



Seasonal selection of key resources by cattle in a mixed savannah-wetland ecosystem increases the potential for conflict with lions

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ABSTRACT

In Africa's pastoral conservation landscapes, apex predators frequently kill livestock. Retaliatory persecution such as poisoning threatens predators, but also non-target biota. Several factors influence conflict severity, including livestock husbandry, overlap in seasonal habitat use, and the degree to which livestock perceive and are able to respond to a landscape of fear. We investigated these factors by GPS-tracking 42 Tswana beef cattle (*Bos taurus*) from 29 herds in 2017 and six lions (*Panthera leo*) from different prides (May 2016–Dec. 2017) in the northern Okavango Delta, Botswana, where cattle depredation significantly impacts the livelihoods of rural agropastoralists. Cattle exhibited seasonal habitat selection patterns similar to wild ungulates in the region. They preferred woodland habitats, with more digestible grasses, during the wet season. During the dry season, they preferred wetland habitats with reliable forage and water availability. Cattle also preferred areas close to human settlements, but the necessity to forage in wetlands during the dry season exposed them to significant depredation risk, especially > 4 km from settlements. Lions killed most cattle in wetlands during the late dry season but the intensity of recent lion presence (previous 14 days) only had a weak negative effect on cattle habitat selection patterns. Cattle used rangelands according to nutritional requirements, irrelevant of the associated predation risk, suggesting that socio-ecologically acceptable conflict solutions cannot rely on the exclusion of livestock from seasonal wetlands. Curbing depredation by lions will best be achieved by a combination of resource- and predation-cognisant seasonal herding strategies with adequate livestock protection. Understanding the ecological constraints that intensify conflict is pertinent to any livestock production landscape with predator presence. It is also a central prerequisite for future land use planning and devolution of legal, controlled resource access rights through policy. Coexistence strategies must account for the strong reliance of people, their livestock, and wildlife on shared key resources. This is particularly important in large trans-frontier conservation areas where the successful merging of biodiversity conservation and rural development is a strategic goal. Omission will foster resentment and resistance to coexistence with apex predators, particularly if livestock productivity and human livelihoods are negatively affected.

1. Introduction

In Africa, where livestock is a key source of income and social status, cattle (*Bos taurus*) numbers are increasing (Thornton, 2010), simultaneously increasing their availability as a food resource for apex predators such as the lion (*Panthera leo*). The resulting conflict can

cause severe financial losses (Baker et al., 2008) that significantly impact rural livelihoods. Consequently, the attitudes of communal land managers towards damage-causing predators are particularly negative (Kansky et al., 2014). Intensive conflict between lions and people living in and around protected areas is probably the greatest challenge facing lion conservation because it results in retaliatory persecution, thereby

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detrimentally affecting lion populations at large spatial scales (Woodroffe and Frank, 2005; Trinkel et al., 2017). Moreover, vulture populations across Africa are being devastated by carcass poisoning intended to kill lions (Ogada et al., 2015). Clearly, conservation strategies are needed to ensure sustainable wildlife persistence in increasingly human-dominated landscapes, such as Africa's large communal coexistence areas that border or connect wildlife reserves and parks. In landscapes where livestock and large predators co-occur, rural residents incur the major cost of coexistence through frequent stock depredation. Therefore, the development of optimal conservation strategies requires knowledge of how livestock use habitats seasonally in relation to predator activity and whether they reduce predation risk by responding to the associated landscape of fear (Laundré et al., 2001). Conservation strategies must take into account the livelihoods of local communities and associated socio-ecological dynamics, with a focus on harmonizing conservation-oriented goals with livelihood-oriented goals (Fynn et al., 2016).

Free-ranging herbivores in African savannas, whether wild or domestic, face several constraints that influence their foraging decisions, movements and seasonal habitat selection. The principal drivers are: (i) strong seasonal and inter-annual variation in forage quantity and quality (Illius and O'Connor, 1999; Owen-Smith, 2008), (ii) predation risk and the associated landscape of fear (Creel and Winnie, 2005; Laundré et al., 2001; Valeix et al., 2009) and (iii) increasing fragmentation of ecosystems by anthropogenic impacts (Fynn and Bonyongo, 2011; Harris et al., 2009). Optimal adaptation by herbivores to strong temporal variation in forage quantity and quality requires access to key aspects of functional resource heterogeneity in ecosystems (Hopcraft et al., 2010; Owen-Smith, 2004). Savannah habitats with low rainfall and productivity support higher forage quality than more productive wetland/high rainfall habitats (Hopcraft et al., 2010), but they are unable to sustain greenery and reliable forage availability during the dry season (Owen-Smith, 2008). Thus, across Africa, many wild and domestic herbivore populations historically migrated seasonally, selecting higher quality forage in woodlands and saline grasslands during the wet season and selecting the only remaining green forage on floodplain systems (especially in deeper-flooded zones) during the dry season (Fynn et al., 2015).

Functional heterogeneity is not only important for providing herbivores with adaptive foraging options, but also for adapting to predation risk and the landscape of fear. The landscape of fear (Laundré et al., 2001) is defined as the impact of relative danger in shaping prey behaviour. It hinges on the trade-off between acquiring food and maintaining safety. A fast-growing body of landscape of fear literature focuses on wild ungulates (Courbin et al., 2016; Creel et al., 2005; Périquet et al., 2010; Valeix et al., 2009), predators (Droge et al., 2016; Haswell et al., 2018; Vanak et al., 2013), and also on predator response to anthropogenic threats (Loveridge et al., 2017). Most studies show that in areas where the perceived risk of predation is high, prey decrease their food intake (Christianson and Creel, 2010), increase their vigilance (Périquet et al., 2010) or simply avoid these locations both in space and time (Courbin et al., 2016; Creel et al., 2005). Where functional heterogeneity of habitats has been modified by anthropogenic influence, such as through ecosystem fragmentation (e.g. fencing, Fynn and Bonyongo, 2011; Harris et al., 2009; Løvschal et al., 2017) or through modification of water availability in the landscape (e.g. dam development, Fynn et al., 2015), herbivore populations may decline as a result of loss of predation refuges (Harrington et al., 1999; Hopcraft et al., 2010; Rettie and Messier, 2008). Thus, it is important to understand how functional heterogeneity may enable herbivores to adapt to predation risk and the landscape of fear, while still maintaining access to sufficient quantity and quality of food (e.g. Rettie and Messier, 2008; Sinclair and Arcese, 1995).

Apart from the problems of ecosystem fragmentation and loss of connectivity between functional seasonal herbivore habitats, another factor leading to declining herbivore populations in African savannas is

that local communities living in and around protected areas are among the poorest, not benefiting adequately from Transfrontier Conservation Areas (TFCAs). TFCAs have been developed to address the problem of ecosystem fragmentation and disruption of wildlife movements over large functional landscapes (Andersson et al., 2013). Another objective of TFCAs is to enhance the livelihoods of local communities through job creation and tourism development (Snell, 2015). International tourism companies often are the main economic benefactors of wildlife presence (Igoe, 2004) and lions are a particularly valuable viewing asset (van der Meer et al., 2016), yet coexistence costs from livestock depredation and compromised human safety directly accrue to those communities adjoining reserves (Weise et al., 2019). The local cost-benefit trade-off often is negatively biased towards rural communities (Igoe, 2004), especially where consumptive utilisation of wildlife is not possible (Mbaiwa, 2018). While the TFCA concept is innovative, and has great potential for addressing these problems, most communities living within TFCAs have seen their livelihoods imperilled by an intensive human-wildlife interface (e.g. Songhurst, 2017; Weise et al., 2019), and also face an inability to access lucrative beef markets owing to the prevalence of foot and mouth disease and associated trade restrictions. Modern conservation strategies must prioritize the well-being of communities living in potential corridors and wildlife dispersal areas (Fynn et al., 2016; Tyrrell et al., 2017) to ensure greater buy-in with conservation objectives (Norton-Griffiths and Said, 2010; Ostrom, 1999). The plural objectives of TFCAs will only be met if the well-being of communities is addressed in a holistic sense. Livestock such as cattle, sheep (*Ovis aries*), and goats (*Capra aegagrus*) contribute critically towards the livelihoods and cultural values of local communities in African savannas. They should, therefore, form a central focus of conservation research and strategy development in TFCAs.

From a community livelihood perspective and their attitudes to conservation objectives, as well as for reducing the killing of predators and other biota, it is important to minimise livestock-predator conflict. Knowledge about movements and seasonal habitat use of free-ranging livestock in relation to wildlife, especially apex predators, could be used to develop an understanding of optimal seasonal livestock habitats and how conflict mitigation strategies may affect nutrient and energy intake by livestock over the annual cycle. In addition, this knowledge can be used to design improved livestock husbandry practices, the most likely variable in successfully reducing depredation and controlling future conflict (Reddy et al., 2016). Although methods are now well developed to study predator-prey interactions in wild ecosystems, for instance using simultaneous GPS tracking (e.g. Courbin et al., 2016; Creel et al., 2005), very few studies have applied these to investigate livestock-predator interactions (e.g. Valeix et al., 2012).

To address the paucity of information on seasonal livestock movements and habitat use in relation to the landscape of fear, we used GPS tracking devices to simultaneously record cattle (29 herds) and lion (six individuals) locations in Botswana's Okavango Delta for one year. We tested whether cattle habitat selection patterns were affected by the landscape of fear, i.e. if cattle were both capable of assessing predation risk by lions and responding to it in the same way that wild prey do. We expected cattle to show similar habitat selection patterns as buffaloes (*Syncerus caffer*) in the region (Sianga and Fynn, 2017; Sianga et al., 2017), i.e. strong seasonal shifts in habitat use corresponding with surface water availability in dry land areas and rainfall-driven grass growth in dry lands. Assuming that cattle are able to detect cues of recent lion presence (e.g. olfactory, vocalisations, encounters and depredation incidents), we also expected that cattle preference would decrease in areas recently (preceding 14 days) used by lions, even more so in less preferred habitats and during the night. Finally, we predicted that cattle should be more sensitive to recent lion presence while far away from human settlements (perceived as safe locations) and during dark nights.

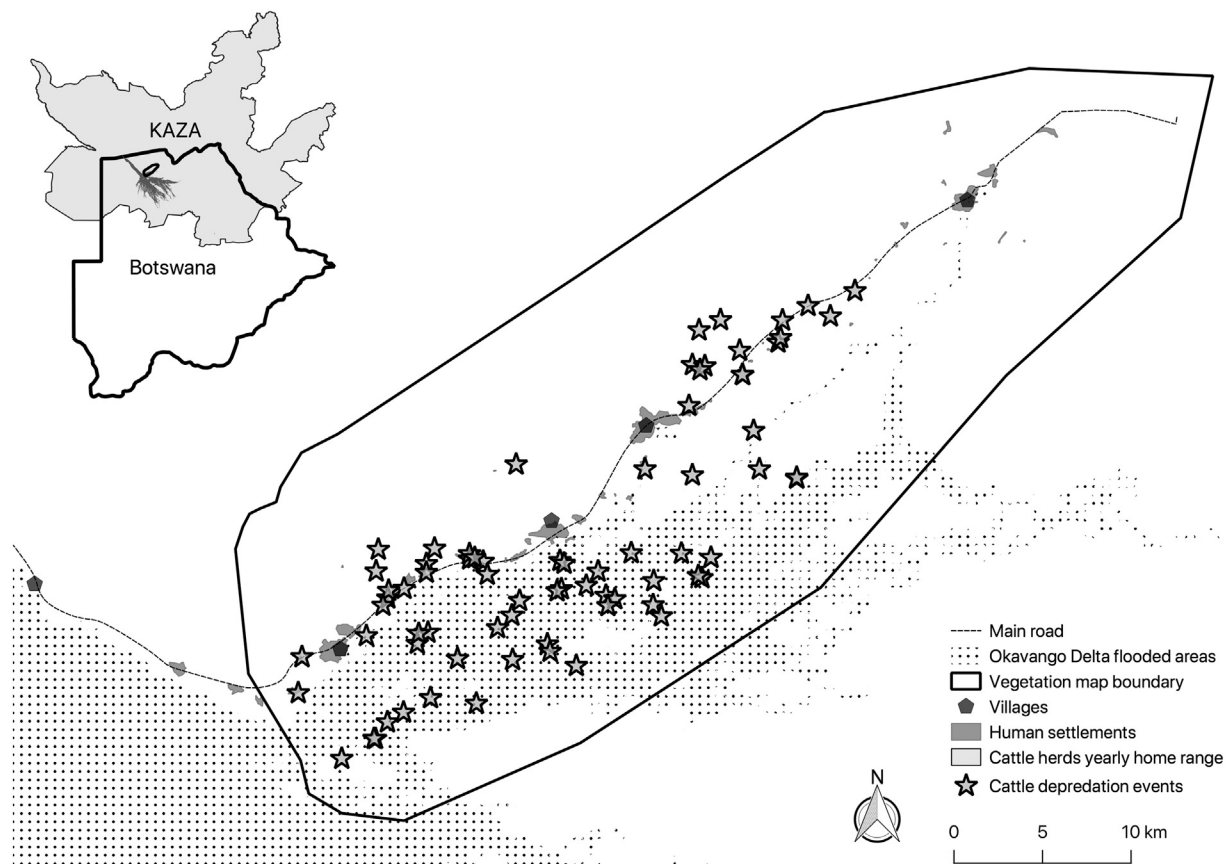


Fig. 1. Map of the study area in the Kavango Zambezi Transfrontier Conservation Area, showing the location of cattle home ranges in 2017, the extent of the vegetation map used and the location of cattle killed by lions between June 2016 and April 2018.

2. Methods and materials

2.1. Study area

We studied lions, cattle, and conflict across communities living at the boundary of NG/11 and NG/12 multi-use areas (settlement, cropping, livestock, and wildlife) located along the northern edge of Botswana's Okavango Delta (Fig. 1) in the Kavango Zambezi Transfrontier Conservation Area (KAZA TFCFA). A key factor for research significance is that the study region maintains critical functional heterogeneity of seasonal habitats for wild and domestic herbivores in the form of extensive floodplains dominated by key dry season forage species such as *Panicum repens*, *Oryza longistaminata* and *Vossia cuspidata*, with adjacent woodlands supporting high-quality grasses for wet season grazing (Fynn et al., 2015). In addition, the study area forms part of an international wildlife corridor, linking Okavango Delta wetlands with the vast interior woodlands extending into NG/13 and ultimately into Bwabwata, Mudumu and Mamili National Parks in Namibia. Thus, the area provides critical ecosystem connectivity that, if maintained, enhances the ecological functionality of the KAZA TFCFA.

Our study area comprised four villages, 44 cattle posts, and intermittent settlements with approximately 5000 residents. The main subsistence activities entail household-specific combinations of agro-pastoralism with small business, and most families subsist on < US\$500 per month. Non-consumptive wildlife tourism in NG/12 floodplains offers seasonal and permanent employment opportunities. Livestock is an important socio-cultural and economic commodity and official cattle numbers have risen from 6300 in 2006 to 11,100 in 2017 (Department of Veterinary Services, Seronga office) – we estimated a total population of approximately 16,500 cattle in 2017. Between October and March, the area receives between 500 mm and 750 mm rainfall

annually (Mendelsohn and el Obeid, 2004). The major dry land habitats in NG/11 are open to dense *Baikiaea-Burkea* woodlands, and mixed mopane (*Colophospermum mopane*) and *Burkea-Terminalia* woodlands on Kalahari Sandveld, whereas NG/12 is characterised by seasonally flooded grasslands and reed beds interspersed with riparian forest on islands (Mendelsohn and el Obeid, 2004; Pröpper et al., 2015; Sianga and Fynn, 2017). In 2017, floodplains were water-logged from January through June.

Across the entire study area, livestock move across unrestricted communal pastures where they coexist with indigenous ungulates such as plains zebra (*Equus quagga*) and blue wildebeest (*Connochaetes taurinus*) as well as an intact guild of large mammalian predators: lion, spotted hyaena (*Crocuta crocuta*), leopard (*P. pardus*), African wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*). Tswana beef cattle (a Sanga breed) are rarely herded (< 10%) and only irregularly confined during night hours (~40%; Weise et al., 2018). Such cavalier husbandry creates an ideal scenario for depredation by lions that cause about 87% of all regional livestock losses (Weise et al., 2018), affecting 67% of livestock owners and resulting in a mean annual loss of 4% of stock owned (Weise et al., 2019). Botswana's government compensates owners for predator-induced livestock losses – owners receive 100% compensation for losses to lions (Department of Wildlife and National Parks, 2003), albeit often with substantial delays (Weise et al., 2019). While lions were reported to kill only 11 cattle in 2010, compensation claims increased by 2300% to 264 cattle in 2017 (Department of Wildlife and National Parks, Seronga office). Despite compensation, lions continue to be persecuted indiscriminately (Weise et al., 2019). Following the nation-wide hunting moratorium in 2013 (Mbaiwa, 2018), the control and mitigation of conflict predominantly depends upon improved cattle husbandry and changes in human behaviour and risk management (Reddy et al., 2016). For these changes to be effective,

it will be imperative to understand the interactions of free-ranging lions and cattle.

Based on surface water levels and rainfall in 2017, we defined three seasons. The wet season was characterised by rising floods and heavy rains from January to April when seasonal pans in the northern part of the study area provided surface water. The early dry season lasted from May through August and was characterised by a progression from peak flooding to low flood levels in NG/12, no rains, cold winter temperatures, and the drying up of seasonal pans in the north. During the late dry season from September to December northern pans were dry, flood levels receded to the last permanent channels in NG/12 and mid-day temperatures consistently exceeded 30 °C. Apart from natural surface water provided by seasonal rains and flooding, there are no artificial waterholes in the area.

2.2. Cattle spatial data

Between January and December 2017, we deployed 28 SPOT Trace™ GPS tracking units on 42 domestic cattle (41 females, one male) from 29 herds (Table S1), representing herds from the four main villages and 18 geographically distinct cattle posts (Fig. 1). The replication of our sample units (29 herds) generated a statistically robust data set of seasonal cattle habitat use, exceeding Bolker et al.'s (2009) rule of thumb of at least six sample units per random effect.

Cattle tracking devices measured 8.7 cm (length) × 5.1 cm (width) × 2.1 cm (height), and weighed 88.0 g, or < 0.0003% of adult body weight (Fig. S1). We tagged cattle in their home kraals or at the community's cattle crush, with assistance from owners and herd men, and as part of routine husbandry procedures such as milking and health assessments, thus minimising the stress and discomfort from handling by unknown personnel. Due to the docility of cattle, we did not immobilise animals chemically. We inserted trackers into custom-made canvas pouches (< 30.0 g) that we attached to the animal's bell collar or around the horn base using soft cotton rope. This simple attachment protocol enabled rapid deployment while removing the necessity for additional collars. We attached pouches in a fashion that ensured an unobstructed interface of the tracker's GPS antenna with the sky (Fig. S1). We defined an immediate stopping rule in case tagged individuals exhibited signs of discomfort or apparent behavioural change such as excessive horning of vegetation, continued attempts to remove the trackers, or any sign of injury such as skin abrasion, laceration, or dipteran infestation resulting from tracker deployment. Owners and herd men monitored signs as part of their routine husbandry practices, also assisting with subsequent battery replacements, while the research team attempted to locate and assess cattle condition weekly. Monitoring had no influence on the herd's management regime. To give best representation of the entire herd's movements, we focussed GPS-tagging on lead cows (as identified by herd men) and, if this was not possible, randomly selected another adult female from the focal herd. We programmed trackers to record and relay GPS positions at hourly intervals, or, if trackers had been stationary for > 1 h, at first detection of movement via an in-built motion sensor. Because our analyses focus on locations instead of movements, variable time lags between successive fixes did not impact our results.

Across our study area, cattle were habituated to return to their home kraals around sunset. To prevent bias from periods in confinement and to focus on habitat selection during grazing times, we discarded any cattle GPS locations within village and cattle post boundaries (cf. Kuiper et al., 2015). Using 2016 Google Earth high resolution imagery, we mapped village and cattle post boundaries manually. Based on local sunrise and sunset times (http://aa.usno.navy.mil/data/docs/RS_OneYear.php), we assigned each cattle location to day or night time.

2.3. Environmental data

2.3.1. Habitat type

Following the vegetation classification and map (30 m × 30 m resolution) of Sianga and Fynn (2017), we mapped cattle, lion and conflict locations according to seven habitat types: *Acacia* grasslands, *Baikiaea* forests, Dry floodplains, Mopane woodlands (hereafter Mopane), Riparian woodlands (Riparian), Sandveld communities (Sandveld), and Wetlands. We discarded the positional data (used and random) of four cattle herds (Table S1) that ranged outside the vegetation map's boundaries as well as any other cattle locations beyond this.

2.3.2. Distance to water: MNDWI

We used satellite imagery from the Sentinel project Level 1C with a 10 m × 10 m resolution to compute monthly Modified Normalized Difference Water Index (MNDWI) to classify pixels as water (MNDWI > 0) or dry land (MNDWI ≤ 0). We calculated MNDWI with SNAP software v.5 (<http://step.esa.int/main/toolboxes/snap/>) using the following formula:
$$= \frac{\text{Green band (B3)} - \text{Mid Infra Red band (B12)}}{\text{Green band (B3)} + \text{Mid Infra Red band (B12)}}$$
. The study area overlapped with two tiles (34KFE and 34KGE, each 100 km × 100 km) and between two and seven images per tile were available for each month of 2017. When possible, we used images from the middle of each month (between the 10th and 20th) with least cloud cover. However, all images from January and March 2017 had extremely high cloud cover (93% - 100%) and we used the MNDWI value from February. Precipitation was very low in December 2016 (80.0 mm recorded in Shakawe, http://www.sasscalweather.net.org/weatherstat_monthly_we.php?loggerid_crit=68026) but high in January (224.2 mm), thus making February's value most representative of water distribution in January. Precipitation was also low in March (83.6 mm) and, therefore, unlikely to result in significantly modified surface water distribution since February. For other months with high cloud cover (February, June, and December), we identified each cloud and its shadow manually and discarded those pixels from calculations. Cloud-covered pixels and those in cloud shadow were assigned an MNDWI value of N/A. For each cattle location (used and random), we calculated the distance to the nearest water pixel's centre. Locations within water pixels were assigned a 0 m distance to water.

2.3.3. Moon illumination index

We assigned each cattle night time location (used and random) to a moon illumination index value ranging from 0 (new moon) to 1 (full moon) extracted from <http://aa.usno.navy.mil/data/docs/MoonFraction.php>. Regardless of moon phase, we set moon illumination to 0 if the moon was below the horizon at the time of the location fix.

2.3.4. Distance to the nearest human settlement (distance to safety)

Cattle may perceive permanent human settlements (i.e. cattle posts and villages) as safer, especially at night (Kuiper et al., 2015). However, since cattle are habituated to return to their homes in the evening, it is likely that they will be found closer to human settlement because of habituation rather than as a result of true habitat selection. We calculated the linear distance to the nearest human settlement (hereafter distance to safety) from the spatial file used to discard locations within cattle posts and villages boundaries.

2.3.5. Intensity of lion use

In 2016 and 2017, we tracked six adult lions (three females, three males, Fig. S2) from different prides and male coalitions via GPS Iridium satellite transponders. Telonics and Vectronic GPS transponders weighed < 1.5% of adult body weight and were equipped with automated drop-offs. During 2016, Telonics transponders recorded and transmitted five daily locations whereas Vectronic transponders fitted

Table 1

Model set. Note that the interaction between the intensity of lion use and moon illumination index were only included in the model including night time cattle data.

Hypothesis	Fixed effects included
1. Null	Intercept only
2. Only environmental variables affect cattle habitat selection	Habitat type + distance to water
3. Only predation risk variables affect cattle habitat selection	Distance to safety + intensity of lion use + distance to safety * intensity of lion use + intensity of lion use * moon illumination
4. Both environmental and predation risk variables affect cattle habitat selection	Habitat type + intensity of lion use + distance to safety + distance to water + distance to safety * intensity of lion use + habitat type * intensity of lion use + intensity of lion use * moon illumination

in December 2016 recorded and relayed positions every 2 h.

For each 10 m × 10 m pixel, we derived a proxy of cattle-lion encounter/predation risk by establishing an intensity of lion use index based on lion home ranges estimated with the Movement-based Kernel Density Estimator (movement kernel) with 5% increments (Calenge, 2006). We calculated movement kernels from lion locations within a 14-day period preceding a given cattle location (used and random). We defined the intensity of lion use as 100 minus the smallest (higher risk) lion 14-days kernel contour that overlapped with a given cattle location. For locations falling into home ranges of different lions, the intensity of lion use was assigned the smallest (i.e. higher risk) contour value. We then generated movement kernels using lion locations for 365 days preceding a given cattle location (used or random). Cattle locations falling outside any yearly and 14-day lion home range were discarded from the analyses. For one lion that died and two transponders that stopped transmitting we set intensity of lion use to N/A for any cattle location taken > 14 days after death or failure.

2.3.6. Livestock depredation locations

As part of a conflict mitigation programme, local cattle owners informed us about livestock depredation events by lions. Between June 2016 and April 2018, we directly investigated and verified 80 incidents, of which 75 overlapped with the vegetation map and were used in the analyses (Fig. 1).

2.4. Statistical analyses

We extracted, processed and analysed data with R version 3.4.5 (R Core Team, 2018) using packages *raster* (Hijmans, 2015), *maptools* (Bivand and Lewin-Koh, 2017), *rgeos* (Bivand and Rundel, 2017), *ade-habitatHR* (Calenge, 2006), *lme4* (Bates et al., 2015), *lmerTest* (Kuznetsova et al., 2017) and *MuMIn* (Bartoń, 2018).

2.4.1. Random location generation

For each cattle location, we generated an associated set of 15 random locations within the herd's 95% annual home range. Excluding locations within cattle posts and villages, we computed home ranges from the herd's complete dataset using fixed kernel density estimator and the reference smoothing factor h_{ref} as recommended by Hemson et al. (2005). We matched each of the 15 random locations to the same date and time as their associated GPS location and therefore the same season and day/night characteristics.

2.4.2. Cattle habitat preference

We first estimated cattle habitat preference by computing Jacobs' selection index (Jacobs, 1974): $D = \frac{r-p}{r+p-2p}$. Based on the proportion of each habitat used by cattle p and availability r , this index standardizes the relationship between the proportions of each habitat type available. D ranges from -1 (maximum avoidance) to $+1$ (maximum preference). We chose Jacobs' index because it minimises bias in preference estimation, especially with proportions < 10% (Jacobs, 1974). Jacobs' index was computed for each herd-season combination, and the proportion of each habitat available for a given herd was computed using random locations (see Section 2.4.1). We used Linear Mixed Models to test for seasonal variation in habitat preferences. The

interaction between season and habitat type was included as a fixed effect and herd identity as a random intercept. We tested for significant differences across factor levels using a post-hoc test. In addition, we tested for seasonal shifts in habitat preferences, fitting the same model to each habitat separately including only season as a fixed effect. Model assumptions were verified by plotting residuals against fitted values, against each model covariate, and against each covariate not included in the model as suggested by Zuur and Ieno (2016).

2.4.3. Cattle resource selection

We then estimated cattle Resource Selection Functions (RSFs) using Generalised Linear Mixed effects Models (GLMMs) with binomial error structure and a logit link for each season and for day and night locations separately. Herd identity was included as a random intercept in each model. We included habitat type, distance to water, distance to safety and intensity of lion use as main effects. Additionally, we included double interactions between habitat type and intensity of lion use, distance to safety and intensity of lion use, and moon illumination index and intensity of lion use. We standardised distance to water and distance to safety to assist with model convergence and parameter estimation. Data from herds with < 10 used locations for any day/night-season combination were removed from subsequent analyses. In the late dry season, cattle used only one location in *Baikiaea* forest and we, therefore, could not test for any interaction in this habitat type. Rather than removing this habitat and intensity of lion use from the final model, we chose to discard all locations (used and random) in this habitat type and computed the full model.

We created a set of four models (Table 1), each corresponding with a discrete hypothesis of which parameters may influence cattle habitat selection. We used Akaike Information Criterion with an exclusion threshold of $\Delta AIC < 2$ to select the model best fitting the data (Burnham and Anderson, 2002). We determined model fit using the Nagelkerke R^2 modified from GLMMs (Nakagawa and Schielzeth, 2013). We report the conditional R^2 value with its variance as computed by the delta method, which measures the response variable's variation as explained by the full model including both fixed and random effects. Finally, we used k -fold cross validation to test how well the model predicted the likelihood of cattle presence at a given location. We followed Boyce et al. (2002) using 80% of the data as a training set, with 100 repetitions, 10 probability bins and Spearman's rank correlation test to assess the model's ability to predict the likelihood of use from the training set. K -fold scores close to 1 indicate better predictive ability.

It has been cautioned that inclusion of colinear variables in a given model might lead to bias and uncertainty in parameter estimates (Zuur et al., 2010). However, Morrissey and Ruxton (2018) showed that correlation between variables does not necessarily lead to bias and that removing variables based on colinearity might indeed be “detrimental to most biological analyses”. We, therefore, retained all fixed effects present in the model best fitting the data. We assessed significant effect of parameters by generating 95% confidence intervals (CIs) using bootstrapping with 200 simulations.

2.4.4. Patterns of cattle depredation by lions

To determine whether distance to safety affected the probability of

cattle being killed by lions, we computed a RSF and Generalised Linear Models with binomial error structure, a logit link, and distance to safety (continuous variable) as the explanatory variable. We computed models separately for each season. Using AICs, we compared this model to the null model including only the intercept. To estimate lion preference patterns for killing cattle in terms of habitat type, we used Jacobs' selection index with r defined as the proportion of cattle depredation locations in each habitat type and p as the proportion of cattle GPS locations recorded in each habitat type (cf. Kuiper et al., 2015). As most depredation events occurred at night (61.3%, $n = 49$), we defined availability of habitat type and distance to safety using cattle night locations for both the RSF and Jacobs' index computations.

3. Results

3.1. Cattle habitat preference

We analysed a total of 13,894 wet season, 9981 early dry season and 20,927 late dry season cattle GPS locations, as well as their 672,045 associated random locations. When compared to the proportion of each habitat type available, cattle exhibited higher use of *Acacia* grasslands during all seasons, with a significant preference during the late dry season when compared with the wet season (Table 2). Based on availability, Dry floodplains were also used more than expected (Fig. 2), with a significant selection during wet and early dry seasons compared with the late dry season (Table 2). The use of Wetlands showed a strong seasonal trend and increased progressively during the year, from less than expected to more than expected, and as seasonal water pans dried up (Fig. 2, Table 2). Cattle used Mopane habitat less than expected during both dry seasons, but more than expected during the wet season. A significant difference, however, only occurred between the wet and early dry season (Fig. 2, Table 2). Cattle used *Baikiaea* forests and Sandveld communities less than expected during all seasons and we found no patterns for Riparian habitat use (Fig. 2, Table 2).

Cattle were found closer to human habitation during both day and night in the wet season when grazing grounds and surface water were available in the immediate vicinity of settlements (Table 3). Conversely, cattle grazed further from settlements and surface water as the dry season progressed (Table 3), reflecting the depletion of grasses around human habitation and the drying up of seasonal water pans in the North, thus limiting access to drinking water to the last wetlands in NG/12 floodplains.

3.2. Cattle resource selection

After removal of cattle locations (used and random) falling outside any yearly lion home range and of herds with < 10 used locations in *Baikiaea* habitats (both used and random) during the late dry season, the positional data used in RSF analyses comprised of 2496 (48,164

random), 3387 (57,159 random) and 10,384 (150,955 random) locations during the wet, early dry and late dry seasons respectively. In all cases, the full model including both environmental and predation risk related variables yielded a better data fit than other models (all $\Delta AICs > 2$, Table S2).

3.2.1. Day time habitat selection

Day time model fit (R^2) and ability to predict accuracy (k -fold cross validation scores) ranged from low in the wet season to medium support in the late dry season. The intensity of lion use affected habitat selection differently in all three seasons (Table S3, Fig. 3). The intensity of lion use had a consistent negative effect (except for Mopane during the wet season), although with varying intensity that depended on season and habitat. During the wet season, Sandveld was the preferred grazing habitat at low intensity of lion use (< 15), whereas Mopane was preferred at higher intensity of lion use > 15 (Fig. 3a). During the early dry season, cattle preferred Dry floodplains and *Acacia* grasslands, with an intensity of lion use > 10 (Fig. 3b). Cattle preference was less sensitive to the intensity of lion use in these preferred habitats. During the late dry season, Wetlands was the preferred habitat at all levels of intensity of lion use, which exerted a weaker negative effect on this habitat type (Fig. 3c). During the wet and the late dry seasons, cattle selected for locations close to water, whereas this covariate had no effect during the early dry season (Table 2, Fig. 4).

Only during the dry seasons was cattle preference for locations close to safety (Table 3) differently affected by the intensity of lion use (Fig. 5). While the intensity of lion use positively affected selection far from safety during the early dry season, the opposite was true during the late dry season (Fig. 5), with a weak effect, however.

3.2.2. Night time habitat selection

Patterns of night-time habitat preference differed between seasons and were affected by the intensity of lion use (Table S3, Fig. 3). In the wet season, Mopane was the preferred habitat from low to medium intensity of lion use and Sandveld became the preferred habitat at high intensity of lion use (Fig. 3d). During the early dry season, cattle preferred *Acacia* grasslands and Mopane over all other habitats (Fig. 3e). During the late dry season, Mopane was avoided and Riparian, Wetlands and *Acacia* grasslands habitat were preferred. In both Riparian habitat and *Acacia* grasslands, the intensity of lion use had a positive effect on selection strength (Fig. 3f).

Cattle preference for locations close to water was consistent during the late dry season, but this pattern reversed during the wet season (Fig. 4). Distance to water also had a statistically significant negative effect on selection strength during the early dry season, albeit a weak one. Cattle preferred locations close to safety and this was affected differently by the intensity of lion use across the three seasons. During wet and early dry seasons, selection strength of locations close to safety decreased with increasing intensity of lion use, but it strongly increased

Table 2

Seasonal differences in Jacobs' selection index for each habitat type. Dark grey and light grey cells indicate significantly positive and negative differences respectively.

Habitat type	Early dry vs. late dry	Early dry vs. wet	Late dry vs. wet
Acacia grasslands	0	0	– (p=0.049)
Baikiaea forests	0	0	0
Dry floodplains	+ (p=0.042)	0	– (p=0.031)
Mopane	0	– (p=0.007)	0
Riparian	0	0	0
Sandveld	0	0	0
Wetland	– (p=0.002)	+ (p=0.009)	+ (p<0.0001)

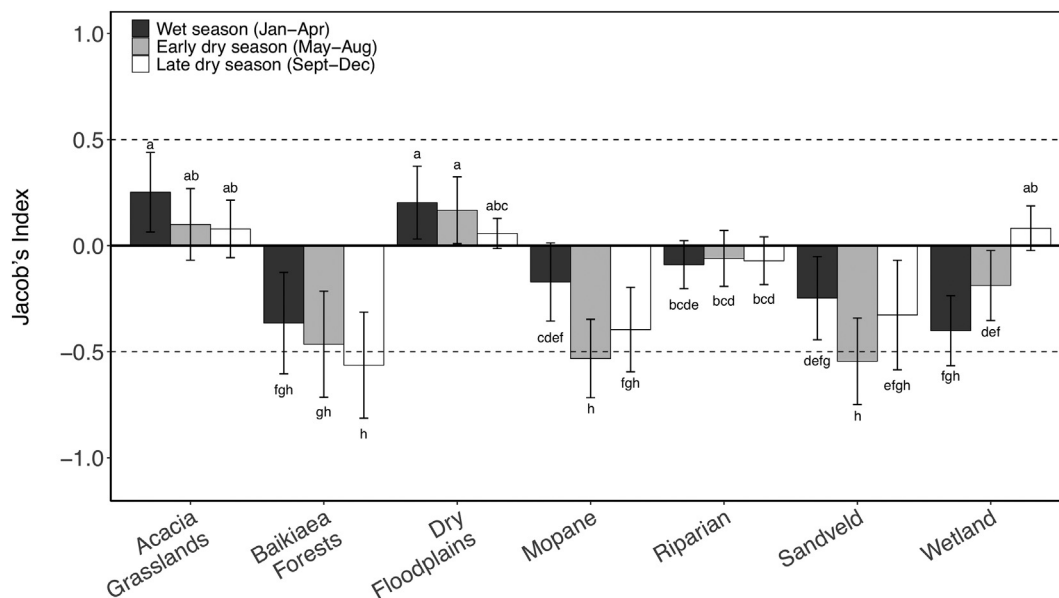


Fig. 2. Cattle habitat use (a) and Jacobs' selection index (b) during the three seasons compared to their availability (derived from random locations) across the study area. Jacobs' index was computed as the average across all herds and error bars show 95% CIs. Letters indicate significant differences.

during the late dry season (Fig. 5). Only during the wet season was the effect of intensity of lion use on location selection affected by night brightness (i.e. moon illumination index). The intensity of lion use had a more pronounced negative effect on selection strength during dark, new moon nights when compared with bright, full moon nights (Fig. 6).

3.3. Spatial patterns of cattle depredation by lions

We recorded 30, 23 and 22 lion depredation events during the wet, early dry and late dry season respectively. Jacobs' index yielded a clear effect of habitat type on the probability of cattle being killed by lions (Fig. 7). Lions did not kill cattle in *Baikiaea* forests and Sandveld. Lions significantly preferred killing cattle in Wetlands during the wet and the late dry seasons. GLMs showed that the effect of distance to safety was significant and positive during all seasons, albeit weaker during the early dry season (wet: 0.0007 ± 0.0001 , $p < 0.001$; early dry: 0.0004 ± 0.0001 , $p = 0.005$; late dry: 0.001 ± 0.0001 , $p < 0.001$). The probability of cattle being killed strongly increased > 4 km from the nearest settlement (Fig. 8). The two patterns might be interlinked as cattle found in Wetlands were far from permanent human settlements (Table S4).

4. Discussion

4.1. Cattle habitat selection patterns

In the northern Okavango Delta, cattle habitat selection patterns were strongly impacted by seasonal changes. Cattle used rangelands according to nutritional requirements, irrelevant of the associated predation risk. Their selection patterns shifted throughout the year following the distribution of the most profitable habitats and surface

water availability. While Wetlands were preferred during the dry season, dry woodlands (Mopane, *Acacia* grasslands and Sandveld) where dominant grasses are more digestible and nutritious were preferred during the wet season when water is available in seasonal pans. Similar to buffalo in the region (Sianga and Fynn, 2017; Sianga et al., 2017), these seasonal habitat selection patterns are driven by the changing distribution of water and forage resources.

High quality, digestible grasses, such as *Digitaria eriantha*, *Panicum maximum* and *Urochloa trichopus* are most abundant in the mosaic of Sandveld communities and Mopane woodlands, together with water in seasonal pans during the wet season (Sianga and Fynn, 2017), providing better energy and protein intake than tougher, less digestible grasses in wetlands (Hopcraft et al., 2010). Saline soils in Mopane woodland (Romanens, 2017) probably provide an essential supply of minerals to pregnant and lactating females through mineral-enriched grasses and drinking water in pans (Murray, 1995; Grant & Scholes, 2006). During the dry season, however, Wetlands with their gradients of flood depth and duration retain soil moisture during the dry season, enabling production of green forage and providing critical access to drinking water and adequate-quality grazing (Hopcraft et al., 2010; Fynn et al., 2015). Across Africa, herbivores follow receding floods to deeper flooded areas as the dry season progresses (Fynn et al., 2015). This pattern is consistent with cattle moving longer distances during the dry season (Weise et al., 2018) in search of water and grazing grounds.

While preference patterns were affected in similar ways by both distance to safety (cf. Valeix et al., 2012; Kuiper et al., 2015) and water between day and night, cattle exhibited slight variations in terms of habitat preferences during the two dry seasons. *Acacia* grasslands were preferred during the day in the early dry season, whereas Mopane was preferred during the night. In the late dry season, Wetlands was least selected for at night, but it was the preferred habitat during the day.

Table 3
Average seasonal distance of cattle GPS locations to the nearest human settlement and surface water in 2017.

	Wet season (January–April)		Early dry season (May–August)		Late dry season (September–December)	
	Day	Night	Day	Night	Day	Night
Distance to nearest human settlement	1440 m	616 m	2448 m	1278 m	2822 m	979 m
Distance to water	348 m	718 m	430 m	762 m	807 m	1675 m

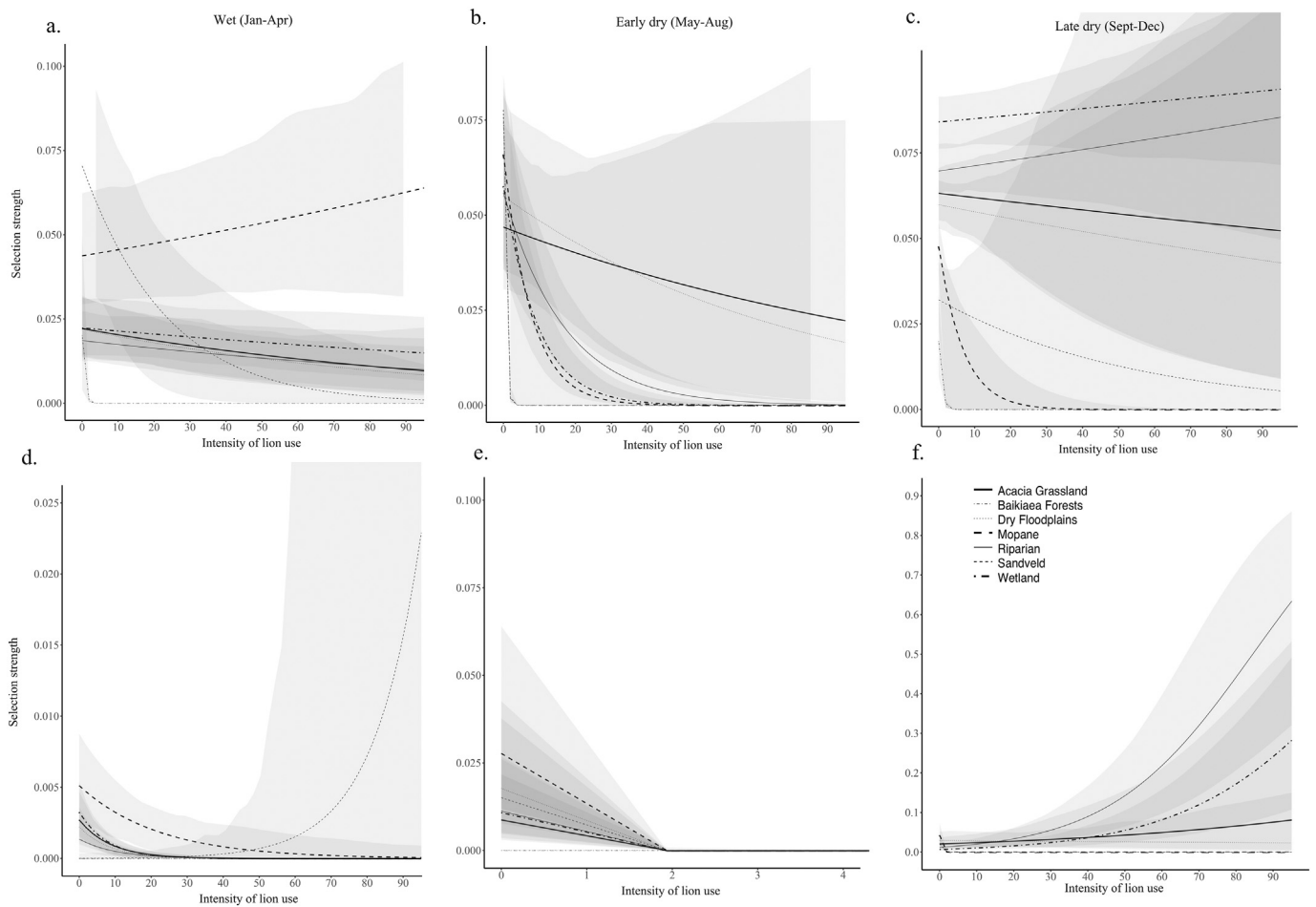


Fig. 3. Effects of the interactions between habitat type and intensity of lion use on cattle habitat selection strength during day (a–c) and night (d–f) across the three seasons. Grey ribbons represent 95% CIs. Note that Baikiaea forests were not considered during the late dry season due to only one used cattle location in this habitat.

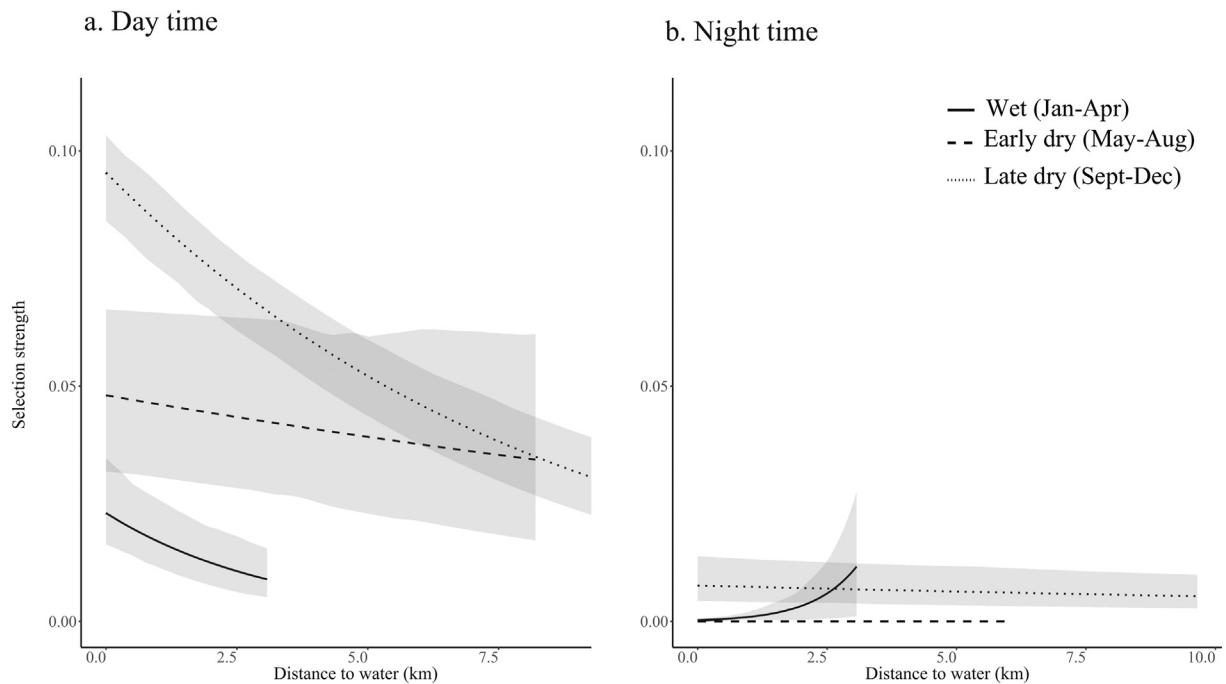


Fig. 4. Effect of distance to water on cattle habitat selection strength during day and night across the three seasons. Grey ribbons represent 95% CIs.

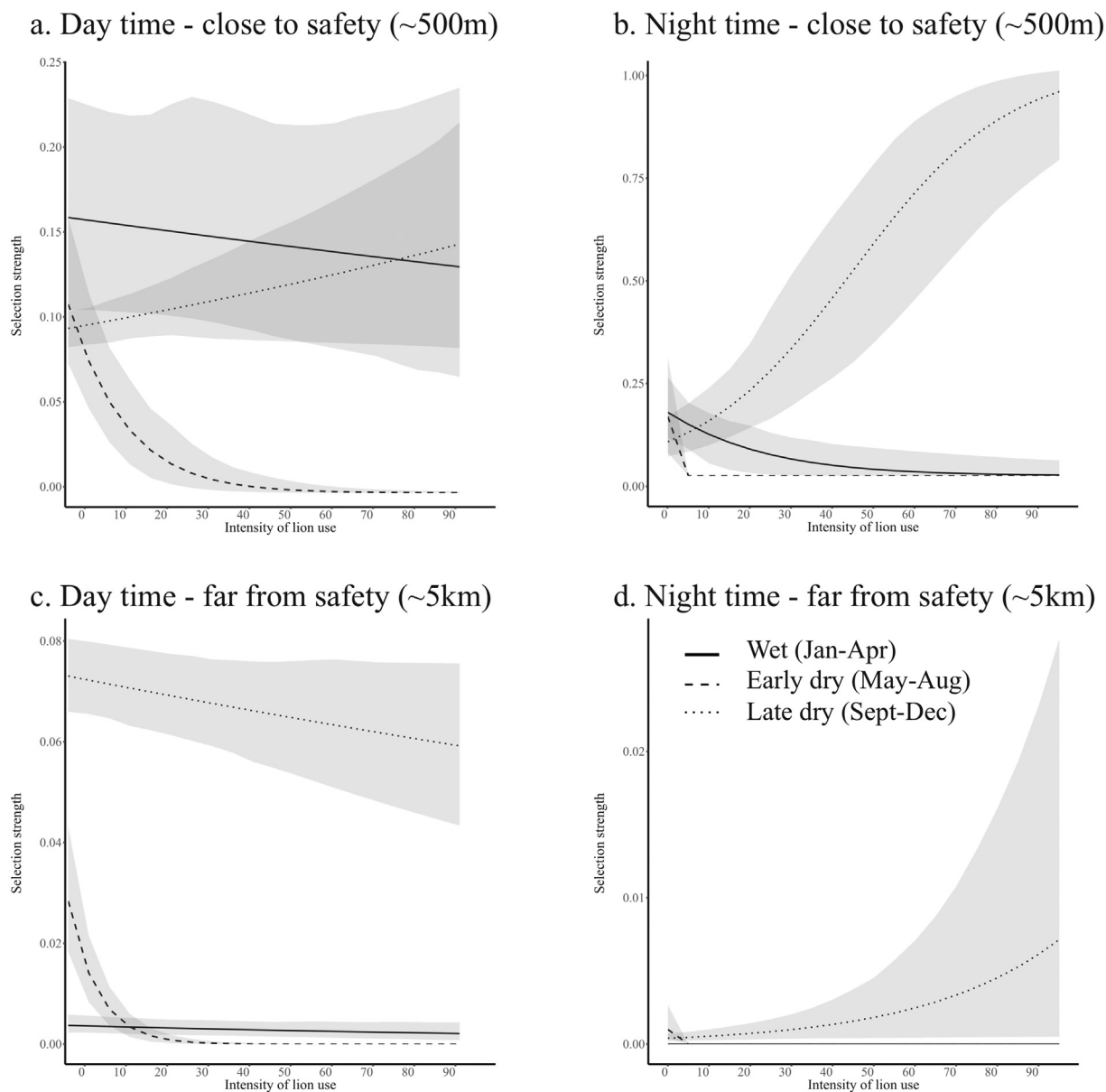


Fig. 5. Effect of distance to safety (i.e. proximity to cattle post or village) on cattle habitat selection strength during day (a) and night (b) across the three seasons. Grey ribbons represent 95% CIs.

Despite removing all cattle locations in villages and cattle posts from the analyses, these contrasting patterns likely reflect habitual returns to human settlements. While cattle graze and ruminant in remote pastures during the day, they mostly rest and remain stationary at night. Hence, we expected cattle to be more selective about their foraging habitat during the day, favouring the best grazing grounds.

4.2. Cattle landscape of fear

Based on the spatiotemporal scales we used to characterise potential predation risk, we conclude that free-ranging Tswana cattle in our study area did not perceive and/or respond strongly to a landscape of fear with frequent depredation by lions. We found that cattle habitat selection was only mildly influenced by the recent presence of lions, even though lions exhibited a clear preference in terms of the habitat where they killed cattle; i.e. mainly in Wetlands. Although the interaction between habitat type and intensity of lion use was statistically significant during the wet and early dry seasons, and also more pronounced in less preferred habitats, the strength of this effect was

insufficient for cattle to avoid the best grazing habitats with higher risk in favour of less profitable ones. Contrary to their wild ungulate counterparts (e.g. elk, *Cervus elaphus*, Creel et al., 2005; several African ungulates, Valeix et al., 2009), cattle neither seemed to avoid risky places nor risky habitats where lions were most active and depredation was highest. In Zimbabwe, seasonal use of wooded habitats distant to villages and close to protected area boundaries increased cattle vulnerability to lion depredation (Kuiper et al., 2015). This apparent lack of fear may result from the process of domestication, during which cattle were specially protected by humans and, therefore, are no longer exposed to the evolutionary selection pressures induced by predation, resulting in a naïve response to lion presence. The absence of a cattle landscape of fear bears strong implications for the future management of depredation by lions because cattle owners cannot rely on an instinctive avoidance response to predation risk by free-ranging cattle. In Botswana, lions preferentially prey upon wild herbivores when these are present; however, resident lions do not follow migratory ungulates and switch to abundant and readily available cattle near protected area boundaries in periods of wild herbivore scarcity (Valeix et al., 2012).

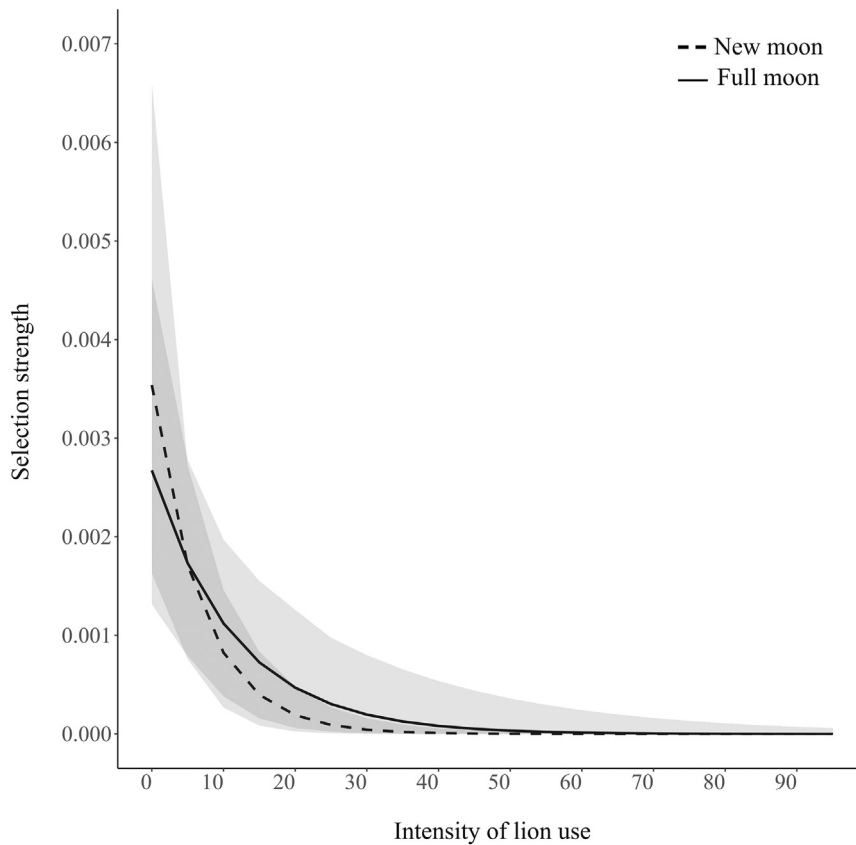


Fig. 6. Effect of interactions between night brightness (i.e. moon illumination index) and intensity of lion use on cattle habitat selection strength at night during the wet season. Grey ribbons represent 95% CIs.

We also found that cattle always preferred locations closer to human settlements. Our assumption was that these locations should be perceived as safer in terms of predation risk. In similar studies, cattle grazing close to villages benefitted from the proximity of people, resulting in a lower incidence of lion depredation (Kuiper et al., 2015) as lions generally avoided the proximity of people, killing cattle afar,

while also adjusting their activity and movements to avoid direct encounters with people (Valeix et al., 2012). Indeed, lions tended to kill cattle farther away from settlements. However, it remains speculative whether this represents a true pattern of habitat selection, or rather an effect of cattle habituation. Even though cattle were rarely herded or corralled (Weise et al., 2018), they are trained to return to home

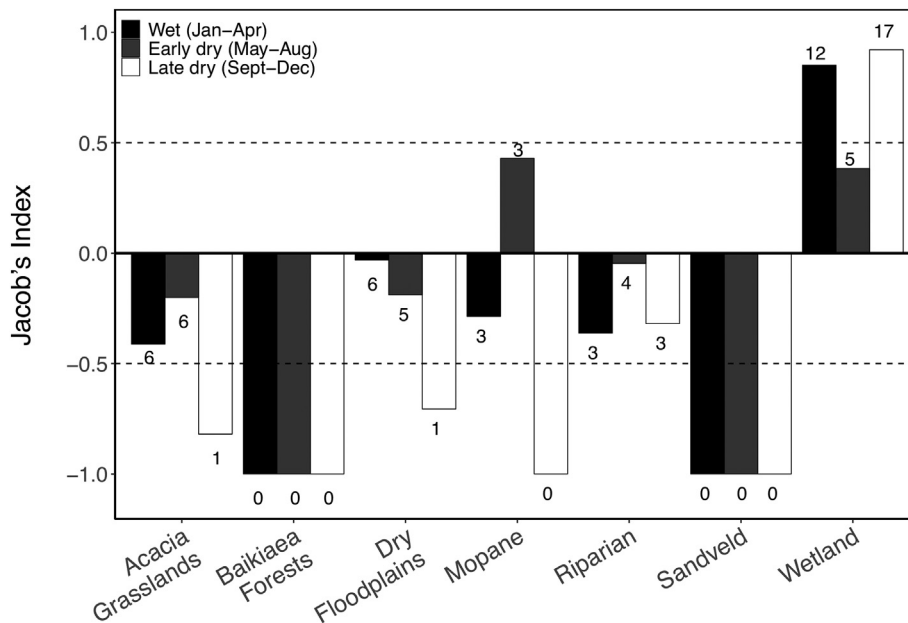


Fig. 7. Lion habitat preferences (Jacob's index) for cattle predation during the wet, early dry and late dry season in 2017. Values indicate the number of records in each habitat type.

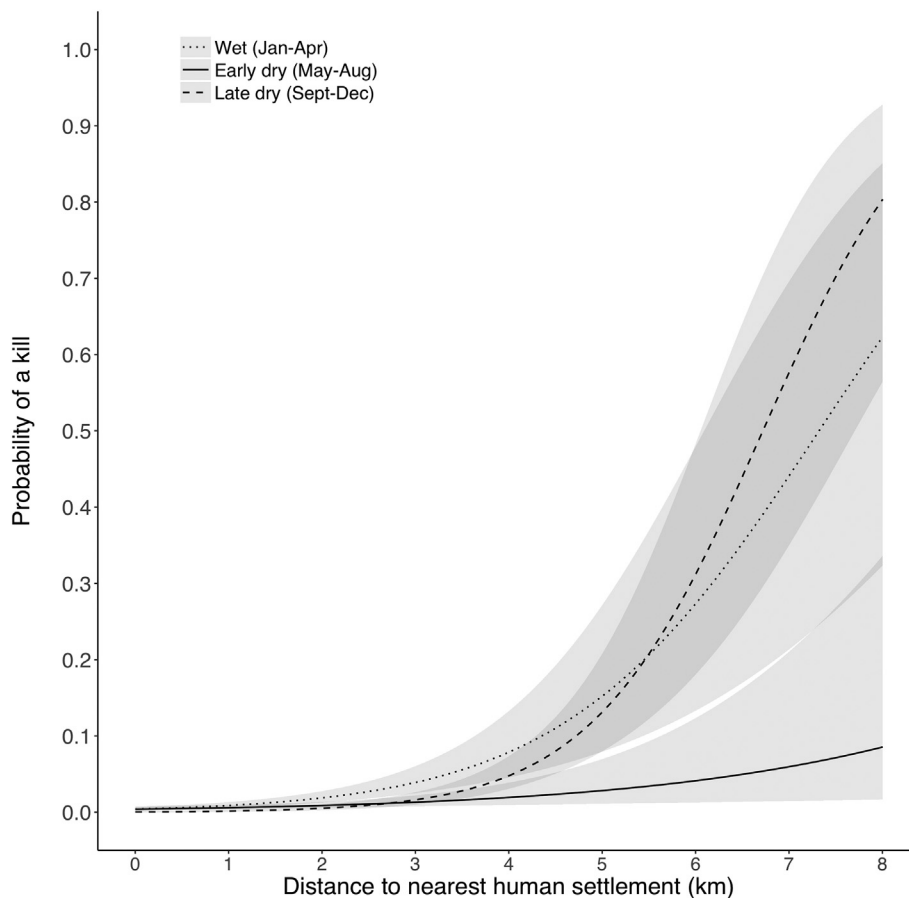


Fig. 8. Effect of distance to nearest human settlement on the probability of lion killing cattle during the wet (dotted line), early dry (dashed line) and late dry (solid line) season in 2017. Grey ribbons represent 95% confidence intervals.

enclosures in the evening. An apparent selection for grazing close to human settlements might, therefore, reflect the repetitive movement to and from corrals, resulting in higher detection rates close to settlements. This is supported by the fact that the interaction between distance to safety and intensity of lion use was only significant during dry season days, unlikely affecting selection strength significantly.

We expected cattle to respond to ambient light levels like wild ungulates (Palmer et al., 2017) and to avoid locations with high intensity of lion use during new moon nights when lion hunting success is highest (Funston et al., 2001). We did observe such an effect during the wet season, but, given its weakness, we question its biological significance.

4.3. Study limitations

The apparent absence of a landscape of fear response in cattle might be due to the coarse spatiotemporal scale we used to characterise predation risk. We cannot rule out its existence at more granular scales. By employing a 14 days proxy for encounter and predation risk, it is plausible that lions had already left used cattle areas identified as risky. It is also plausible that cattle might only respond to the immediate presence of lions, in which case the landscape of fear manifests at a finer scale. While several prey species have been shown to respond to long term predation risk by lions (Valeix et al., 2009), many also adjust their behaviour to the actual presence of predators in their vicinity (Périquet et al., 2010) or following recent encounters (Courbin et al., 2016). Opportunistic field observations ($n = 7$) of cattle-lion encounters showed that cattle instantly increased vigilance, stopped feeding, and refused to approach lions when detecting their olfactory cues in the immediate vicinity (< 300 m distance), warranting additional research into this topic at refined spatiotemporal scales.

With only six lions equipped with GPS transponders we caution that interactions with un-collared lions likely were obscured. Used cattle positions classified as low risk may have been located in the core home range of unmonitored lions. Valeix et al. (2012) demonstrated that lion space use differed between periods of wild prey abundance and scarcity, influencing the frequency of lion encounters with livestock. While we cannot estimate the frequency of such events, unknown interactions are unlikely to have biased our results significantly as these would have masked a potential response rather than created one, rendering our results conservative. However, our small sample size in terms of lion GPS locations resulted in a small number of used cattle locations in *Baikiaea* forests with a high intensity of lion use. This might explain the peculiar avoidance of this habitat by cattle in different seasons.

Our statistical approach yielded low values for model fits and also low predictive accuracy scores from cross-validation. Low model fit scores likely resulted from system complexity and our failure to measure interacting components at finer resolutions. While our results probably reflect true biological patterns, models with weak fit scores provide less reliable inference, limiting our ability to predict cattle habitat selection patterns.

5. Conclusion: conservation implications

Our study region is characterised by well-developed functional habitat heterogeneity in the form of extensive wetlands, which provide important dry season foraging options, and woodlands, which provide important wet season foraging options. This combination provides optimal adaptive foraging options over the annual cycle for wild and domestic herbivores (Fryxell and Sinclair, 1988; Fynn et al., 2015; Hopcraft et al., 2010). The functional nature of wetlands with their

abundance of dry season key resources (reliable green forage and water) is demonstrated by seasonal livestock movements and habitat selection. Cattle are effectively utilizing functional habitat heterogeneity, similar to buffalo in the region (Sianga and Fynn, 2017). Considering that the frequency and severity of drought events is predicted to increase under global change (Hoerling et al., 2004), continued, but controlled, access to extensive wetlands will be critical for the long-term well-being of livestock owners in the region.

The factors discussed above need to be carefully considered when developing herding strategies and measures to mitigate the conflict between lions and livestock owners. Our results clearly demonstrate that the greatest predation of cattle occurs in wetlands far from settlements, probably because most of the Okavango Delta is protected, providing a core reservoir for a significant lion population (Riggio et al., 2013). A seemingly obvious solution would be to develop boreholes in the northern woodlands so that cattle can remain away from wetlands and their associated higher concentrations of lions all year round. However, woodlands do not provide reliable green forage and drinking water throughout the year; cattle deprived of these critical resources would likely lose condition much more than those with access to wetlands. During drought years, much greater mortality could be expected for those cattle without access to key wetland resources (Illius and O'Connor, 2000; Owen-Smith, 2004). Therefore, it is unlikely that restricting livestock to woodland habitats can provide a sustainable solution to the severe lion-livestock conflict in the area. Instead of separating livestock from lions, minimising depredation by lions will best be achieved by a combination of resource- and predation-cognisant seasonal herding strategies with vigilant livestock herding and night-time corralling (see also Valeix et al., 2012; Kuiper et al., 2015; Weise et al., 2018). Together, these strategies provide several advantages: (1) cattle depredation by lions can be greatly reduced; and (2) holistic rangeland management strategies can be implemented to improve rangeland condition and livestock performance (Odadi et al., 2017; Odadi et al., 2018). Mobile corrals may be necessary to facilitate safe cattle confinement in areas with the best seasonal forage, thus also greatly reducing cattle energy expense from walking long distances between a permanent corral and the best foraging sites (Odadi et al., 2018). When cattle are herded and their spatial distribution is managed to create functional heterogeneity in the form of short and tall grassland, both wildlife and livestock benefit (Fynn et al., 2016; Tyrrell et al., 2017). Moreover, traditional herding with night-time corralling creates long-lasting nutrient hotspots that produce high-quality forage, attract wildlife, and increase spatial heterogeneity (Marshall et al., 2018). Conversely, strategies that attempt to minimise conflict by separation of livestock and wildlife are inherently flawed in that they result in ecosystem fragmentation (e.g. by fencing) and loss of access to functional heterogeneity for both wildlife and livestock (Fynn et al., 2016).

While livestock access to critical seasonal resources clearly is important to ensure the long-term well-being of communities living in and around conservation areas, the process needs to be managed in a sustainable fashion. For example, commodity-based trade of free-range cattle could provide an important value-added market outlet for local beef, with associated improvement in economic security of cattle owners. Limiting the number of livestock in this ecologically sensitive area requires determination of carrying capacities and maximum stocking rates that acknowledge regional variability in rainfall and primary production. In the northern Okavango Delta, cattle access to seasonal wetlands also needs to be facilitated in a manner that is compatible with tourism in one of Africa's prime wildlife viewing areas. Under a herding strategy that aims to improve rangeland condition and functional habitat heterogeneity in pastoral areas and wildlife corridors (Fynn et al., 2016; Marshall et al., 2018; Odadi et al., 2017; Odadi et al., 2018; Tyrrell et al., 2017), the potential for maintenance of wildlife range well beyond the boundaries of protected areas is greatly increased. Simple and straightforward improvements in cattle husbandry

together with implementation of holistic rangeland management strategies that improve habitat condition and functional heterogeneity could help facilitate the coexistence of people and their livestock with lions, while promoting the rural development and biodiversity conservation objectives of the KAZA TFCA. Herded cattle can be marketed as value-added, wildlife-friendly beef to safari lodges under a conservation agreement with the tourism industry. Major safari company managers in Botswana have already committed to buying beef from herding programs at higher prices, having recognized the conservation value of range-fed beef, now known to have health advantages over the grain-fed animals common to western societies (Provenza et al., 2019). We emphasise that wildlife-friendly beef can be a key strategy for developing cattle herding programs around protected areas in Africa.

Understanding the ecological constraints that intensify conflict is pertinent to any livestock production landscape with predator presence. It is also a central prerequisite for future land use planning and devolution of legal, but controlled, resource access rights through policy. Coexistence strategies must account for the strong reliance of people, their livestock, and wildlife on shared key resources. This is particularly important in large trans-frontier conservation areas where the successful merging of biodiversity conservation and rural development is a strategic goal. Omission will foster resentment and resistance to coexistence with apex predators, particularly if livestock productivity and human livelihoods are negatively affected.

Declaration of Competing Interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.06.031>.

References

- Andersson, J., de Garine-Wichatitsky, M., Cumming, D., Dzingirai, V., Giller, K., 2013. *Transfrontier Conservation Areas: People Living on the Edge*. Routledge, London & New York.
- Baker, P.J., Boitani, L., Harris, S., Saunders, G., White, P.L., 2008. Terrestrial carnivores and human food production: impact and management. *Mammal Rev.* 38 (2&3), 123–166. <https://doi.org/10.1111/j.1365-2907.2008.00122.x>.
- Bartoń, K., 2018. MuMIn: Multi-Model Inference. Retrieved from. <https://CRAN.R-project.org/package=MuMIn>.
- Bates, D.M., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48 doi:arXiv:1406.5823.
- Bivand, R.S., Lewin-Koh, N., 2017. mapproj: Tools for Reading and Handling Spatial Objects (Version 0.9-2).
- Bivand, R.S., Rundel, C., 2017. rgeos: Interface to Geometry Engine - Open Source ('GEOS') (Version 0.3-26).
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24, 127–135. <https://doi.org/10.1016/j.tree.2008.10.008>.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K., 2002. Evaluating resource selection functions. *Ecol. Model.* 157, 281–300.
- Burnham, K., Anderson, D., 2002. *Model Selection and Multimodal Interference: A Practical Information-Theoretic Approach*, 2nd edition. Springer, New York, USA.
- Calenge, C., 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* 197, 516–519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>.

- Christianson, D.A., Creel, S., 2010. A nutritionally mediated risk effect of wolves on elk. *Ecology* 91, 1184–1191. <https://doi.org/10.1890/09-0221.1>.
- Courbin, N., Loveridge, A.J., Macdonald, D.W., Fritz, H., Valeix, M., Makuwe, E.T., Chamailé-Jammes, S., 2016. Reactive responses of zebras to lion encounters shape their predator–prey space game at large scale. *Oikos* 125, 829–838. <https://doi.org/10.1111/oik.02555>.
- Creel, S., Winnie, J., 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Anim. Behav.* 69, 1181–1189. <https://doi.org/10.1016/j.anbehav.2004.07.022>.
- Creel, S., Winnie, J., John, A., Maxwell, B., Hamlin, K., Creel, M., 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86, 3387–3397. <https://doi.org/10.1890/05-0032>.
- Department of Wildlife and National Parks, 2003. Compensation Guidelines for Damages Caused by Elephants and Lion. Department of Wildlife and National Parks, Ministry of Environment, Wildlife and Tourism, Gaborone, Botswana.
- Droge, E., Creel, S., Becker, M.S., M'Soka, J., 2016. Spatial and temporal avoidance of risk within a large carnivore guild. *Ecol. Evol.* 7, 189–199. <https://doi.org/10.1002/ece3.2616>.
- Fryxell, J.M., Sinclair, A.R.E., 1988. Causes and consequences of migration by large herbivores. *Trends Ecol. Evol.* 3, 237–241. [https://doi.org/10.1016/0169-5347\(88\)90166-8](https://doi.org/10.1016/0169-5347(88)90166-8).
- Funston, P.J., Mills, M.G.L., Biggs, H.C., 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. *J. Zool.* 253, 419–431. <https://doi.org/10.1017/S0952836901000395>.
- Fynn, R.W.S., Bonyongo, M.C., 2011. Functional conservation areas and the future of Africa's wildlife. *Afr. J. Ecol.* 49, 175–188. <https://doi.org/10.1111/j.1365-2028.2010.01245.x>.
- Fynn, R.W.S., Murray-Hudson, M., Dhliwayo, M., Scholte, P., 2015. African wetlands and their seasonal use by wild and domestic herbivores. *Wetl. Ecol. Manag.* 23, 559–581. <https://doi.org/10.1007/s11273-015-9430-6>.
- Fynn, R.W.S., Augustine, D.J., Peel, M.J.S., de Garine-Wichatitsky, M., 2016. Strategic management of livestock to improve biodiversity conservation in African savannahs: a conceptual basis for wildlife–livestock coexistence. *J. Appl. Ecol.* 53, 388–397. <https://doi.org/10.1111/1365-2664.12591>.
- Grant, C., Scholes, M., 2006. The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biol. Cons.* 130, 426–437.
- Harrington, R., Owen-Smith, N., Viljoen, P.C., Biggs, H.C., Mason, D.R., Funston, P.J., 1999. Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biol. Conserv.* 90, 69–78. [https://doi.org/10.1016/S0006-3207\(98\)00120-7](https://doi.org/10.1016/S0006-3207(98)00120-7).
- Harris, G., Thirgood, S., Hopcraft, J.G.C., Croomsight, J., Berger, J., 2009. Global decline in aggregated migrations of large terrestrial mammals. *Endanger. Species Res.* 7, 55–76. <https://doi.org/10.3354/esr00173>.
- Haswell, P.M., Jones, K.A., Kusak, J., Hayward, M.W., 2018. Fear, foraging and olfaction: how mesopredators avoid costly interactions with apex predators. *Oecologia* 187, 573–583. <https://doi.org/10.1007/s00442-018-4133-3>.
- Hemson, G., Johnson, P., South, A., Kenward, R.E., Ripley, R., Macdonald, D.W., 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *J. Anim. Ecol.* 74, 455–463. <https://doi.org/10.1111/j.1365-2656.2005.00944.x>.
- Hijmans, R.J., 2015. raster: Geographic Data Analysis and Modeling (Version 2.5-2).
- Hoerling, M.P., Hurrell, J.W., Xu, T., Bates, G.T., Phillips, A.S., 2004. Twentieth century North Atlantic climate change. Part II: understanding the effect of Indian Ocean warming. *Clim. Dyn.* 23, 391–405. <https://doi.org/10.1007/s00382-004-0433-x>.
- Hopcraft, J.G.C., Olf, H., Sinclair, A.R.E., 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends Ecol. Evol.* 25, 119–128. <https://doi.org/10.1016/j.tree.2009.08.001>.
- Igoe, J., 2004. Conservation and Globalization: A Study of National Parks and Indigenous Communities From East Africa to South Dakota. Thomson Learning, London and Belmont, California.
- Illius, A.W., O'Connor, T.G., 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecol. Appl.* 9, 798–813. [https://doi.org/10.1890/1051-0761\(1999\)009\[0798:OTRONC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[0798:OTRONC]2.0.CO;2).
- Illius, A.W., O'Connor, T.G., 2000. Resource heterogeneity and ungulate population dynamics. *Oikos* 89, 283–294. <https://doi.org/10.1034/j.1600-0706.2000.890209.x>.
- Jacobs, J., 1974. Quantitative measurement of food selection. *Oecologia* 14, 413–417. <https://doi.org/10.1007/BF00384581>.
- Kansky, R., Kidd, M., Knight, A.T., 2014. Meta-analysis of attitudes toward damage causing mammalian wildlife. *Conserv. Biol.* 28, 924–938.
- Kuiper, T.R., Loveridge, A.J., Parker, D.M., Johnson, P.J., Hunt, J.E., ... Macdonald, D.W., 2015. Seasonal herding practices influence predation on domestic stock by African lions along a protected area boundary. *Biol. Conserv.* 191, 546–554. <https://doi.org/10.1016/j.biocon.2015.08.012>.
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* 82, 1–26. <https://doi.org/10.18637/jss.v082.i13>.
- Laundré, J.W., Hernández, L., Altendorf, K.B., 2001. Wolves, elk, and bison: re-establishing the 'landscape of fear' in Yellowstone National Park, U.S.A. *Can. J. Zool.* 79, 1401–1409. <https://doi.org/10.1139/cjz-79-8-1401>.
- Loveridge, A.J., Valeix, M., Elliot, N.B., Macdonald, D.W., 2017. The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. *J. Appl. Ecol.* 54, 815–825. <https://doi.org/10.1111/1365-2664.12794>.
- Løvschal, M., Böcher, P.K., Pilgaard, J., Amoke, I., Odingo, A., Thuo, A., Svenning, J.-C., 2017. Fencing bodes a rapid collapse of the unique Greater Mara ecosystem. *Nat. Publ. Group* 7 (1). <https://doi.org/10.1038/srep41450>.
- Marshall, F., Reid, R.E.B., Goldstein, S., Storozum, M., Wreschnig, A., ... Ambrose, S.H., 2018. Ancient herders enriched and restructured African grasslands. *Nature* 561, 387–390. <https://doi.org/10.1038/s41586-018-0456-9>.
- Mbawai, J.E., 2018. Effects of the safari hunting tourism ban on rural livelihoods and wildlife conservation in Northern Botswana. *S. Afr. Geogr. J.* 100, 41–61. <https://doi.org/10.1080/03736245.2017.1299639>.
- Mendelsohn, J., el Obeid, S., 2004. Okavango River - The Flow of a Lifeline. Struik Publishers, Cape Town, South Africa.
- Morrissey, M.B., Ruxton, G.D., 2018. Multiple regression is not multiple regressions: the meaning of multiple regression and the non-problem of collinearity. *Philos. Theory Pract. Biol.* 10, 1–24. <https://doi.org/10.3998/ptpbio.16039257.0010.003>.
- Murray, M.G., 1995. Specific nutrient requirements and migration of wildebeest. In: Sinclair, A.R.E., Arcese, P. (Eds.), *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem*. The University of Chicago Press, Chicago, pp. 231–256.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>.
- Norton-Griffiths, M., Said, M.Y., 2010. The future for wildlife on Kenya's rangelands: an economic perspective. In: Toit, J.T. du, Kock, R., Deutsch, J.C.R. (Eds.), *Wild Rangelands*. Blackwell, Chichester, pp. 367–392.
- Odadi, W.O., Fargione, J., Rubenstein, D.I., 2017. Vegetation, wildlife, and livestock responses to planned grazing management in an African pastoral landscape. *Land Degrad. Dev.* 28, 2030–2038. <https://doi.org/10.1002/ldr.2725>.
- Odadi, W.O., Riginos, C., Rubenstein, D.I., 2018. Tightly bunched herding improves cattle performance in African savanna rangeland. *Rangel. Ecol. Manag.* 71, 481–491. <https://doi.org/10.1016/j.rama.2018.03.008>.
- Odaga, D., Shaw, P., Beyers, R.L., Buij, R., Murn, C., Thiollay, J.M., ... Sinclair, A.R.E., 2015. Another continental vulture crisis: Africa's vultures collapsing toward extinction. *Conserv. Lett.* 9, 89–97. <https://doi.org/10.1111/conl.12182>.
- Ostrom, E., 1999. Revisiting the commons: local lessons, global challenges. *Science* 284, 278–282. <https://doi.org/10.1126/science.284.5412.278>.
- Owen-Smith, N., 2004. Functional heterogeneity in resources within landscapes and herbivore population dynamics. *Landscape Ecol.* 19, 761–771. <https://doi.org/10.1007/s10980-005-0247-2>.
- Owen-Smith, N., 2008. Effects of temporal variability in resources on foraging behaviour. In: Prins, H.H.T., van Langevelde, F. (Eds.), *Resource Ecology: Spatial and Temporal Dynamics of Foraging*. Springer, Netherlands, pp. 159–181.
- Palmer, M.S., Fieberg, J., Swanson, A., Kosmala, M., Packer, C., 2017. A 'dynamic' landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. *Ecol. Lett.* 20, 1364–1373. <https://doi.org/10.1111/ele.12832>.
- Périquet, S., Valeix, M., Loveridge, A.J., Madzikanda, H., Macdonald, D.W., Fritz, H., 2010. Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. *Anim. Behav.* 79, 655–671. <https://doi.org/10.1016/j.anbehav.2009.12.016>.
- Pröpper, M., Gröngroft, A., Finck, M., Stirn, S., De Cauwer, V., Lages, F., ... Jürgens, N., 2015. The Future Okavango – Findings, Scenarios and Recommendations for Action. *Research Project Final Synthesis*.
- Provenza, F., Kronberg, S., Gregorini, P., 2019. Is grassed meat and dairy better for human and environmental health? *Front. Nutr.* 6, 26. <https://doi.org/10.3389/tnut.2019.00026>.
- R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing (version 3.4.5).
- Reddy, S.M.W., Montambault, J., Masuda, Y.J., Keenan, E., Butler, W., Fisher, J.R.B., ... Gneezy, A., 2016. Advancing conservation by understanding and influencing human behavior. *Conserv. Lett.* 10, 248–256. <https://doi.org/10.1111/conl.12252>.
- Rettie, W.J., Messier, F., 2008. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23, 466–478. <https://doi.org/10.1111/j.1600-0587.2000.tb00303.x>.
- Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M.S., Dickman, A.J., ... Pimm, S., 2013. The size of savannah Africa: a lion's (*Panthera leo*) view. *Biodivers. Conserv.* 22, 17–35. <https://doi.org/10.1007/s10531-012-0381-4>.
- Romanens, R. (2017). Organic Matter Dynamics and Soil Diversity in the Chobe Enclave, Botswana. Unpublished Master thesis, University of Lausanne, Switzerland.
- Sianga, K., Fynn, R., 2017. The vegetation and wildlife habitats of the Savuti-Mababe-Linyanti ecosystem, northern Botswana. *Koedoe* 59. <https://doi.org/10.4102/koedoe.v59i2.1406>.
- Sianga, K., Fynn, R., Bonyongo, M.C., 2017. Seasonal habitat selection by African buffalo *Syncerus caffer* in the Savuti-Mababe-Linyanti ecosystem of northern Botswana. *Koedoe* 59 (2), a1382. <https://doi.org/10.4102/koedoe.v59i2.1382>.
- Sinclair, A.R.E., Arcese, P., 1995. Population consequences of predation-sensitive foraging: the Serengeti wildebeest. *Ecology* 76, 882–891. <https://doi.org/10.2307/1939353>.
- Snell, M., 2015. Kavango Zambezi Transfrontier Conservation Area Master Integrated Development Plan 2015–2020. pp. 1–81.
- Songhurst, A., 2017. Measuring human-wildlife conflicts: comparing insights from different monitoring approaches. *Wildl. Soc. Bull.* 41, 351–361. <https://doi.org/10.1002/wsb.773>.
- Thornton, P.K., 2010. Livestock production: recent trends, future prospects. *Philos. Trans. R. Soc. B* 365, 2853–2867. <https://doi.org/10.1098/rstb.2010.0134>.
- Trinkel, M., Fleischmann, P.H., Slotow, R., 2017. Electrifying the fence or living with consequences? Problem animal control threatens the long-term viability of a free-ranging lion population. *J. Zool.* 301, 41–50. <https://doi.org/10.1111/jzo.12387>.
- Tyrell, P., Russell, S., Western, D., 2017. Seasonal movements of wildlife and livestock in a heterogeneous pastoral landscape: implications for coexistence and community based conservation. *Glob. Ecol. Conserv.* 12, 59–72. <https://doi.org/10.1016/j.gecco.2017.05.001>.

- 2017.08.006.
- Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., Macdonald, D.W., 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* 90, 23–30. <https://doi.org/10.1890/08-0606.1>.
- Valeix, M., Hemson, G., Loveridge, A.J., Mills, M.G.L., Macdonald, D.W., 2012. Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *J. Appl. Ecol.* 49, 73–81. <https://doi.org/10.1111/j.1365-2664.2011.02099.x>.
- van der Meer, E., Badza, M.N., Ndhlovu, A., 2016. Large carnivores as tourism flagship species for the Zimbabwe component of the Kavango Zambezi Transfrontier Conservation Area. *Afr. J. Wildl. Res.* 46, 121–134. <https://doi.org/10.3957/056.046.0121>.
- Vanak, A.T., Fortin, D., Thaker, M., Ogden, M., Owen, C., Greatwood, S., Slotow, R., 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology* 94, 2619–2631. <https://doi.org/10.1890/13-0217.1>.
- Weise, F.J., Hayward, M.W., Casillas Aguirre, R., Tomeletso, M., Gadimang, P., Somers, M.J., Stein, A.B., 2018. Size, shape and maintenance matter: a critical appraisal of a global carnivore conflict mitigation strategy – livestock protection kraals in northern Botswana. *Biol. Conserv.* 225, 88–97. <https://doi.org/10.1016/j.biocon.2018.06.023>.
- Weise, F.J., Hauptmeier, H., Stratford, K.J., Hayward, M.W., Aal, K., Heuer, M., ... Stein, A.B., 2019. Lions at the gates: trans-disciplinary design of an early warning system to improve human-lion coexistence. *Front. Ecol. Evol.* 6, 242. <https://doi.org/10.3389/fevo.2018.00242>.
- Woodroffe, R., Frank, L.G., 2005. Lethal control of African lions (*Panthera leo*): local and regional population impacts. *Anim. Conserv.* 8, 91–98. <https://doi.org/10.1017/S1367943004001829>.
- Zuur, A.F., Ieno, E.N., 2016. A protocol for conducting and presenting results of regression-type analyses. *Methods Ecol. Evol.* 7, 636–645. <https://doi.org/10.1111/2041-210X.12577>.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.