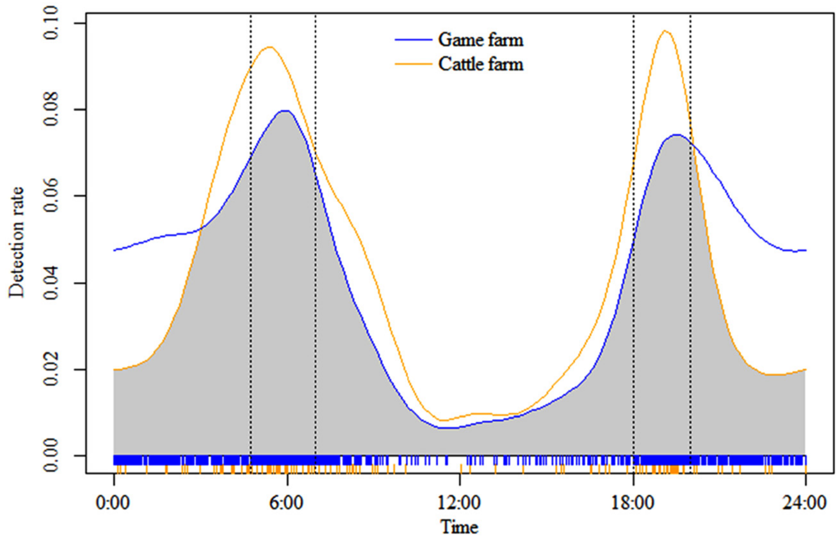

Figure 2. Cheetah daily activity patterns based on independent cheetah camera trap observations at cattle (n = 129) and game (n = 937) farms in Ghanzi district between October 2019 and November 2021. The grey shading under the curve represents the overlap in cheetah activity between cattle and game farms. Dotted lines represent twilight.

in areas with livestock, but rather more nocturnal in areas without livestock. This could be related to cattle activity with regards to their grazing behaviour. While we assumed cattle to be active during the day, analyses of temporal activity and grazing patterns of free-ranging cattle in arid lands of central Australia showed that cattle are more active and restless at night until sunrise (Low et al. 1981). Indeed, nocturnal grazing has been described for the arid regions of Botswana, where animals under free-range conditions spend a significant amount of time grazing at night, whereas they are resting at mid-day or chewing the cud (Butler 1971). On game farms, on the other hand, we recorded nocturnal cheetah activity. This may be explained by the presence of resources and absence of risks on game farms, the two main biotic factors shaping activity patterns (Kronfeld-Schor and Dayan 2003). Without grazing livestock, a lower human-induced mortality risk and with more wild prey availability than on cattle farms, there are fewer risks and more resources, which may encourage more nocturnal activity for cheetahs on game farms (Boast and Houser 2012, Boast 2014, Boast et al. 2016), also because there are no nocturnal lions or spotted hyenas in the study region (Cheetah Conservation Botswana unpubl.). Research on marking tree visits by cheetahs in farmlands in South Africa and Namibia also suggests that cheetahs

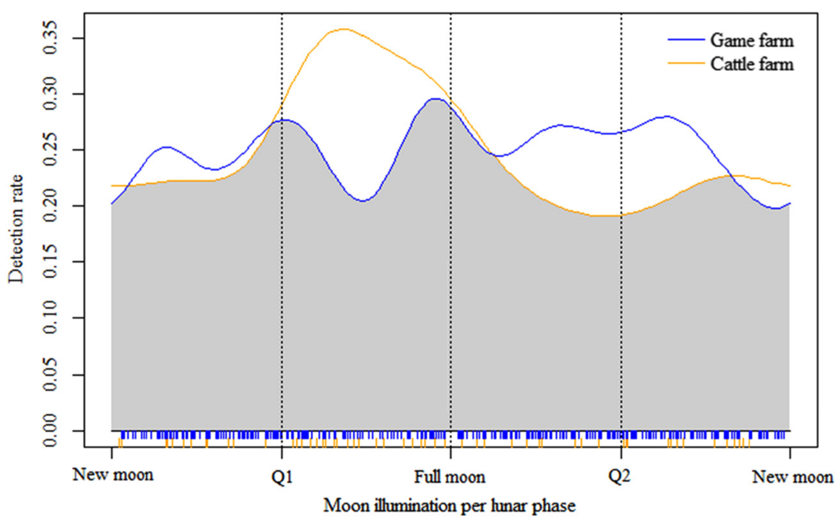

Figure 3. Cheetah circalunar activity patterns based on independent nocturnal observations recorded at cattle (n = 51) and game (n = 557) farms in Ghanzi district between October 2019 and November 2021. The lunar phases new moon, first quarter (Q1), full moon and last quarter (Q2) are based on moon illumination of the respective dates of the nocturnal observations. The grey shading under the curve represents the overlap in cheetah activity between cattle and game farms. Dotted lines represent the different lunar phases.

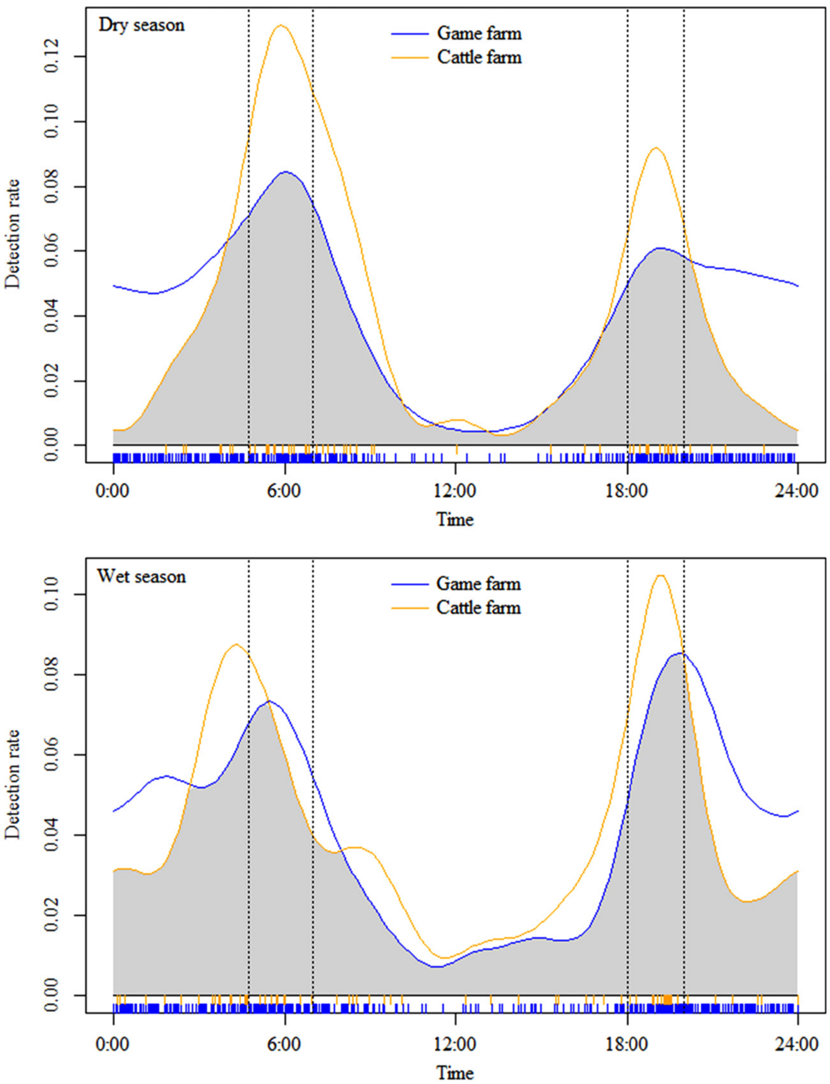

Figure 4. Cheetah daily activity patterns based on independent cheetah observations during the dry season on cattle (n = 57) and game (n = 435) farms (top) and wet season on cattle (n = 72) and game (n = 502) farms (bottom) in Ghanzi district between October 2019 and November 2021. The dry season spans from 1 April to 31 October and the wet season from 1 November to 31 March.

may have been nocturnal in areas because of human activity; however, they do not differentiate between game or livestock presence and associated mortality risk (Marnewick et al. 2005, Verschueren et al. 2021). In terms of daily activity patterns across different seasons, we did not observe a significant difference in cheetah activity between game and cattle farms during the hot, wet season. However, during the cold, dry season, we did find a significant difference in cheetah activity between game and cattle farms. This could be because cattle are more active at night during the dry season, as this is essential for nutritional intake (Butler 1971, Low et al. 1981, Ayantunde et al. 2000, Puls et al. 2021). Although we did detect significant differences in daily activity between cattle and game farms, it should be noted that 88% of the total cheetah observations were recorded on game farms where livestock is absent. We suspect that this reflects patchy space use by cheetah with higher detection rates being driven by repeated use of the same preferred selected sites – one specific game farm in this case. Therefore, partitioning in this mixed-use landscape is most likely spatial in addition to temporal. Indeed, this has been described for several carnivore species (Boydston et al. 2003, Oriol-Cotterill et al. 2015a).

We expected that cheetahs are more active on cattle farms compared to game farms during full moon periods. However, we found no difference in cheetah activity in relation to moonlight illumination. Increased activity during lunar phases with higher moonlight availability has been reported for many carnivores including diurnal African wild dogs (*Lycaon pictus*, Rasmussen and Macdonald 2011, Cozzi et al. 2012, Broekhuis et al. 2014). It is therefore possible that we were unable to detect such a pattern due to a small sample size. Furthermore, with the expansion of livestock on the continent, we would also advise for more studies on cattle behaviour in areas where cattle and wildlife share their resources, to develop targeted mitigation strategies for human–wildlife conflict.

Our results demonstrate differences in daily and seasonal activity patterns of a carnivore in areas with and without livestock. The results suggest usage of human-transformed areas when risk is lowest. Here, we illustrate that by taking longer-term cycles such as season into account, variations in carnivore behaviour in response to land use and mortality risk may be detected. Overall, cheetah showed temporal partitioning while visiting marking trees, avoiding inferred cattle activity at night and human activity during the day, especially during the dry season. Olfactory communication forms an important part of cheetah social interactions (Wachter et al. 2019, Melzheimer et al. 2020) and this may affect territory defences, attraction of mates, warning of conspecifics, protection of offspring and the attraction of cubs by their mother (Bradbury and Vehrencamp 1998), impacting fitness and survival. Therefore, conservation actions intended to modify the ways people and wildlife interact in time and space may consider the context-specific management implications on a local scale (e.g. temporal zoning of human activities or the nocturnal and/or seasonal kraaling of cattle during the dry winter season) to promote human–carnivore coexistence and the long-term conservation of free-ranging carnivores (Carter et al. 2012). This study sheds new light on behaviour of a carnivore outside of protected areas that has generally been considered diurnal, and contributes to our understanding of the impact of land use on the activity patterns of free-ranging cheetah in the face of livestock production increasing on the African continent.

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Author contributions

Michelle J. C. Kral: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Investigation (lead); Methodology (lead); Project administration (lead); Resources (equal); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Pablo Rios Tubio**: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Writing – review and editing (equal). **Femke Broekhuis**: Conceptualization (equal); Supervision (lead); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Ignas M. A. Heitkönig**: Conceptualization (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Christopher Mbisana**: Data curation (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Lucas Motlhabane**: Data curation (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Rebecca Klein**: Funding acquisition (lead); Project administration (equal); Resources (lead); Supervision (equal); Writing – review and editing (supporting). **Frank van Langevelde**: Conceptualization (equal); Investigation (equal); Methodology (equal); Supervision (lead); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

The data that support the findings of this study are available upon reasonable request from the corresponding author (M. J. C. Kral). The data are not publicly available because of the conservation status of the species.

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