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

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32 **Summary**

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

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

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

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

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

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

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

61

62 **Introduction**

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

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

82 Access to resources, such as dry season forage for herbivores, is a key determinant for both
83 wildlife population dynamics (Illius & O'Connor 2000) and the livelihoods of people living at
84 the edge of protected areas (Murwira *et al.* 2013). Ecological theory predicts that one of the
85 conditions for sustainable coexistence between species is resource partitioning (Roughgarden
86 1976). Wild and domestic herbivores provide a good model to study spatiotemporal
87 partitioning because they have similar resource requirements implying they can share the
88 same habitat or compete for its resources (Butt 2011; Odadi *et al.* 2011; Fynn *et al.* 2016).
89 Whether wild or domestic, the distribution of water-dependent herbivores is primarily driven
90 by surface water availability (De Leeuw *et al.* 2001; Ogutu *et al.* 2014). At large scales,
91 pastoralists (Adriansen & Nielsen 2002) and migratory herbivores (Hopcraft & Morales 2014)
92 distribute themselves according to foraging opportunities during the rainy season when they
93 are not constrained by access to water. However, they congregate around the remaining water
94 sources during the dry season and are forced to make the best of areas within commuting
95 distance of water (Butt 2010; Cornélis *et al.* 2011; Chamaillé-Jammes *et al.* 2013)

96 Wildlife populations in protected areas in savanna ecosystems are particularly vulnerable to
97 droughts (Walker *et al.* 1987). In southern Africa, droughts have worsened over the past
98 decades (Chamaillé-Jammes, Fritz & Murindagomo 2007) and recent climatic scenarios
99 predict decreasing rainfall and increasing temperatures during the 21st century (Giannini *et al.*
100 2008). During a drought, one might expect hot dry season conditions to prevail earlier in the
101 season and persist longer in the case of delayed rains. Cattle will likely range even further
102 inside the protected area (Butt 2014) and wildlife will aggregate in larger numbers around the
103 remaining water pans. As a result, human-wildlife conflicts such as disease transmission
104 (Miguel *et al.* 2013), livestock depredation (Kuiper *et al.* 2015) or raiding by elephants
105 (Guerbois, Chapanda & Fritz 2012) are likely to increase.

106 To understand how wildlife simultaneously managed to exploit dwindling resources and
107 minimise interaction with cattle and herders, we quantified the role of the distribution of
108 surface water on habitat selection and the spatial overlap between cattle (*Bos taurus* &
109 *indicus*) and two locally dominant wild herbivore species; the African elephant (*Loxodonta*
110 *Africana*) and the African buffalo (*Syncerus caffer caffer*), at the edge of Sikumi Forest, a
111 protected area in North-Western Zimbabwe (Fig. 1). All three of the studied species are
112 water-dependent (Hempson, Archibald & Bond 2015). Unlike inside the protected areas
113 where elephant are the dominant herbivore species at waterholes (Valeix, Chamaillé-Jammes
114 & Fritz 2007), the association of cattle with people implies they may effectively exclude wild
115 herbivores from waterholes when they come to drink or forage in close proximity (Western
116 1975; Sitters *et al.* 2009; Ogutu *et al.* 2014). In response to cattle presence, wild herbivores
117 could operate a temporal niche shift towards nocturnal activity to continue using the same
118 water sources yet avoid the disturbances caused by cattle and people.

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

131 **Methods**

132 *Study area*

133 We conducted the study in an area covering 190 km² of Sikumi Forestry Commission land
134 (26.9°E, 18.6°S) on the boundary of Hwange National Park, Zimbabwe. There is currently no
135 fence between the Communal Land, Sikumi, Hwange National Park and adjacent
136 photographic or trophy hunting safari areas (Fig. 1). Homesteads and fields are located
137 immediately across the boundary or a few hundred meters away (Guerbois, Chapanda & Fritz
138 2012). A veterinary fence had been erected between Sikumi and the communal land in the
139 1960's. After the 1992 drought, gates were installed along the fence to allow cattle to enter.
140 The fence rapidly became ineffective due to lack of maintenance during the economic crisis
141 and was finally dismantled after the year 2000.

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

148 Mean annual precipitation is 600mm with large variations between years (Chamaillé-Jammes,
149 Fritz & Murindagomo 2006). Climate is characterized by a rainy season that extends from
150 November to April followed by the dry season which can be subdivided in a cold dry season
151 (May-August) and a hot dry season (September-November). There are no perennial rivers in
152 the study area, natural depressions and dams fill up with water during the rainy season but
153 gradually dry up throughout the dry season. By the end of the dry season, surface water can

154 only be found at 13 artificial waterholes in which groundwater is continuously pumped.
155 Surface water availability for each season was determined following the systematic
156 monitoring of 78 natural water pans in the area throughout the 2013 and 2014 dry seasons
157 (Fig. 1).

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

169 *Modelling cattle incursions*

170 Cattle owners usually keep their cattle in kraals located close to their homesteads overnight to
171 protect livestock from predators and thieves. Kraals act as central places from which cattle
172 depart in the morning and return to before sundown. Cattle from 11 different kraals were
173 equipped with GPS collars recording 1 location every hour. Five cows were tracked in 2010-
174 2011 and 9 in 2012-2014.

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

178 They range about 1.6km from the boundary but may reach up to 5.4km and spend on average
179 4.3h per day inside. During the cold dry season, cattle are no longer herded and roam freely in
180 the villages, feeding on communal pastures and crops residues left in the fields. They enter the
181 Sikumi less than one day out of five. Some herds are briefly driven into Sikumi to drink but
182 most drink at boreholes inside the communal area. Incursions are briefer (mean=1.8h) and
183 closer to the boundary (mean=0.8km, max=3.8km). As for the hot dry season, cattle enter
184 Sikumi to graze on their own more often (one day out of three), stay longer (mean=3.1h) and
185 travel further (mean=1.4 km, max=6.0 km). Herders only enter to collect them in the late
186 afternoon (Valls-Fox & Perrotton unpublished data).

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

196 *Modelling buffalo distribution and habitat selection*

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

202 UD. To understand how buffalo foraging decisions are influenced by the presence of cattle we
203 used Step Selection Functions (Thurfjell, Ciuti & Boyce 2014). Resource selection was
204 estimated by pairing each one hour step with 10 random controls having a different direction
205 and length. At fine scales, buffalo alternate foraging bouts lasting a few hours with periods of
206 resting and ruminating (Sinclair 1977). We restricted our analyses to foraging periods by
207 removing steps that were shorter than 30m. To account for spatio-temporal correlation
208 between our GPS data we identified three foraging bouts: morning (4am-12pm), evening
209 (12pm-8pm) and night (8pm-4am) (Appendix S3). Step Selection Functions were estimated
210 independently for each foraging bout, predictor variables included vegetation, distance to
211 water, distance to the boundary and cattle density.

212 *Modelling elephant distribution and habitat selection*

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

222 **Results**

223 *Cattle use of Sikumi Forest.*

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

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

232 Buffalo remain within the boundaries of Sikumi and their home range is delimited by the
233 extent of cattle excursions as long as water is widely distributed. During the rainy season,
234 buffalo only spend 2.5% of their time within the areas used by cattle (Fig. 3a). During the
235 cold dry season, buffalo spend twice as much time within 3km of the boundary (from 7% to
236 13%, Fig. 3b). However, cattle incursions are shorter, briefer and less frequent so the overlap
237 remains minimal (2.5%). During the hot dry season, buffalo contract their home range around
238 the remaining water pans and stay further away from the boundary. However, cattle range
239 further inside Sikumi as well. As a result, buffalo spend 11% of their time in the area used by
240 cattle. Cattle and buffalo home ranges particularly around permanent waterholes or corridors
241 between them (Fig. 3c).

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

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

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

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

262 Unlike previous seasons, buffalo select areas close to water during both the morning and
263 evening bouts during the hot dry season (Fig. 4) suggesting they drink twice a day, increasing
264 the likelihood of contact with cattle at waterholes. Buffalo stay away from the boundary but
265 hardly respond to cattle presence suggesting the main driver of their movement is access to
266 water. Elephant bulls range closer to the boundary in the hot dry season (3-4km) and take
267 advantage of the night to forage in areas that cattle use during the daytime (Fig. 5).

268 Occasionally, elephant bulls make nightly excursions into the communal land. Over the study

269 period, we recorded only 79 excursions out of the 1960 nights spent by the six collared bulls
270 in the study area (226 - 334 nights per individual). Half of the excursions occurred during the
271 hot dry season and 25% at the end of the cropping season between March and May.

272

273 **Discussion**

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

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

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

294 *Seasonal changes drive cattle-wildlife interactions*

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

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

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

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

314 *Can surface water management mitigate the effects drought?*

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

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

327 *Avoidance of cattle or avoidance of people?*

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

335 Rather than avoiding cattle per se, buffalo and elephants might in fact be avoiding humans.

336 During the rainy season, herd boys drive cattle into Sikumi and stay with them all day. During

337 the dry season, cattle range freely and often enter unaccompanied. Unfortunately, seasonal
338 changes in cattle movement are confounded with changing herding practices, and we cannot
339 tell whether elephant and buffalo's usage of areas closer to the boundary result from the
340 absence of herd boys or from shorter and less frequent cattle incursions. Even though cattle
341 are not systematically accompanied by people, the association may be sufficiently strong for
342 wildlife to consider them as cues for human presence.

343 Free ranging cattle can displace wild herbivores even in the absence of humans (Stewart *et al.*
344 2002; Cooper *et al.* 2008) and the presence of cattle herders does not necessarily imply a
345 greater displacement of wild herbivores. In East-African savannas, sedentarisation of nomadic
346 pastoral communities resulted in a decline in herbivore abundance attributed to displacement
347 from key grazing resources by resident livestock (Western, Groom & Worden 2009). The
348 decline neither resulted from increased offtake nor from higher cattle densities. A
349 neighbouring nomadic community with similar human and livestock population growth
350 witnessed an increase in wildlife abundance over the same period. In southern Kenya, Maasai
351 pastoralists preferentially take their cattle to forage far from water during dry periods and
352 commute large distances between their pastures and water. Such practices ease coexistence
353 with wild herbivores that select foraging grounds along the distance to water gradient
354 according to their water dependency (Sitters *et al.* 2009). Herding practices in Sikumi consist
355 in repeated incursions by sedentary livestock to the same areas close to water. Unlike patterns
356 reported by Sitters *et al.* (2009) and as suggested by Western *et al.* (2009) in Kenya, herding
357 practices in Sikumi may effectively exclude wild herbivores from the vicinity of the Forest
358 boundary.

359 *Edge effects at an unfenced interface*

360 Despite the absence of any physical barrier to movement, buffalo never cross into the
361 communal land and elephant bulls make rare excursions during the rainy and hot dry seasons.
362 Both species avoid Sikumi boundary but bunch up against a virtual fence (Jachowski, Slotow
363 & Millspaugh 2014) corresponding to the contour of the area used by cattle. The boundary of
364 Sikumi has edge effects on wildlife that are comparable to effects of real barriers (Loarie, van
365 Aarde & Pimm 2009). However, our study focuses on elephant bulls and adult female buffalo,
366 individuals from different sex and age classes could perceive the boundary differently as has
367 been recently demonstrated for sub-adult buffalo in the Greater Limpopo TFCA (Caron *et al.*
368 2016).

369

370 **Conclusion**

371 Cattle are ubiquitous and highly valued in most agro-pastoral societies that live around
372 protected areas worldwide. However, cattle incursions into protected areas are often perceived
373 as “unnatural” and considered as a threat to wildlife via overgrazing (Butt 2014).

374 Displacement of wildlife on the boundary of protected areas over a distance of a few
375 kilometers does not entail substantial habitat loss, however it can promote coexistence by
376 delimiting a buffer zone that protects people from wildlife (e.g. livestock predation, crop
377 destruction, zoonosis transmission). The implementation of such buffering strategies are
378 particularly relevant for large conservation areas such as the Kavango-Zambezi TFCA that
379 encompasses multiple protected areas as well as communal land.

380 In order to maintain the integrity of protected area boundaries, two mechanisms may be
381 mobilized: fear of humans and resource availability. In arid lands, water provisioning may be

382 designed to allow for the segregation of livestock and wildlife in order to minimise conflict.
383 However, in more mesic landscapes or situations, such as savannas during the rainy season,
384 the relation between cattle and wildlife may be one of facilitation rather than competition
385 (Fynn *et al.* 2016). Nonetheless, cattle may only be perceived as cues for human presence,
386 thus traditional herding practices, that often rely on people accompanying cattle, may be
387 paramount to maintaining segregation between cattle and wildlife.

388

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398

399 **Authors' Contributions**

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

404

405 **References**

- 406 Adriansen, H. & Nielsen, T. (2002) Going where the grass is greener: on the study of pastoral
407 mobility in Ferlo, Senegal. *Human Ecology*, **30**, 215–226.
- 408 Atickem, A. & Loe, L.E. (2014) Livestock-wildlife conflicts in the Ethiopian highlands:
409 Assessing the dietary and spatial overlap between mountain nyala and cattle. *African*
410 *Journal of Ecology*, **52**, 343–351.
- 411 Butt, B. (2010) Pastoral resource access and utilization: Quantifying the spatial and temporal
412 relationships between livestock mobility, density and biomass availability in southern
413 Kenya. *Land Degradation & Development*, **21**, 520–539.
- 414 Butt, B. (2011) Coping with Uncertainty and Variability: The Influence of Protected Areas on
415 Pastoral Herding Strategies in East Africa. *Human Ecology*, **39**, 289–307.
- 416 Butt, B. (2014) the Political Ecology of ‘Incursions’: Livestock, Protected Areas and Socio-
417 Ecological Dynamics in the Mara Region of Kenya. *Africa*, **84**, 614–637.
- 418 Caron, A., Cornelis, D., Foggin, C., Hofmeyr, M. & de Garine-Wichatitsky, M. (2016)
419 African Buffalo movement and zoonotic disease risk across transfrontier conservation
420 areas, Southern Africa. *Emerging Infectious Diseases*, **22**, 277–280.
- 421 Caron, A., Miguel, E., Gomo, C., Makaya, P., Pfukenyi, D.M., Foggin, C., Hove, T. & de
422 Garine-Wichatitsky, M. (2013) Relationship between burden of infection in ungulate
423 populations and wildlife/livestock interfaces. *Epidemiology and Infection*, **141**, 1522–35.
- 424 Chamaillé-Jammes, S., Fritz, H. & Madzikanda, H. (2009) Piosphere contribution to
425 landscape heterogeneity: a case study of remote-sensed woody cover in a high elephant
426 density landscape. *Ecography*, **32**, 871–880.
- 427 Chamaillé-Jammes, S., Fritz, H. & Murindagomo, F. (2006) Spatial patterns of the NDVI–
428 rainfall relationship at the seasonal and interannual time scales in an African savanna.
429 *International Journal of Remote Sensing*, **27**, 5185–5200.
- 430 Chamaillé-Jammes, S., Fritz, H. & Murindagomo, F. (2007) Detecting climate changes of
431 concern in highly variable environments: Quantile regressions reveal that droughts
432 worsen in Hwange National Park, Zimbabwe. *Journal of Arid Environments*, **71**, 321–
433 326.
- 434 Chamaillé-Jammes, S., Mtare, G., Makuwe, E. & Fritz, H. (2013) African elephants adjust
435 speed in response to surface-water constraint on foraging during the dry-season. *PloS*
436 *one*, **8**, e59164.
- 437 Chamaillé-Jammes, S., Valeix, M., Bourgarel, M., Murindagomo, F. & Fritz, H. (2009)
438 Seasonal density estimates of common large herbivores in Hwange National Park,
439 Zimbabwe. *African Journal of ...*, 804–808.
- 440 Cooper, S.M., Perotto-Baldivieso, H.L., Owens, M.K., Meek, M.G. & Figueroa-Pagán, M.
441 (2008) Distribution and interaction of white-tailed deer and cattle in a semi-arid grazing
442 system. *Agriculture, Ecosystems & Environment*, **127**, 85–92.
- 443 Cornélis, D., Benhamou, S., Janeau, G., Morellet, N., Ouedraogo, M. & de Visscher, M.-N.
444 (2011) Spatiotemporal dynamics of forage and water resources shape space use of West
445 African savanna buffaloes. *Journal of Mammalogy*, **92**, 1287–1297.
- 446 Courbin, N., Loveridge, A.J., Macdonald, D.W., Fritz, H., Valeix, M., Makuwe, E. &

- 447 Chamailé-Jammes, S. (2016) Reactive responses of zebras to lion encounters shape their
448 predator-prey space game at large scale. *Oikos*, **125**, 829–838.
- 449 Craigie, I.D., Baillie, J.E.M., Balmford, A., Carbone, C., Collen, B., Green, R.E. & Hutton,
450 J.M. (2010) Large mammal population declines in Africa's protected areas. *Biological
451 Conservation*, **143**, 2221–2228.
- 452 Cross, P.C., Lloyd-Smith, J.O. & Getz, W.M. (2005) Disentangling association patterns in
453 fission–fusion societies using African buffalo as an example. *Animal Behaviour*, **69**,
454 499–506.
- 455 Cumming, D.H.M., Osofsky, S.A., Atkinson, S.J. & Atkinson, M.W. (2015) Beyond Fences :
456 Wildlife , Livestock and Land Use in Southern Africa. *One health: The theory and
457 practice of integrated health approaches* (eds J. Zinsstag), E. Schelling), D. Waltner-
458 Toews), M. Whittaker), & M. Tanner), pp. 243–257. C. A. B. International.
- 459 Dohna, H.Z., Peck, D.E., Johnson, B.K., Reeves, A. & Schumaker, B. a. (2014) Wildlife-
460 livestock interactions in a western rangeland setting: Quantifying disease-relevant
461 contacts. *Preventive Veterinary Medicine*, **113**, 447–456.
- 462 Fischer, J., Batory, P., Bawa, K.S., Brussaard, L., Chappell, M.J., Clough, Y., Daily, G.C.,
463 Dorrough, J., Hartel, T., Jackson, L.E., Klein, A.M., Kremen, C., Kuemmerle, T.,
464 Lindenmayer, D.B., Mooney, H.A., Perfecto, I., Philpott, S.M., Tschardtke, T.,
465 Vandermeer, J., Wanger, T.C. & Von Wehrden, H. (2011) Conservation: Limits of Land
466 Sparing. *Science*, **334**, 593–593.
- 467 Fynn, R.W.S., Augustine, D.J., Peel, M.J.S. & de Garine-Wichatitsky, M. (2016) Strategic
468 management of livestock to improve biodiversity conservation in African savannahs: A
469 conceptual basis for wildlife-livestock co-existence. *Journal of Applied Ecology*, **53**,
470 388–397.
- 471 Giannini, A., Biasutti, M., Held, I.M. & Sobel, A.H. (2008) A global perspective on African
472 climate. *Climatic Change*, **90**, 359–383.
- 473 Graham, M.D., Douglas-Hamilton, I., Adams, W.M. & Lee, P.C. (2009) The movement of
474 African elephants in a human-dominated land-use mosaic. *Animal Conservation*, **12**,
475 445–455.
- 476 Guerbois, C., Chapanda, E. & Fritz, H. (2012) Combining multi-scale socio-ecological
477 approaches to understand the susceptibility of subsistence farmers to elephant crop
478 raiding on the edge of a protected area. *Journal of Applied Ecology*, **49**, 1149–1158.
- 479 Hempton, G.P., Archibald, S. & Bond, W.J. (2015) A continent-wide assessment of the form
480 and intensity of large mammal herbivory in Africa-supplemental. *Science*, **1056**.
- 481 Hibert, F., Calenge, C., Fritz, H., Maillard, D., Bouché, P., Ipavec, A., Convers, A.,
482 Ombredane, D. & Visscher, M.-N. (2010) Spatial avoidance of invading pastoral cattle
483 by wild ungulates: insights from using point process statistics. *Biodiversity and
484 Conservation*, **19**, 2003–2024.
- 485 Hopcraft, J. & Morales, J. (2014) Competition, predation, and migration: individual choice
486 patterns of Serengeti migrants captured by hierarchical models. *Ecological ...*, **84**, 355–
487 372.
- 488 Illius, A.W. & O'Connor, T.G. (2000) Resource heterogeneity and ungulate population
489 dynamics. *Oikos*, **89**, 283–294.
- 490 Jachowski, D.S., Slotow, R. & Millsaugh, J.J. (2014) Good virtual fences make good

- 491 neighbors: Opportunities for conservation. *Animal Conservation*, **17**, 187–196.
- 492 Johnson, D.S., Hooten, M.B. & Kuhn, C.E. (2013) Estimating animal resource selection from
493 telemetry data using point process models. *Journal of Animal Ecology*, **82**, 1155–1164.
- 494 Juffe-Bignoli, D., Burgess, N.D., Bingham, H., Belle, E.M.S., de Lima, M.G., Deguignet, M.,
495 Bertzky, B., Milam, a N., Martinez-Lopez, J., Lewis, E., Eassom, A., Wicander, S.,
496 Geldmann, J., van Soesbergen, A., Arnell, a P., O'Connor, B., Park, S., Shi, Y.N.,
497 Danks, F.S., MacSharry, B. & Kingston, N. (2014) *Protected Planet Report 2014*.
498 Cambridge, UK.
- 499 Kartzinel, T.R., Chen, P. a., Coverdale, T.C., Erickson, D.L., Kress, W.J., Kuzmina, M.L.,
500 Rubenstein, D.I., Wang, W. & Pringle, R.M. (2015) DNA metabarcoding illuminates
501 dietary niche partitioning by African large herbivores. *Proceedings of the National*
502 *Academy of Sciences*, **112**, 201503283.
- 503 Kuiper, T.R., Loveridge, A.J., Parker, D.M., Johnson, P.J., Hunt, J.E., Stapelkamp, B.,
504 Sibanda, L. & Macdonald, D.W. (2015) Seasonal herding practices influence predation
505 on domestic stock by African lions along a protected area boundary. *Biological*
506 *Conservation*, **191**, 546–554.
- 507 De Leeuw, J., Waweru, M.N., Okello, O.O., Maloba, M., Nguru, P., Said, M.Y., Aligula,
508 H.M., Heitko, I.M.A., Reid, R.S., De Leeuw, J., Waweru, M.N., Okello, O.O., Maloba,
509 M., Nguru, P., Said, M.Y., Aligula, H.M., Heitkonig, I. & Reid, R.S. (2001) Distribution
510 and diversity of wildlife in northern Kenya in relation to livestock and permanent water
511 points. *Biological Conservation*, **100**, 297–306.
- 512 Loarie, S.R., van Aarde, R.J. & Pimm, S.L. (2009) Fences and artificial water affect African
513 savannah elephant movement patterns. *Biological Conservation*, **142**, 3086–3098.
- 514 Miguel, E., Grosbois, V., Caron, A. & Bouludier, T. (2013) Contacts and foot and mouth
515 disease transmission from wild to domestic bovines in Africa. *Ecosphere*, **4**, 1–32.
- 516 Murwira, A., De Garine-wichatitsky, M., Zengeya, F.M., Poshiwa, X., Matema, S., Caron, A.,
517 Guerbois, C., Hellard, E. & Fritz, H. (2013) Resource gradients and movement across
518 the edge of transfrontier parks. *Transfrontier conservation areas: people living on the*
519 *edge* (eds J.A. Andersson, M. De Garine-Wichatitsky, D.H.M. Cumming, V.
520 Dzingirai), & K.E. Giller), pp. 123–136. Routledge, London and New York.
- 521 Newmark, W.D. (2008) Isolation of African protected areas. *Frontiers in Ecology and the*
522 *Environment*, **6**, 321–328.
- 523 Odadi, W.O., Karachi, M.K., Abdulrazak, S. a & Young, T.P. (2011) African wild ungulates
524 compete with or facilitate cattle depending on season. *Science*, **333**, 1753–5.
- 525 Ogutu, J.O., Reid, R.S., Piepho, H.-P., Hobbs, N.T., Rainy, M.E., Kruska, R.L., Worden, J.S.
526 & Nyabenge, M. (2014) Large herbivore responses to surface water and land use in an
527 East African savanna: implications for conservation and human-wildlife conflicts.
528 *Biodiversity and Conservation*, **23**, 573–596.
- 529 Palomo, I., Montes, C., Martín-López, B., González, J.A., García-Llorente, M., Alcorlo, P. &
530 Mora, M.R.G. (2014) Incorporating the social-ecological approach in protected areas in
531 the anthropocene. *BioScience*, **64**, 181–191.
- 532 Redpath, S.M., Young, J., Evely, A., Adams, W.M., Sutherland, W.J., Whitehouse, A., Amar,
533 A., Lambert, R.A., Linnell, J.D.C., Watt, A. & Gutiérrez, R.J. (2013) Understanding and
534 managing conservation conflicts. *Trends in Ecology and Evolution*, **28**, 100–109.

- 535 Roughgarden, J. (1976) Resource partitioning among competing species--a coevolutionary
536 approach. *Theoretical population biology*, **9**, 388–424.
- 537 Sinclair, A.E. (1977) *The African Buffalo A Study of Ressource Limitation of Populations* (ed
538 GB Schaller). The University of Chicago Press, Chigago and London.
- 539 Sitters, J., Heitkönig, I.M.A., Holmgren, M. & Ojwang, G.S.O. (2009) Herded cattle and wild
540 grazers partition water but share forage resources during dry years in East African
541 savannas. *Biological Conservation*, **142**, 738–750.
- 542 Somers, M.J. & Hayward, M.W. (eds). (2011) *Fencing for Conservation: Restriction of
543 Evolutionary Potential or a Riposte to Threatening Processes?* Springer Science &
544 Business Media.
- 545 Stewart, K.M., Bowyer, R.T., Kie, J.G., Cimon, N.J. & Johnson, B.K. (2002) Temporospatial
546 Distributions of Elk, Mule Deer, and Cattle: Resource Partitioning and Competitive
547 Displacement. *Journal of Mammalogy*, **83**, 229–244.
- 548 Thurfjell, H., Ciuti, S. & Boyce, M.S. (2014) Applications of step-selection functions in
549 ecology and conservation. *Movement Ecology*, **2**, 26.
- 550 Valeix, M., Chamaillé-Jammes, S. & Fritz, H. (2007) Interference competition and temporal
551 niche shifts: elephants and herbivore communities at waterholes. *Oecologia*, **153**, 739–
552 748.
- 553 Valeix, M., Loveridge, A.J., Davidson, Z., Madzikanda, H., Fritz, H. & Macdonald, D.W.
554 (2010) How key habitat features influence large terrestrial carnivore movements:
555 waterholes and African lions in a semi-arid savanna of north-western Zimbabwe.
556 *Landscape Ecology*, **25**, 337–351.
- 557 Walker, B.H., Emslie, R.H., Owen-Smith, N. & Scholes, R.J. (1987) To Cull or Not to Cull :
558 Lessons from a Southern African Drought. *Journal of Applied Ecology*, **24**, 381–401.
- 559 Western, D. (1975) Water availability and its influence on the structure and dynamics of a
560 savannah large mammal community. *East African Wildlife Journal*, **13**, 265–286.
- 561 Western, D., Groom, R. & Worden, J. (2009) The impact of subdivision and sedentarization
562 of pastoral lands on wildlife in an African savanna ecosystem. *Biological Conservation*,
563 **142**, 2538–2546.
- 564 Williamson, B.R. (1975) The condition and nutrition of elephant in Wankie National Park.
565 *Arnoldia*, **7**, 1–16.
- 566 Young, T.P., Palmer, T.M. & Gadd, M.E. (2005) Competition and compensation among
567 cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biological
568 Conservation*, **122**, 351–359.
- 569 Zengeya, F.M., Murwira, A., Caron, A., Cornélis, D., Gandiwa, P. & de Garine-Wichatitsky,
570 M. (2015) Spatial overlap between sympatric wild and domestic herbivores links to
571 resource gradients. *Remote Sensing Applications: Society and Environment*, **2**, 56–65.
- 572
- 573