Water and cattle shape habitat selection by wild herbivores at the edge of a protected area

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Surface water availability and cattle herding practices shape the human-wildlife interface at the edge of a protected area.

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Running title: water and avoidance of cattle by wildlife

Total Word count: 6735

summary 350, main text: 4304, acknowledgements 123, references 1753, tables and figure legends 282

Tables: 0, Figures: 5, number of references: 57

Summary

1. Coexistence between wildlife and human activities is increasingly perceived as a key to successful conservation. To understand the drivers of coexistence, we investigated the role of surface water, a key resource, on the interactions between livestock and wild herbivores at the edge of an unfenced protected area in a semi-arid savanna.

2. We used GPS data to quantify avoidance between African elephant (Loxodonta Africana), African buffalo (Syncerus caffer caffer) and cattle (Bos taurus & indicus) at multiple scales, according to seasonal changes in surface water distribution, in Sikumi Forest, at the edge of Hwange National Park, Zimbabwe.

3. The range and duration of cattle incursions within a few kilometres of the boundary of Sikumi Forest vary seasonally by shifting from consistent selection of open habitats close to water pans during the rainy season, to the less predictable selection of areas far away from the dried up water pans at the end of the dry season.

4. During the rainy and cold dry season, buffalo successfully avoid cattle at the home-range scale and at the scale of foraging bouts. By the end of the dry season, buffalo herds, which are restricted in their movement to the vicinity of water, still avoid using areas used by cattle but tolerate higher overlap with cattle and cannot afford to avoid them as strongly at fine scales.

5. Elephant home ranges overlap extensively with cattle throughout the year but elephant avoid cattle by staying away from the boundary during the day and getting closer at night. As the dry season advances, elephant bulls range closer to the boundary especially at night and may even make excursions into the communal land in their search for forage.

6. Synthesis and applications: Wild herbivores strongly avoid livestock and people as long as their foraging and drinking resources allow. During the rainy season, when resources are abundant, cattle herding create a buffer zone between wildlife areas and human settlements. When resources are scarce (during a drought) long term planning of artificial water provisioning is essential to maintain spatial segregation and mitigate conflicts such as disease transmission or crop-raiding.

Key words: coexistence, conflict, habitat selection, livestock, temporal shift, resource partitioning, wildlife/livestock interface.

Introduction

To date, setting aside land for conservation remains one of the core conservation strategies (Palomo *et al.* 2014). Yet, protected areas only cover 15% of the land surface worldwide (Juffe-Bignoli *et al.* 2014) and their implementation has not been sufficient to curtail the decline of large mammal populations (Craigie *et al.* 2010). Land sharing in addition to land sparing is increasingly being considered as a necessary and effective option to maintain biodiversity (Fischer *et al.* 2011). However, the effectiveness of conservation within these multiple use areas depends on how wildlife responds to human activities (Fynn *et al.* 2016).

Despite increasing population densities and encroachment by agriculture (Newmark 2008), livestock husbandry and subsistence agro-pastoralism remain the primary land-uses around wildlife areas in semi-arid rangeland ecosystems, particularly near African protected savannas (Caron *et al.* 2013). The partitioning of rangelands into different land-uses, including protected areas, commercial ranching or communal agro-pastoralism, has often been accompanied by the establishment of fences to hinder the movement of wildlife, livestock and people (Somers & Hayward 2011). However, many areas have remained unfenced or have seen their fences decommissioned over the past decades (Cumming *et al.* 2015). In the absence of fences, livestock and wildlife ranges may overlap. Current land-tenure implies that this overlap can generate conservation conflicts (*sensu* Redpath *et al.* 2013) resulting from cattle incursions into protected areas (Hibert *et al.* 2010; Butt 2011) or wildlife excursions outside of protected areas (Graham *et al.* 2009).

Access to resources, such as dry season forage for herbivores, is a key determinant for both wildlife population dynamics (Illius & O'Connor 2000) and the livelihoods of people living at the edge of protected areas (Murwira *et al.* 2013). Ecological theory predicts that one of the conditions for sustainable coexistence between species is resource partitioning (Roughgarden 1976). Wild and domestic herbivores provide a good model to study spatiotemporal partitioning because they have similar resource requirements implying they can share the same habitat or compete for its resources (Butt 2011; Odadi *et al.* 2011; Fynn *et al.* 2016). Whether wild or domestic, the distribution of water-dependent herbivores is primarily driven by surface water availability (De Leeuw *et al.* 2001; Ogutu *et al.* 2014). At large scales, pastoralists (Adriansen & Nielsen 2002) and migratory herbivores (Hopcraft & Morales 2014) distribute themselves according to foraging opportunities during the rainy season when they are not constrained by access to water. However, they congregate around the remaining water sources during the dry season and are forced to make the best of areas within commuting distance of water (Butt 2010; Cornélis *et al.* 2011; Chamaillé-Jammes *et al.* 2013)

Wildlife populations in protected areas in savanna ecosystems are particularly vulnerable to droughts (Walker *et al.* 1987). In southern Africa, droughts have worsened over the past decades (Chamaillé-Jammes, Fritz & Murindagomo 2007) and recent climatic scenarios predict decreasing rainfall and increasing temperatures during the 21st century (Giannini *et al.* 2008). During a drought, one might expect hot dry season conditions to prevail earlier in the season and persist longer in the case of delayed rains. Cattle will likely range even further inside the protected area (Butt 2014) and wildlife will aggregate in larger numbers around the remaining water pans. As a result, human-wildlife conflicts such as disease transmission (Miguel *et al.* 2013), livestock depredation (Kuiper *et al.* 2015) or raiding by elephants (Guerbois, Chapanda & Fritz 2012) are likely to increase.

To understand how wildlife simultaneously managed to exploit dwindling resources and minimise interaction with cattle and herders, we quantified the role of the distribution of surface water on habitat selection and the spatial overlap between cattle (*Bos taurus & indicus*) and two locally dominant wild herbivore species; the African elephant (*Loxodonta Africana*) and the African buffalo (*Syncerus caffer caffer*), at the edge of Sikumi Forest, a protected area in North-Western Zimbabwe (Fig. 1). All three of the studied species are water-dependent (Hempson, Archibald & Bond 2015). Unlike inside the protected areas where elephant are the dominant herbivore species at waterholes (Valeix, Chamaillé-Jammes & Fritz 2007), the association of cattle with people implies they may effectively exclude wild herbivores from waterholes when they come to drink or forage in close proximity (Western 1975; Sitters *et al.* 2009; Ogutu *et al.* 2014). In response to cattle presence, wild herbivores could operate a temporal niche shift towards nocturnal activity to continue using the same water sources yet avoid the disturbances caused by cattle and people.

Segregation between cattle and wildlife may also result from competition for forage. Evidence for exploitation competition is scarce (Kartzinel *et al.* 2015). We hypothesize exploitation competition may occur throughout the year for buffalo and cattle that are both grazers, whereas it is more likely to be limited to the rainy season for elephant that essentially browse during the dry season (Williamson 1975). Exploitation competition is expected to be strongest during the dry season when forage is limiting and may be negligible or even outweighed by facilitation during the rainy season (Odadi *et al.* 2011). However, competition can be asymmetrical: Cattle have been reported to compensate for forage depletion by wildlife whereas wild herbivores do not (Young, Palmer & Gadd 2005). As a result, buffalo are expected to strongly avoid areas that are heavily grazed by cattle throughout the year whereas elephant may still find browse in these areas and attempt to exploit them when cattle are absent.

Methods

Study area

We conducted the study in an area covering 190 km^2 of Sikumi Forestry Commission land (26.9°E, 18.6°S) on the boundary of Hwange National Park, Zimbabwe. There is currently no fence between the Communal Land, Sikumi, Hwange National Park and adjacent photographic or trophy hunting safari areas (Fig. 1). Homesteads and fields are located immediately across the boundary or a few hundred meters away (Guerbois, Chapanda & Fritz 2012). A veterinary fence had been erected between Sikumi and the communal land in the 1960's. After the 1992 drought, gates were installed along the fence to allow cattle to enter. The fence rapidly became ineffective due to lack of maintenance during the economic crisis and was finally dismantled after the year 2000.

Human presence inside Sikumi mainly consists in game viewing from 4x4 vehicles and patrols by Forestry Commission scouts and anti-poaching units. People living on the edge of Sikumi also enter within the first few kilometres of the boundary. Their main activity is cattle herding although they regularly collect natural resources such as firewood and thatching grass. The exact distance cattle are allowed to enter is unclear and remains a bone of contention between cattle owners and the Forestry Commission.

Mean annual precipitation is 600mm with large variations between years (Chamaillé-Jammes, Fritz & Murindagomo 2006). Climate is characterized by a rainy season that extends from November to April followed by the dry season which can be subdivided in a cold dry season (May-August) and a hot dry season (September-November). There are no perennial rivers in the study area, natural depressions and dams fill up with water during the rainy season but gradually dry up throughout the dry season. By the end of the dry season, surface water can only be found at 13 artificial waterholes in which groundwater is continuously pumped. Surface water availability for each season was determined following the systematic monitoring of 78 natural water pans in the area throughout the 2013 and 2014 dry seasons (Fig. 1).

Vegetation is typical of dystrophic semi-arid savanna dominated by the trees *Baikiaea plurijuga*, *Colophospermum mopane*, *Kirkia acuminata* and *Bauhinia petersiana*. Herbivore aggregations around water pans create piospheres due to repeated grazing and trampling. Vegetation in Sikumi is similar to Hwange National Park, woody cover generally increases with distance from water pans (Chamaillé-Jammes, Fritz & Madzikanda 2009). A simplified vegetation map was adapted from Courbin *et al.* (2016). Four classes were defined according to the proportion of woody cover: Open Grasslands (0.8%) only found within 500m of water pans, Bushed Grasslands (16.6%) and Bushland (26.8%) both found within 2km of water and Bushed Woodland (55.8%) that predominantly occupies the areas farthest from water (Fig. S1). Communal land consists of dispersed homesteads in a matrix of fields and native vegetation, however tree cover is much reduced.

Modelling cattle incursions

Cattle owners usually keep their cattle in kraals located close to their homesteads overnight to protect livestock from predators and thieves. Kraals act as central places from which cattle depart in the morning and return to before sundown. Cattle from 11 different kraals were equipped with GPS collars recording 1 location every hour. Five cows were tracked in 2010-2011 and 9 in 2012-2014.

Cattle incursions in Sikumi follow the seasonal changes in herding strategies, water availability and forage abundance. During the rainy season, cattle are driven into Sikumi nearly every single day, mainly to prevent them from destroying crops in adjacent fields.

They range about 1.6km from the boundary but may reach up to 5.4km and spend on average 4.3h per day inside. During the cold dry season, cattle are no longer herded and roam freely in the villages, feeding on communal pastures and crops residues left in the fields. They enter the Sikumi less than one day out of five. Some herds are briefly driven into Sikumi to drink but most drink at boreholes inside the communal area. Incursions are briefer (mean=1.8h) and closer to the boundary (mean=0.8km, max=3.8km). As for the hot dry season, cattle enter Sikumi to graze on their own more often (one day out of three), stay longer (mean=3.1h) and travel further (mean=1.4 km, max=6.0 km). Herders only enter to collect them in the late afternoon (Valls-Fox & Perrotton unpublished data).

For each one of the three seasons, we modelled the probability of cattle presence inside Sikumi as an Inhomogeneous Poisson Point process (IPP) using GPS locations (Johnson, Hooten & Kuhn 2013). Independent variables included vegetation structure, distance to water, distance to the kraal, distance to the boundary and distance between the kraal and boundary. Model predictions were computed for each one of the 321 kraals within 2km of the boundary (Fig. 1) and summed to produce a map of cattle intensity of use covering the entire study area for each season. The area used by cattle was defined by drawing the 95th percentile of the summed utilization distributions. A detailed description of model design, validation and predictions is given in Appendix S2.

Modelling buffalo distribution and habitat selection

Sikumi harbours a single herd of approximately 500 buffalo. Five adult females were tracked with GPS collars between November 2012 and August 2014. Collars recorded 1 location per hour. We calculated seasonal occupancy by summing the individual Utilization Distributions (UD) calculated with biased random bridges (Cornélis *et al.* 2011). Spatial overlap was defined as the percentage of the buffalo UD that was within the 95th percentile of the cattle

UD. To understand how buffalo foraging decisions are influenced by the presence of cattle we used Step Selection Functions (Thurfjell, Ciuti & Boyce 2014). Resource selection was estimated by pairing each one hour step with 10 random controls having a different direction and length. At fine scales, buffalo alternate foraging bouts lasting a few hours with periods of resting and ruminating (Sinclair 1977). We restricted our analyses to foraging periods by removing steps that were shorter than 30m. To account for spatio-temporal correlation between our GPS data we identified three foraging bouts: morning (4am-12pm), evening (12pm-8pm) and night (8pm-4am) (Appendix S3). Step Selection Functions were estimated independently for each foraging bout, predictor variables included vegetation, distance to water, distance to the boundary and cattle density.

Modelling elephant distribution and habitat selection

Elephant bulls are responsible for most of the crop-raiding incidents (Guerbois, Chapanda & Fritz 2012). Ten individuals were equipped with GPS collars recording 1 location per hour between December 2010 and February 2013. Unfortunately, only 6 provided sufficiently long datasets within the study area for us to conduct statistical analyses. We measured elephant's spatial overlap with cattle and resource selection using the same methods than the ones used for buffalo. However, elephants being monogastric herbivores, they do not have the clear-cut foraging bouts (Fig. S5, Appendix S4). Since cattle enter the Forest area during the daytime and elephant excursions into Communal land generally occur at night, day-time and night-time Step Selection Functions were estimated separately for each season.

Results

Cattle use of Sikumi Forest.

Cattle habitat selection patterns reflect the strong central place effect of their home kraal; as shown by the strong decrease in probability of selection as distance to the boundary increases, regardless of distance to water and habitat type (Fig. 2, Appendix S2). Cattle also select areas close to water pans during the rainy season. The pattern dampens in the cold dry season and is actually reversed when the pans are dry in the hot dry season. Unsurprisingly, cattle select the most open habitats, especially near water pans. However, as the dry season advances, the difference between habitats decreases and cattle distribution becomes less predictable.

The home-range scale: buffalo avoid cattle but elephants do not.

Buffalo remain within the boundaries of Sikumi and their home range is delimited by the extent of cattle excursions as long as water is widely distributed. During the rainy season, buffalo only spend 2.5% of their time within the areas used by cattle (Fig. 3a). During the cold dry season, buffalo spend twice as much time within 3km of the boundary (from 7% to 13%, Fig. 3b). However, cattle incursions are shorter, briefer and less frequent so the overlap remains minimal (2.5%). During the hot dry season, buffalo contract their home range around the remaining water pans and stay further away from the boundary. However, cattle range further inside Sikumi as well. As a result, buffalo spend 11% of their time in the area used by cattle. Cattle and buffalo home ranges particularly around permanent waterholes or corridors between them (Fig. 3c).

Conversely, the home ranges of elephant bulls extend up to the Sikumi boundary, overlapping the area occupied by cattle (Fig. 3) albeit with considerable variation between individuals and seasons (15% to 68% UD overlap).

The foraging scale: daytime avoidance and night-time opportunism.

Both buffalo and elephant prefer foraging further away from the boundary and are strongly deterred by the presence of cattle whenever they come closer, as shown by the difference between the full line and the dashed line in Figs. 4 & 5. Both species prefer areas with less woody cover throughout the year. However, buffalo select these areas more strongly when they are closer to the boundary (Appendix S3).

During the rainy and cold dry seasons, encounters between cattle and buffalo are even less likely since buffalo select areas away from water during the morning bout and only return towards water during the evening bout when cattle are no longer present (Fig. 4). Similarly, elephant bulls prefer areas further away from water during the day than during the night (Fig. 5). Interestingly, distance to water no longer appears to be a decisive criterion during the day or during the night when elephant bulls forage close to the boundary and particularly in areas where cattle are present (Fig. 5). Overall, both species range closer to the boundary during the cold dry season than the rainy season. Buffalo select area closer to the Sikumi boundary during the evening and night (~4km) than during the morning but strongly avoid areas used by cattle within 2km of the boundary. Elephant bulls prefer areas between 3km and 4km from the boundary.

Unlike previous seasons, buffalo select areas close to water during both the morning and evening bouts during the hot dry season (Fig. 4) suggesting they drink twice a day, increasing the likelihood of contact with cattle at waterholes. Buffalo stay away from the boundary but hardly respond to cattle presence suggesting the main driver of their movement is access to water. Elephant bulls range closer to the boundary in the hot dry season (3-4km) and take advantage of the night to forage in areas that cattle use during the daytime (Fig. 5). Occasionally, elephant bulls make nightly excursions into the communal land. Over the study period, we recorded only 79 excursions out of the 1960 nights spent by the six collared bulls in the study area (226 - 334 nights per individual). Half of the excursions occurred during the hot dry season and 25% at the end of the cropping season between March and May.

Discussion

Cattle, elephant and buffalo share a preference for open grassland habitats found close to water in Sikumi but have different constraints resulting from their relationship to humans. Cattle incursions are strongly constrained by the central place effect of their home kraal that keeps them from wandering beyond a few kilometres from the boundary. Buffalo and elephant avoid cattle by staying away from the boundary at large scales but can also fine-tune their diel behaviour to exploit the area close to the boundary at night. These patterns are consistent with avoidance of cattle by wild herbivores in African (Hibert *et al.* 2010; Ogutu *et al.* 2014) and North-American (Stewart *et al.* 2002) rangelands.

Buffalo predominantly rely on avoidance at the home range scale (Fig. 3) whereas elephant appear to favour temporal niche shift, by avoiding direct encounters with cattle (or people) during the day but coming closer to the boundary and to water at night (Fig. 5). This difference could result from competitive exclusion of buffalo by cattle (both species being grazers) whereas elephant bulls have access to a broader niche being mixed feeders (Kartzinel *et al.* 2015). Alternatively, solitary elephant bulls are more likely to adopt a cryptic behaviour allowing a more flexible and adaptive foraging strategy, whereas buffalo splinter groups usually include at least a few dozen or even several hundred individuals (Cross, Lloyd-Smith & Getz 2005), reducing their ability to remain inconspicuous during the daytime. Seasonal changes suggest access to key resources is one of the key drivers of cattle-wildlife interactions

(Zengeya *et al.* 2015) but ecological differences between species lead to different behavioural responses.

Seasonal changes drive cattle-wildlife interactions

During the rainy season, herd boys drive cattle into Sikumi daily to keep their livestock out of fields and to exploit the pastures around waterholes. Widespread distribution of water pans allows buffalo and elephant to successfully avoid cattle. Although waterholes still constitute key habitats for all species, buffalo shift their home range at large scales to exploit the open areas around water pans further inside Sikumi whereas elephant only visit waterholes at night when they range closer to the boundary.

During the dry season, cattle are no longer herded, they initially spend most of their time in the communal land feeding on crop residues, but eventually return to Sikumi and gradually travel further away from the boundary and from water suggesting that intraspecific competition (Young, Palmer & Gadd 2005; Odadi *et al.* 2011) is stronger than the risk of encountering predators (Kuiper *et al.* 2015) or than competition with wild herbivores.

As the dry season advances, buffalo water dependence takes precedence over avoidance of cattle. They strongly contract their home-range around waterholes (Cornélis *et al.* 2011) and only venture further away from water during their nocturnal foraging bout (Fig. 4). Buffalo and cattle home-range overlap increases fivefold, heightening the likelihood of contacts between both species and the risk of disease transmission (Miguel *et al.* 2013).

As resources dwindle, elephant bulls select areas closer and closer to the boundary at night, suggesting that they avoid intraspecific competition as well by foraging in areas with lower browser densities when forage becomes most limiting rather than the attractiveness of crops.

Can surface water management mitigate the effects drought?

In Sikumi, the 1992 drought was a turning point when traditional authorities and the Forestry Commission came to an informal agreement to tolerate cattle incursions within the first few kilometres to mitigate a massive die-off in domestic livestock due to forage and water shortages. Current water management is already a key determinant of human-wildlife coexistence. The spatial overlaps between buffalo and cattle reflect the distribution of water pans pumped by safari operators (Fig. 3) and cattle owners can manipulate the behaviour of their livestock by providing water from boreholes (pers. obs.).

Local stakeholders may reduce conflicts by shifting artificial waterholes further away from unfenced protected area boundaries and increasing access to boreholes for cattle in the communal lands. Such policies might also reduce livestock depredation as predators will select for areas with higher wild prey densities and remain close to permanent waterholes (Valeix *et al.* 2010).

Avoidance of cattle or avoidance of people?

Whereas cattle and buffalo hardly overlap and almost never meet in Sikumi, up to 60% of elephant bull's seasonal home-range can be found within the area utilized by cattle. In other ecosystems, livestock can displace other herbivore species completely (Stewart *et al.* 2002; Hibert *et al.* 2010), they may overlap in space but not in time (Cooper *et al.* 2008; Atickem & Loe 2014) or even co-mingle (Dohna *et al.* 2014). Moreover, buffalo strongly avoid cattle in Sikumi whereas their range overlap extensively with cattle around the Greater Limpopo Transfrontier Conservation Area (Miguel *et al.* 2013).

Rather than avoiding cattle per se, buffalo and elephants might in fact be avoiding humans. During the rainy season, herd boys drive cattle into Sikumi and stay with them all day. During the dry season, cattle range freely and often enter unaccompanied. Unfortunately, seasonal changes in cattle movement are confounded with changing herding practices, and we cannot tell whether elephant and buffalo's usage of areas closer to the boundary result from the absence of herd boys or from shorter and less frequent cattle incursions. Even though cattle are not systematically accompanied by people, the association may be sufficiently strong for wildlife to consider them as cues for human presence.

Free ranging cattle can displace wild herbivores even in the absence of humans (Stewart *et al.* 2002; Cooper *et al.* 2008) and the presence of cattle herders does not necessarily imply a greater displacement of wild herbivores. In East-African savannas, sedentarisation of nomadic pastoral communities resulted in a decline in herbivore abundance attributed to displacement from key grazing resources by resident livestock (Western, Groom & Worden 2009). The decline neither resulted from increased offtake nor from higher cattle densities. A neighbouring nomadic community with similar human and livestock population growth witnessed an increase in wildlife abundance over the same period. In southern Kenya, Maasai pastoralists preferentially take their cattle to forage far from water during dry periods and commute large distances between their pastures and water. Such practices ease coexistence with wild herbivores that select foraging grounds along the distance to water gradient according to their water dependency (Sitters *et al.* 2009). Herding practices in Sikumi consist in repeated incursions by sedentary livestock to the same areas close to water. Unlike patterns reported by Sitters *et al.* (2009) and as suggested by Western *et al.* (2009) in Kenya, herding practices in Sikumi may effectively exclude wild herbivores from the vicinity of the Forest boundary.

Edge effects at an unfenced interface

Despite the absence of any physical barrier to movement, buffalo never cross into the communal land and elephant bulls make rare excursions during the rainy and hot dry seasons. Both species avoid Sikumi boundary but bunch up against a virtual fence (Jachowski, Slotow & Millspaugh 2014) corresponding to the contour of the area used by cattle. The boundary of Sikumi has edge effects on wildlife that are comparable to effects of real barriers (Loarie, van Aarde & Pimm 2009). However, our study focuses on elephant bulls and adult female buffalo, individuals from different sex and age classes could perceive the boundary differently as has been recently demonstrated for sub-adult buffalo in the Greater Limpopo TFCA (Caron *et al.* 2016).

Conclusion

Cattle are ubiquitous and highly valued in most agro-pastoral societies that live around protected areas worldwide. However, cattle incursions into protected areas are often perceived as “unnatural” and considered as a threat to wildlife via overgrazing (Butt 2014). Displacement of wildlife on the boundary of protected areas over a distance of a few kilometers does not entail substantial habitat loss, however it can promote coexistence by delimiting a buffer zone that protects people from wildlife (e.g. livestock predation, crop destruction, zoonosis transmission). The implementation of such buffering strategies are particularly relevant for large conservation areas such as the Kavango-Zambezi TFCA that encompasses multiple protected areas as well as communal land.

In order to maintain the integrity of protected area boundaries, two mechanisms may be mobilized: fear of humans and resource availability. In arid lands, water provisioning may be designed to allow for the segregation of livestock and wildlife in order to minimise conflict. However, in more mesic landscapes or situations, such as savannas during the rainy season, the relation between cattle and wildlife may be one of facilitation rather than competition (Fynn *et al.* 2016). Nonetheless, cattle may only be perceived as cues for human presence, thus traditional herding practices, that often rely on people accompanying cattle, may be paramount to maintaining segregation between cattle and wildlife.

Acknowledgments

We are grateful to the cattle owners and Forestry scouts for their time and their trust. This research was authorized by the Research Council of Zimbabwe, the Forestry Commission, the Zimbabwe Parks and Wildlife Management Authority, the Hwange District Administrator and chief Nelukoba. Funding was provided by the grant ANR-11-CEPS-003 of the French ‘Agence National de la Recherche’ and a PhD fellowship from the Ecole Normale Supérieure & Université de Montpellier. This work was conducted within the framework of the Research Platform “Production and Conservation in Partnership” (www.rp-pcp.org) and the FSP-RenCaRe project (FSP n°2011-36).

Authors' Contributions

HVF, SCJ, MDGW & HF conceived the ideas and designed methodology; HFV, AP, BS, MM, and EM collected the data; HVF analysed the data with guidance from NC and SCJ; HVF led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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