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Spatial avoidance of invading pastoral cattle by wild ungulates: insights from using point process statistics

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Abstract Traditional rangelands in many developing countries are currently being encroached by cultivation, driving some herders to illegally use protected areas for grazing their cattle. Since cattle are an exotic species in these ecosystems, they might have an impact on the local wild herbivore communities, notably through competition. We used point pattern statistics to characterise the spatial relationships between wild ungulate species and cattle herds within a protected area in west Africa undergoing seasonal intrusions by cattle. We predicted that the wild ungulate species that are ecologically and morphologically similar to cattle, in terms of body mass and diet, would be more sensitive to grass depletion by cattle and would be separated from cattle to a larger extent. The spatial distribution of browsing and mixed-feeding antelopes did not seem to be affected much by cattle presence, whereas most grazing species showed spatial separation from cattle. Interestingly, elephants also showed significant separation from cattle herds. We discuss the likely processes that may have contributed to the observed spatial patterns. The

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spatial displacement of certain wild species, including megaherbivores, affects the whole community structure and, thus, other components of the ecosystem.

Keywords Cattle · Competition · Ungulate community · Distribution · West Africa · Ripley function

Abbreviations
WRP   W Regional Park

Introduction

In many developing countries, and particularly in sub-Saharan Africa, increasing human and associated livestock populations have resulted in the enhanced use of the last 'natural' areas for grazing (Sayer 1979; De Bie 1991; Prins 1992, 2000; Sournia 1998). The sustainability of pastoral activities is questionable from an ecological point of view when most of the endangered biodiversity, notably the large herbivore community, is supported by these areas (Prins 1992). Several studies have reported potential or actual effects of the introduction of livestock on native wild ungulates (Kie et al. 1991; Loft et al. 1991; Prins 1992; Fritz et al. 1996; Khan et al. 1996; Voeten and Prins 1999; Voeten 1999; Stephens et al. 2001; Coe et al. 2001, 2005; Mishra et al. 2004; Young et al. 2005). Most of these showed that, in the presence of competing cattle, wild species adapt their foraging behaviour by using a 'refuge' habitat or by modifying their diet. However, only a few of these studies focused on the resulting spatial partitioning between wild and domestic species (Sinclair 1982; Bergström and Skarpe 1999; Madhusudan 2004) and how it shapes the whole ungulate community when animals are free to move over large areas. Furthermore, the large herbivore community is assumed to play a key role in the functioning of African savanna ecosystems (e.g. McNaughton and Geordiadis 1992; Olff and Ritchie 1998). Hence, other components of the biodiversity of the remnant savanna areas may be indirectly impacted if pastoral activities affect the large herbivores.

In this paper, we investigate the potential impact of pastoral activities on the diverse ungulate community of a west African savanna (Hibert et al. 2004) by focusing on the spatial behavioural responses of wild species. We used spatial statistics to analyse the ungulate spatial distribution observed during two aerial surveys conducted in 2002 and 2003 over the 10,200 km^2 trans-frontier W Regional Park (WRP) in Burkina Faso, Benin and Niger (Fig. 1). This paper presents a geographical approach as a prelude to follow-up multivariate studies of spatial patterns integrating environmental variables.

Pastoral activities may affect spatial distributions of wild ungulates through different processes. First, wildlife displacement may result from competition by livestock for pastures (e.g. Madhusudan 2004). In addition, some species, particularly if they are poached, might tend to avoid the human presence (herders) associated with cattle (e.g. de Leeuw et al. 2001; Bonnington et al. 2007). In this paper, we focus on potential competition following massive introduction of cattle (>20,000 head) into WRP at the end of the dry season—a period of low forage resource availability—but we will also discuss the possible effects of other factors.

Owing to allometric relationships between digestive systems (Gordon and Illius 1994), forage selection and mouth morphology (Gordon and Illius 1988), herbivore species of
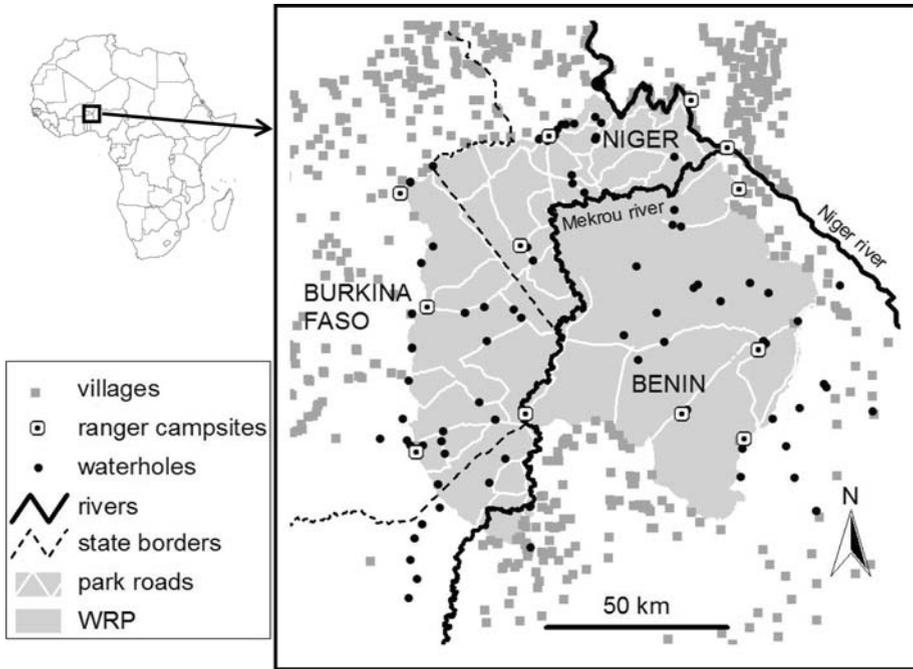
Fig. 1 Map of the west Africa's W Regional Park (WRP) in April 2003

similar body weights and feeding styles are expected to show a high degree of habitat overlap (Illius and Gordon 1987; Robbins et al. 1995; Basset 1995; Ritchie and Olff 1999; Pérez-Barbería and Gordon 1999). They might thus compete for food resources when they co-occur (Belovsky 1986; Prins and Olff 1998; Voeten and Prins 1999; Ritchie and Olff 1999; Prins et al. 2006). Large and medium sized grazing ungulates are expected to have food requirements close to those of grazing cattle (Van Soest 1982; Hofmann 1989). Local depletion of grass by cattle might compel wild grazers to forage on stands that are not yet depleted whereas species that do not exclusively feed on grass, such as mixed feeders, browsers or species that feed on rhizomes and roots, should be less affected. Although less mobile (Sinclair 1977; Owen-Smith 1988; Basset 1995), smaller grazers use smaller patches of grass that might have insufficient forage for larger cattle, which have greater requirements (Illius and Gordon 1987). Under the hypothesis of competition by resource depletion, large grazing ungulates should be the most spatially impacted by cattle since they cannot find enough food in the area where cattle concentrate. Hence, we expect (1) large grazers to be spatially separated from cattle groups even at large scales, (2) smaller grazers to be separated at smaller scales only, and (3) other guilds to be less separated or independent of cattle distribution. Furthermore, since cattle herds are known to mainly concentrate on a certain part of the WRP (Toutain et al. 2001; Convers 2002), the wild community structure, in terms of guild abundance, should be locally affected. Wild grazers, unlike other guilds, are expected to occur in lower densities in areas occupied by cattle than in the rest of the Park (4). Their density in the rest of the park should, however, not exceed the natural limit set by the resource availability (see Fritz et al. 2002). Hence, the presence of cattle should result in a lower density of wild grazers and, consequently, of

the overall herbivore assemblage at the scale of the whole WRP (5) than expected under 'natural' undisturbed conditions.

Materials and methods

Study site

The W Regional Park (WRP) (N 12°, E 2°30′) comprises three contiguous National Parks crossing the borders of Benin (5,500 km²), Burkina Faso (2,500 km²) and Niger (2,200 km²) (Fig. 1). This World Heritage area is emblematic of the remaining transitional areas from sahelian to savanna vegetation in west Africa and hosts a high diversity of endangered wildlife (Poché 1973; Hibert et al. 2004). The vegetation is structured along the southwest–northeast climatic gradient (annual rainfall: 600 mm in the north and 1,000 mm in the south), with an increase in density and height of ligneous species towards the south (Arbonnier 2002; Dulieu 2004). Rainfall only occurs during the well defined rainy season (May/June–September/October). A few first rain storms (total <40 mm) that fell during the 3 weeks before each aerial count (cf. data on animal distribution) were, however, sufficient to ensure the regrowth of nutrient-rich perennial grasses and forbs in patches. These rains also filled temporary ponds in the south-eastern and western parts of the WRP (Fig. 1).

Pastoral activities

In the 1970s and 1980s, the combination of severe droughts in the Sahel region, the control of tsetse fly and increasing vaccination of livestock and people against diseases of the more humid, southern areas, have favoured the massive southward dispersal of cattle (Bourn and Wint 1994; Boutrais 1997). The traditional pasture ranges surrounding the WRP are being encroached by agriculture as a consequence of increasing human demography and development of cotton cultivation. As a consequence, the settlers have been searching for new land to crop and water and pastures for their livestock in the protected areas (Hempe 1975; Sinsin 1998). This has resulted in serious conflicts with the authorities who have had few means for countering the intrusions (Toutain et al. 2004; Newby 2005; Binot et al. 2006).

Livestock movement in the region surrounding the WRP is more marked at the end of the dry season, between February and May when forage and water become scarce (Convers 2002). Herders from Niger and Burkina Faso leave their villages either for short movements in the country, or to cross the borders to Benin or Togo (Toutain et al. 2001). Some herders illegally lead their herds to the WRP in search of better pastures in the main drainage lines and secondary valleys. Their residence in an area can last from a few days to a week, depending on the size of their herds, the availability of resources and the local level of control by the Park rangers. Herds are usually grouped together for protection from predators, livestock raiders and ranger patrols, and because they concentrate on areas with high quality forage. This usually results in both large and small scale aggregations. Until recently, herders mainly used the southeastern part of the WRP where the Park lacked roads and quick access for ground patrols (Convers 2002). Herds are composed of 90% cattle (*Bos indicus, Bos taurus* × *Bos indicus*), 10% sheep (*Ovis aries*) and goats (*Capra hircus*) and less than 1% pack animals such as donkeys, horses and camels (Convers 2002;

Bouché et al. 2004). Herders return to their villages when rain starts to fall in great amounts, mostly in July.

Animal distribution data

Aerial surveys of wild and domestic ungulates were carried out in the WRP region in the late, hot dry season, from the end of April to the beginning of May in 2002 and at the end of April 2003. Each detected group was located on a map using a global positioning system (GPS) (Fig. 2). Both surveys were conducted along straight and parallel transects. In 2002, the survey was carried out according to a sampling method (Norton-Griffiths 1978). The area was divided into blocks in which flight lines were systematically spaced 5 km apart, surveying a 200 m wide strip on each side of the aircraft and resulting in a 8.6% sampling rate (Rouamba et al. 2002). In 2003, the survey consisted of a total count (Douglas-Hamilton 1996). Flight lines were spaced every kilometre, allowing the survey of a 500 m wide strip on each side of the aircraft and resulting in a total count of large ungulates throughout the WRP (Bouché et al. 2004). In both surveys, four seated CESSNA 172 and 175 aircrafts were used, flying at an average altitude of 200–400 feet above the ground level and at a mean speed of 130–150 km/h.
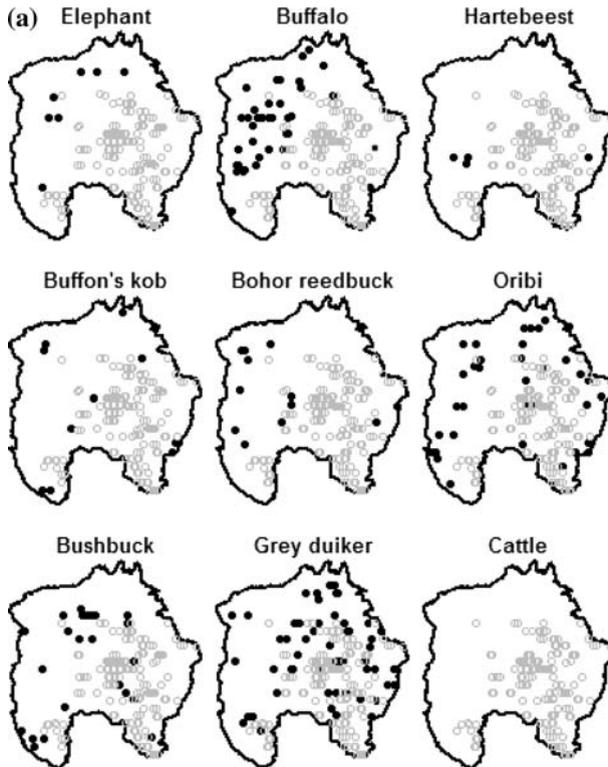

Fig. 2 Spatial distributions of wild and domestic ungulates in W Regional Park at the end of dry season **a** in 2002 (sample aerial survey) and **b** in 2003 (total aerial survey). *Solid black circles* represent groups of wild species (or individuals of solitary species) and *hollow grey circles* show locations of cattle herds
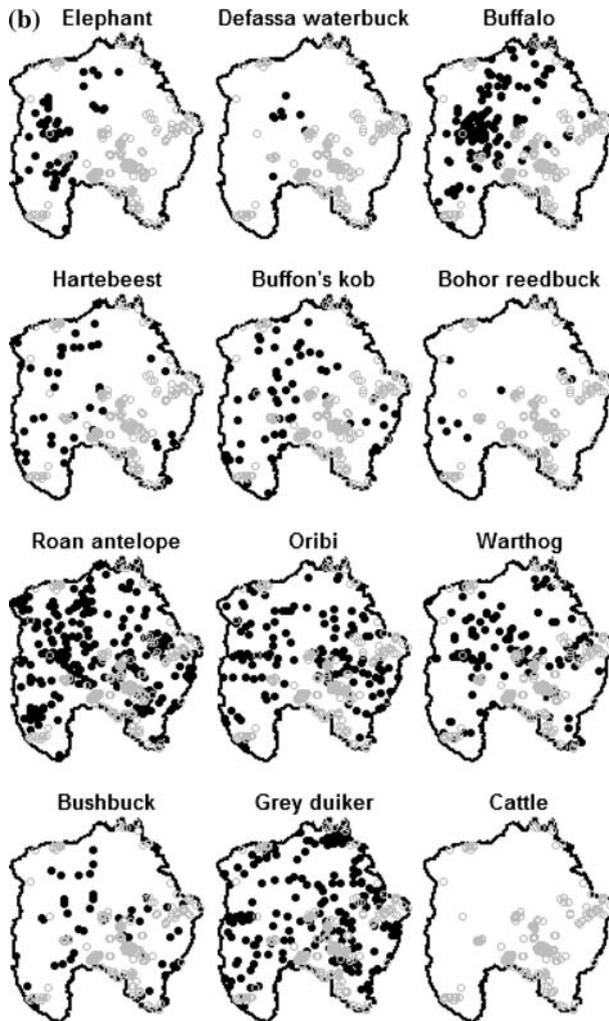
Fig. 2 continued

Aerial surveys are appropriate for surveying large sized gregarious species such as elephant and buffalo, but tend to underestimate the abundance of other ungulates (Jachmann 2002; Redfern et al. 2002). Nevertheless, the 2003 aerial survey provided substantial numbers of animal locations, allowing spatial distribution analyses for 11 of the 14 terrestrial ungulate species living in the WRP (Table 1). We could not conduct analyses for warthog and roan antelope in 2002 because data were not available for these species.

Animal body masses and diets

Data on the body mass and diet of the wild ungulates of the WRP region were taken from the field guide of Lamarque (2004) (Table 1). Schuette et al. (1998) confirm the categorization of the roan antelope (*Hippotragus equinus*) as a mixed-feeder (<50% grass in the

Table 1 Body mass and feeding style of W Regional Park ungulate species and results of the aerial surveys conducted in 2002 and 2003

Species		Body mass (kg)	Main feeding style at the end of dry season	2002 sample survey		2003 total survey		
Common name	Scientific name			Groups	Individuals	Groups	Individuals	Maximum group size
Cattle	*Bos indicus, Bos taurus × Bos indicus*	300	Grazer	153	19,492	200	20,881	1,000
Roan antelope	*Hippotragus equinus* Desmarest, 1804	265	Mixed-feeder	–	–	251	1,641	37
Grey duiker	*Sylvicapra grimmia* Linnaeus, 1758	15	Browser	53	55	184	213	2
Buffalo	*Syncerus caffer brachyceros* Sparrman, 1779	415	Grazer	40	550	148	3,094	100
Oribi	*Ourebia ourebi* Zimmermann, 1783	16	Mixed-feeder	35	48	134	176	3
Warthog	*Phacochoerus africanus* Gmelin, 1788	83	Grazer/rhizome eater	–	–	112	298	14
Elephant	*Loxodonta africana* Blumenbach, 1797	3,925	Mixed-feeder/browser	9	64	74	935	150
Buffon's kob	*Kobus kob* Erxleben, 1777	76	Grazer	10	18	62	118	6
Bushbuck	*Tragelaphus scriptus* Pallas, 1766	51	Browser	23	28	48	59	2
Western hartebeest	*Alcelaphus buselaphus major* Pallas, 1766	160	Grazer	4	28	43	250	22
Bohor reedbuck	*Redunca redunca* Pallas, 1767	48	Grazer	12	18	10	13	3
Defassa waterbuck	*Kobus ellipsiprymnus defassa* Ogilby, 1833	200	Grazer	–	–	9	29	7
Topi	*Damaliscus lunatus korrigum* Burchell, 1824	120	Grazer	–	–	2	4	2
Red-fronted gazelle	*Gazella rufifrons* Gray, 1846	28	Mixed-feeder/browser	–	–	2	6	5
Red-flanked duiker	*Cephalophus rufilatus* Gray, 1846	11	Browser	–	–	–	–	–

diet) in the late, hot dry season in Burkina Faso. This is surprising since the species has been classified as mainly a grazer by most studies in eastern and southern Africa (e.g. Estes 1997; Child and Wilson 1964). At the end of the dry season, the warthog, which is usually a grazer, specializes on the underground rhizomes of perennial grasses and sedges, and on bulbs and tubers (Estes 1997; Lamarque 2004).

The average body masses of local breeds of cattle (*Bos indicus* and *Bos taurus* × *Bos taurus*) were taken from local enquiries (Convers 2002) (Table 1). According to interviewed local herders, cattle forage non-selectively on dry culms and a bit on browse when entering the WRP. A few studies in west Africa describe this browsing behaviour of cattle during the dry season (Le Houérou 1989; de Leeuw and Tothill 1990; De Bie 1991; Houinato and Sinsin 2000). However, the cattle were said to quickly and completely abandon browse once led to greener stands, as they selectively searched for fresh grass items.

Spatial relationships between wild and domestic ungulates

We used the bivariate K_{12} function (Lotwick and Silverman 1982) to study the spatial relationship between each wild species and the cattle herds at different scales, i.e. to see whether cattle and wild species were segregated, independently distributed or aggregated. For a given wild species, this function measures the average number of groups located within a distance s of a randomly chosen cattle herd, divided by the overall density of the wild species' groups. This function was estimated with the approximately unbiased estimator given by Lotwick and Silverman (1982). To facilitate the graphical interpretation of the relationship between cattle herds and wild species groups, we calculated the linearized corresponding L_{12} function defined by $\hat{L}_{12}(s) = \sqrt{\hat{K}_{12}(s)/\pi} - s$ (Lotwick and Silverman 1982; Diggle 1983). Under the assumption of independence between two types of points, the locations of type 2 events (wild species groups) should be random with respect to those of type 1 events (herds of cattle) (Bailey and Gatrell 1995). The expected number of type 2 events within a distance s of a randomly chosen type 1 event is $\lambda_2 \pi s^2$ in the case of a uniform distribution, with λ_2 the density of type 2 events. Thus, theoretically, if the two types of events are independent, $\hat{K}_{12}(s) = \pi s^2$ and hence $\hat{L}_{12}(s) = 0$. If there are more neighbours of type 2 within a distance s of an arbitrary event of type 1 than expected under the assumption of independence, then $\hat{K}_{12}(s) > \pi s^2$ and $\hat{L}_{12}(s) > 0$. This indicates a positive dependence between the two types of events (Diggle 1983) and can be interpreted as an attraction between the two populations. On the other hand, $\hat{K}_{12}(s) < \pi s^2$ and $\hat{L}_{12}(s) < 0$ indicate negative dependence, which can be interpreted as a repulsion between the types of events (Goreaud and Pélissier 2003).

We simulated independence by keeping the location of cattle points unchanged while randomly shifting the locations of the wild ungulates over the study area 1,000 times. The study area was considered as a torus to allow this shifting operation (i.e. top boundary of the area connected to the bottom boundary, and left boundary connected to the right boundary), as advised by several authors (Lotwick and Silverman 1982; Diggle 1983; Goreaud and Pélissier 2003). For each distance value s, the intervals encompassing 95, 90, 80 and 50% of the 1,000 simulated values of $\hat{K}_{12}(s)$ around their median were delineated by the sample quantiles corresponding to the probabilities 2.5–97.5, 5–95, 10–90 and 25–75%, respectively. Corresponding limits of the linearised

$\hat{L}_{12}$ were then derived to graphically identify areas where the empirical data were more extreme than the random simulations.

All spatial analyses were performed using the *ade4* (Dray and Dufour 2007) and *splancs* (Rowlingson et al. 2007) packages in the R.2.7.1 software (R Development Core Team 2008).

Ungulate community structure

The concentration of cattle in some parts of the WRP may have affected the structure of herbivore community in terms of local and overall abundances. We therefore compared the biomass densities of wild and domestic ungulates observed in the park with the densities expected for this type of area under predictive statistical models fitted from a sample of African protected areas.

First, we browsed the 1998 African Antelope Database (East 1999), the African Elephant Database (1995–2007: http://iucn.org/themes/ssc/sgs/afesg/aed/indexfr.htm) the Equids Database (Moehlman 2002) and data compiled by Delany and Happold (1979), Eltringham (1979), Milligan et al. (1982) and Douglas-Hamilton (1987) to collect information on ungulate abundances in 31 reference sites in Africa. We chose the reference sites from among African savanna protected areas known to be relatively well preserved at the times of the surveys (see Appendix 1). We then built a linear regression model to predict the biomass densities of herbivores expected in an area according to the annual rainfall (RAIN), the soil nutrient status (SOIL) and a proxy for vegetation production (PROD) derived from Normalised Difference Vegetation Indices (NDVI) (Hibert and Fritz 2007, unpublished data). We fitted linear regression models to this new dataset for: (i) the total herbivore biomass density (TOTAL), (ii) the megaherbivore (herbivores weighing more than 1 ton) biomass density (MEGA), and (iii) the mesograzer biomass density (grazers weighing less than 1 ton) (MESOG). So far, no environmental model has been found to satisfactorily explain the variability in biomass density for mesobrowsers (browsers weighing less than 1 ton). Biomass densities were calculated as following: $BD_i = \frac{1}{A} * \sum_{j=1}^{ni} \sum_{k=1}^{nj} s_{jk} * m_j^{0.75}$, with BD_i: the biomass density of guild i in the considered area A, n_i: the number of species of guild i, n_j: the number of observed groups of species j in area A and s_{jk}: the observed size of group k of species j.

For low quality soils such as in the WRP area, the selected biomass density models fitted to the data from the 31 African reference sites are:

$$\text{Log}_{10}\text{TOTAL} = 0.5382 \cdot \text{Log}_{10}\text{RAIN} + 1.0741 \; (R^2 = 0.45),$$
$$\text{Log}_{10}\text{MEGA} = 2.85 \cdot \text{Log}_{10}\text{PROD} + 2.28 \; (R^2 = 0.48) \text{ and}$$
$$\text{Log}_{10}\text{MESOG} = 0.875 \cdot \text{Log}_{10}\text{RAIN} - 0.2917 \; (R^2 = 0.54).$$

Annual rainfall is expressed in mm year^{-1}, biomass densities in kg$^{0.75}$ km^{-2}. To take into account their behaviour as partial grazers, we included half of the biomasses of warthog, oribi and roan antelope in the calculation of the total wild mesograzer abundance of the WRP.

We used these models to predict the biomass density of each guild in: (i) the whole WRP, (ii) the illegal pastoral area, (iii) outside the illegal pastoral area. The illegal pastoral area was estimated by the area encompassing 80% of cattle herd locations, using the classical kernel method with a smoothing parameter h value of 10.7 km given by the reference method (calculations were computed with the R function *kernelUD* of the package *adehabitat*; Calenge 2006). Finally, we compared these predicted densities with

the densities of the different guilds observed during the 2003 total count in these areas. We did not carry out comparisons with 2002 density estimates since records for roan antelope and warthog were not available. Confidence intervals around predicted values were computed using the R function *predict.lm* of the package *stats*.

Results

Spatial relationships

For both years, aerial surveys showed encroachment of aggregated herds of cattle in the south-eastern part of the WRP (Fig. 2). The analysis of the bivariate *L* functions (Appendix 2, summarised in Table 2) revealed that, except for elephant, the species assumed to partly or completely use alternative resources to grass (Table 1) did not appear to be separated from cattle, unlike most 'pure' grazers. As expected, for larger grazers (buffalo, Defassa waterbuck, hartebeest), separation from cattle tended to occur even at large scales (>10 km), whereas for smaller grazers (Buffon's kob, Bohor reedbuck) it occured only at smaller scales (Appendix 2, Table 2). The tendency for separation from cattle was not confirmed for Bohor reedbuck or in buffalo, however, by the 2003 survey in spite of negative values of *L* similar to the 2002 pattern in buffalo.

The most spectacular deviation from expectations was for the elephant, which, in both years, exhibited extreme separation compared with simulated independent distributions, even at large scales (>10 km) (Appendix 2, Table 2). In contrast, oribi tended to aggregate with cattle herds at small scales in 2002, as did warthog, bushbuck and grey duiker at larger scales in 2003.

Community structure

We compared herbivore densities measured during the 2003 survey with the 95% confidence intervals (CI) of the predictions of the models of biomass density for each guild. The total wild herbivore density calculated for the whole WRP appeared significantly lower than the model predictions for similar environmental conditions [1.94 $\log_{10}(\text{kg}^{0.75}\ \text{km}^{-2})$, model (95% confidence interval on the prediction): $2.65 \pm 0.67\ \log_{10}(\text{kg}^{0.75}\ \text{km}^{-2})$]. The elephant and wild mesograzer densities were also lower than predicted values but not significantly [elephant: 1.66, model: $2.06 \pm 0.67\ \log_{10}(\text{kg}^{0.75}\ \text{km}^{-2})$; wild mesograzers: 1.55, model CI: $2.26 \pm 0.77\ \log_{10}(\text{kg}^{0.75}\ \text{km}^{-2})$]. However, in the illegal pastoral area, i.e. mainly the south-eastern part of the WRP, both elephant and wild mesograzer densities were significantly lower than predicted densities unlike outside the illegal pastoral area (Fig. 3). Interestingly, the biomass density of wild grazers combined with domestic grazers reached the predicted value at the scale of the entire park ($2.26\ \log_{10}(\text{kg}^{0.75}\ \text{km}^{-2})$). These patterns strongly suggest a functional substitution of wild grazers by domestic ones in the illegal pastoral area.

Discussion

Sinclair (1985) suggested that interspecific competition in African ungulates might induce "an avoidance of the overcompeting ungulates through greater spacing; group distances

Table 2 Summary of spatial relationships between cattle and wild ungulates on the W Regional Park at the end of dry season

Diet (end of dry season)	Species	Spatial interaction			Scales of significant interaction between the wild species groups and cattle herds (km)					
		Expected	2002	2003	2002			2003		
					$P < 0.025$	$P < 0.05$	$P < 0.10$	$P < 0.025$	$P < 0.05$	$P < 0.10$
Large grazers	Buffalo	–	–	o	9.5–10; 13–15	3–18	3–20			
	Defassa waterbuck	–	No data	(–)	No data	No data	No data			11.5
	Hartebeest	–	(–)	(–)	No data	No data	8–8.5; 14–15.5		10–11; 12–14	1.5; 9–15.5
Smaller grazers	Buffon's kob	–	–	(–)	5.5–7	4–9	2–9.5		7–10.5	5.5–11
	Bohor reedbuck	–	–	o	4.5–5	3.5–5.5	2.5–5.5; 8.5–10			
/rhizome eater	Warthog	o/-	No data	(+)	No data	No data	No data		0.5	0.5–4.5
Mixed-feeders	Oribi	o/-	(+)	o			0–0.5			
	Roan antelope	o/-	No data	o	No data	No data	No data			
/browser	Elephant	o/-	–	–	12–14.5; 18–18.5	5–6; 8–15.5; 17–19	>2.5	13–16	11–16.5	1.5; 9.5–18
Browsers	Bushbuck	o	o	(+)					0.5	0.5–3.5
	Grey duiker	o	o	(++)						11.5–16.5

This table summarizes the scales at which aggregation or repulsion between cattle and wild ungulates occur. Spatial relationships were analyzed with L_{12} functions using cattle herd and wild ungulate group locations observed during the 2002 and 2003 aerial surveys. The graphical version of these results is given in Appendix 2. For positive estimators L_{12}, the P-value were estimated as: (number of random values equal to or greater than the observed one + 1)/(number of permutations + 1). In the case of negative estimators, the P-value was estimated as: (number of random values equal to or less than the observed one + 1)/(number of permutations + 1). The null hypothesis (no spatial interaction) was rejected if the P-value was less than the significance level

–, separation at large scale (>10 km); (–), trend to separation at large scale; -, separation at small scale (<10 km); (-), trend to separation at small scale; o/-, separation at low scale or independence; o, independence; (+), trend to aggregation at small scale; (++), trend to aggregation at small scale; +, trend to aggregation at large scale

(a) **Outside the illegal pastoral area**
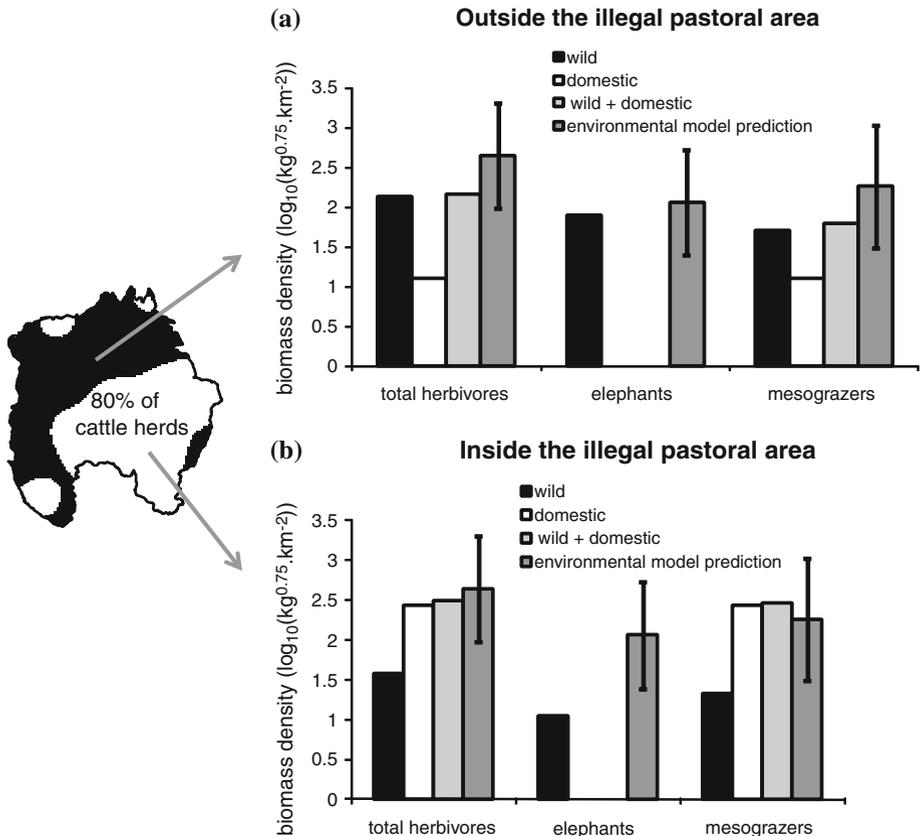
(b) **Inside the illegal pastoral area**

Fig. 3 Comparisons of the observed biomass densities of ungulate guilds of the W Regional Park with those predicted by environmental models, **a** outside the illegal pastoral area, **b** inside the illegal pastoral area, i.e. the area encompassing 80% of cattle herds. Biomass densities in the WRP were calculated from data collected during the 2003 aerial total count, at the end of the dry season. They were compared with the values predicted by biomass density models fitted to the data of 31 African reference sites (Hibert and Fritz 2007, unpublished data) with environmental conditions similar to those of the WRP. Error bars associated to the predicted values represent the 95% confidence intervals

between species should be greater than expected from random". We used point pattern statistics to characterize the spatial relationships between wild ungulate species and intruding cattle herds in the WRP when both green forage and water were scarce. Our two aerial 'snapshots' of the ungulate distribution patterns are admittedly not in themselves sufficient to infer competition between cattle and wild ungulates (see Sinclair 1982; Putman and Wratten 1985; Rosenzweig et al. 1985; Putman 1996; Prins and Olff 1998; Mishra et al. 2004). However, the patterns that we observed were close to those expected under the competition hypothesis: (1) except for elephants, separation from cattle at large scales was only observed in larger grazers, (2) small grazers were separated at smaller scales, (3) other guilds did not show any strong repulsion shift in respect to cattle. As an expected consequence (4), wild grazers appeared to be less abundant in the illegal pastoral area than in the rest of the park and (5), the total herbivore abundance in WRP was lower than expected

under 'natural' undisturbed conditions. However, this latter result might also be due to a deficit in megaherbivores.

Interspecific competition process may result in spatial segregation of species (e.g. in vertebrates, Diamond 1973 or Hairston 1980), as was illustrated on a small scale (<200 ha) by Madhusudan (2004) in the case of resource-mediated competition between wild ungulates and livestock in India. Our approach provides additional measures of scales at which repulsion seems to occur within a much larger area in an African context. A likely scenario of the impact of cattle is that, on exploited pastures just left by cattle herds (mean herd size = 139, SD = 271 in 2002), the sward height was reduced to such a level that the intake rate was not sufficient anymore for large wild grazers (Murray and Illius 2000). If these species—i.e. buffalo and Defassa waterbuck in the vicinity of water points, and more selective grazers feeding on higher swards such as hartebeest (Estes 1997)—could not cope with a lower quality diet and a lower energy intake, they had to move elsewhere (Illius and Gordon 1987). In Kenya, Ego et al. (2003) observed a huge dietary overlap between hartebeest and cattle, suggesting that competition between the two species is likely when resource availability is low. Buffaloes are known to tolerate coarse fodder (Estes 1997; Lamarque 2004) and could thus be less affected than smaller species. Nevertheless, like cattle and other grazers, they are likely to prefer fresh green and nutrient rich grassland to balance any diet deficiencies developed during the dry season.

The distribution of smaller grazers and other species that partially feed on grass at the end of dry season appeared to be less affected at large scales. Smaller grazers, such as Buffon's kob and Bohor reedbuck, have lower food requirements compared to larger species living in larger groups (Jarman 1974). They may be able to afford to remain nearer to cattle, on patches where cattle do not stay long. They may even benefit from residual vegetation if this forage is of sufficient quality, or from a little regrowth soon after the passage of cattle if rain falls (Vesey-Fitzgerald 1960; Gwynne and Bell 1968; Arsenault and Owen-Smith 2002). Indeed, such regrowth is often of higher quality and may suit their requirements.

Bohor reedbuck may be less affected than kobs, as observed in 2003, owing to smaller family units and possible subsistence in habitats with very tall dry and less palatable grass (Estes 1997; Lamarque 2004, pers. obs.). These habitats are usually avoided by cattle herds, according to interviewed herders. Oribi, roan antelope and warthog could also be less frequently ousted from depleted grasslands if they feed on alternatives to grass, such as browse and underground items.

This should also be the case for elephant if this species is a mixed-feeder mainly browsing on sprouting trees and shrubs during the dry season (Cerling et al. 1999; Lamarque 2004). However, we observed a strong spatial separation between cattle and elephants. Competition for grass cannot be totally discarded. Cerling et al. (2006) showed in Kenya that the elephant's diet could shift quickly, with elephants actively searching for grasslands providing a sufficient amount of growing grass after the first rains. There may also be competition for forbs between cattle and elephants as suggested by Odadi et al. (2007) in eastern Africa. Further study of seasonal diet shifts in ungulates of west Africa is still needed. Nevertheless, alternative mechanisms to competition must be considered here.

Before their evacuation following the creation of the W National Parks in the 1950s, local inhabitants traditionally hunted for subsistence. Between the 1950s and 1970s, WRP wildlife then suffered from commercial poaching for ivory (elephant), meat (antelopes) and skins (crocodile, leopard, lion) (Poché 1973, 1974; Hempe 1975).

Commercial poaching has decreased since then, but still occurred in the 1990s in the Beninese part, particularly during the dry season, due to an increasing demand from the cities for bush meat and animal products for traditional pharmacopoeia (Adjakpa 1990; Siddikou 1998; CENAGREF 1999). Long-lived animals such as elephants, whose past experience largely influences their behaviour (Estes 1997), might continue to avoid human beings. Herders of the WRP region, unlike cattlemen of other countries (e.g. Prins 1992), are not known to hunt. However, WRP animals might associate the smell and noise of cattle with human presence and hence avoid areas where cattle roam (Bates et al. 2007; Sam et al. 2002; Georgiadis et al. 2007). Herds are usually led by two people or more in the case of larger herds (Toutain et al. 2001; Convers 2002). Thus, there were certainly more than 400 herders (2×20 herds; Table 1) in the area in 2003. The monitoring of two radio-collared elephants in 2004 during the cattle grazing season confirmed the avoidance of the south-east of WRP that was occupied by cattle (Ipavec et al. 2008). We also cannot either completely exclude a possible direct effect of poaching during the survey periods. The 2003 flight detected four poacher camps in this area and only one in the north-west. However, local studies of poaching do not report any preference for grazers or elephants compared to other guilds, as most ungulate species are targeted (Siddikou 1998; CENAGREF 1999).

Larger predators might also displace wild ungulates (e.g. Creel and Winnie 2005; Mao et al. 2005). However, lions, the main ungulate predators in the WRP, seem to be more abundant in the northern Nigerian part than in the south-eastern Beninese part of the park (Di Silvestre 2008). This suggests a response to prey distribution and human disturbance rather than avoidance of predators by ungulates at a large spatial scale.

Environmental heterogeneity is another factor likely to shape the spatial structure of savanna ungulate communities (Du Toit and Cumming 1999; Chamaillé-James et al. 2007). The intertype K_{12} function is designed to reveal second-order effects corresponding to interactions between points, but only if the assumptions of stationarity and isotropy are met (Pélissier and Goreaud 2001; Goreaud and Pélissier 2003; Cornulier and Bretagnolle 2006). In the WRP, environmental conditions (water availability, structure of vegetation communities) linked to the monsoon vary mainly along a south west–north east axis, making the southern part of the park more attractive for wildlife than the northern one after the first rains. However, this large-scale ecological gradient does not fit with the observed ungulate distribution pattern either (Fig. 2). This supports the hypothesis of a real avoidance of areas where cattle and their herders concentrate by responsive ungulates. Furthermore, if ecologically similar species selected the same resources without competition, they should be aggregated in the same habitat instead of being separated. At smaller scales, similar requirements for water might explain the observed and unexpected tendency of bushbuck, oribi and warthog to aggregate with cattle but does not satisfactorily explain the aggregation of the less water-dependent grey duiker. Further multifactorial studies integrating environmental variables, such as vegetation maps and Normalised Difference Vegetation Index (NDVI), and analyses of ecological niches of both domestic and wild herbivores, will complete this preliminary study of spatial patterns.

As a consequence of behaviourally mediated segregation (direct disturbance by both cattle and humans) and/or competitive processes, the area actually hosting most grazing species and elephants in the WRP is restricted to the north-western part of the park at the end of the dry season. This has certainly been the case for many years, for cattle have regularly encroached on the south-east of the WRP since the 1970s. Grettenberger (1984) stressed that the great increase in grazing of cattle in the 1970s had effectively displaced

wildlife from the most productive habitat in the park and noted 'an influx of elephants from the Benin and Upper Volta (now Burkina Faso) sectors to the Niger W National Park […]. Even within the Niger sector, the amount of illegal activity along the borders had resulted in concentrations of elephants in the middle of the park.' Our comparisons of guild densities to the ones expected in relatively non disturbed conditions strongly suggest that cattle have now functionally replaced wild grazers and ousted the megaherbivores (elephants) from the pastoral area, at least during the end of dry season. The resulting restriction of available space for these guilds seems to explain the large-scale spatial variation in community structure over the park and the marked deficit of large herbivores in the WRP.

In order to better understand the involved processes and to see whether the responses of wildlife to cattle use are season-dependent, we encourage the park's managers to also conduct aerial surveys during the wet season, when forage is not a limiting factor. Continued separated distributions of cattle and wild grazers/elephants in the rainy season would indicate ongoing disturbance by human and cattle presence, whereas independent distributions would imply that domestic and wild animals were separated in the late dry season mainly because of competition for scarce resources. If a further survey is conducted later in the rainy season, when cattle have left the park, and show a concentration of wild ungulates in the south-eastern sector, then it may be possible that cattle have facilitative effects on wild ungulates.

Conclusion

Our approach provides original insights into observed interactions between cattle herds and wild large herbivores by describing the spatial scale at which they occur. It also highlights the risk of major transformation of important components of the biodiversity due to uncontrolled human activities in sites of high natural interest. These sites are indeed often among the less protected ones. Projects funding the operational functioning of natural areas of Africa and other developing countries have been able to slow down the degradation of wildlife populations but most of the time for only the short term period that they last (e.g. see Kremen et al. 1994). Furthermore, our example illustrates how transborder natural areas such as the WRP can suffer from historically different management (or lack of it) in each of their administrative components. The main challenge is to offer sustainable economic alternatives to poaching and herding in the protected areas to surrounding communities.

Appendix 1

See Table 3.

Table 3 List of the African savanna protected areas used as reference ecosystems for the predictive statistical models of ungulate abundance

| Country	Protected area	Period of survey
Benin	Boucle de la Pendjari	1990s
Burkina Faso	Deux Bales	1970s
	Kabore-Tambi	1970s
	Arly	1980s
Cameroon	Bouba Ndjida	1970s
Central African Republic	Manovo-Gounda-Saint Floris	1970s
Congo	Garamba	1960s
	Virunga	1950s
Ivory Coast	Comoe	1970s
Kenya	Samburu Isiolo	1990s
	Tsavo	1970s
Namibia	Etosha	1990s
Nigeria	Kainji Lake	1980s
	Yankari	1970s
South Africa	Kruger	1990s
Tanzania	Serengeti	1990s
	Ugalla River	1990s
	Selous	1990s
	Tarangire	1990s
	Mikumi	1990s
	Moyowosi	1990s
	Mkomazi	1990s
	Ruaha	1990s
	Ngorongoro	1990s
Uganda	Rwenzori Mountains	1970s
Zambia	North Luangwa	1990s
	South Luangwa	1990s
	Kafue	1960s
Zimbabwe	Matusadona	1990s
	Hwange	1990s
	Chizarira	1990s

Appendix 2

See Fig. 4.
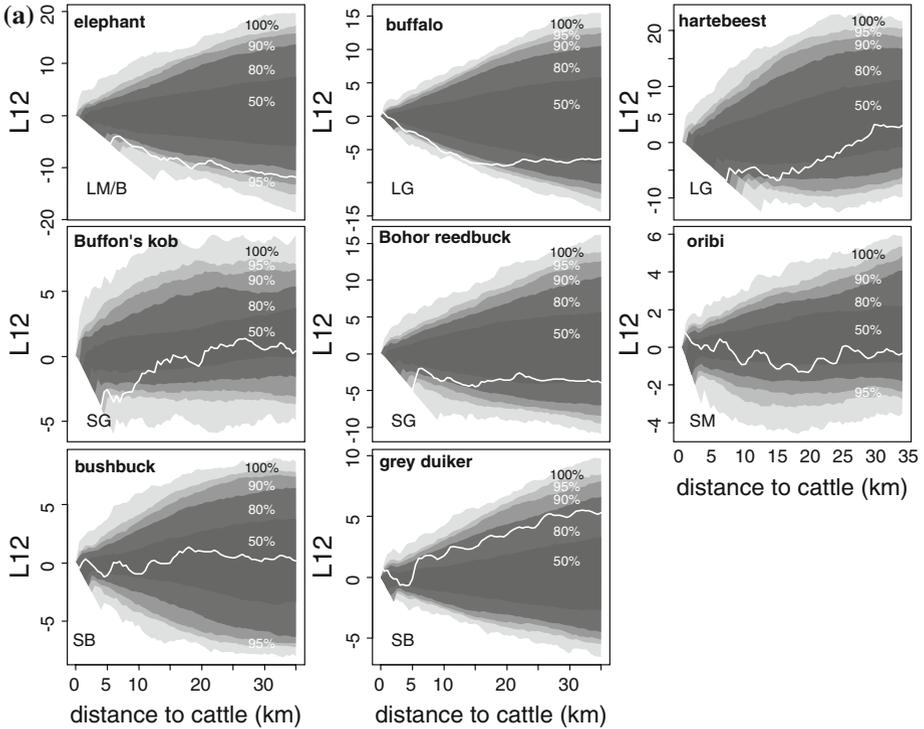
Fig. 4 Plots of bivariate *L* functions against scale showing spatial interaction between wild ungulate species groups and cattle herds in the W Regional Park at the end of the dry season, **a** from animal distributions observed during the 2002 aerial survey and **b** from animal distributions observed during the 2003 aerial survey. The L_{12} values are represented by the *white lines*. The confidence intervals around the simulated values for independence are represented by the *shaded areas*. Values of L_{12} inside the confidence intervals indicate a random distribution; values of L_{12} above (or below) the upper (or lower) confidence interval indicate that the association between the cattle and the wild species is positive (or negative) at the scale considered. Ungulate species were classified according to their size and feeding style as large (L), small (S), mixed-feeder (M), browser (B), grazer (G) and rhizome eaters (RE)
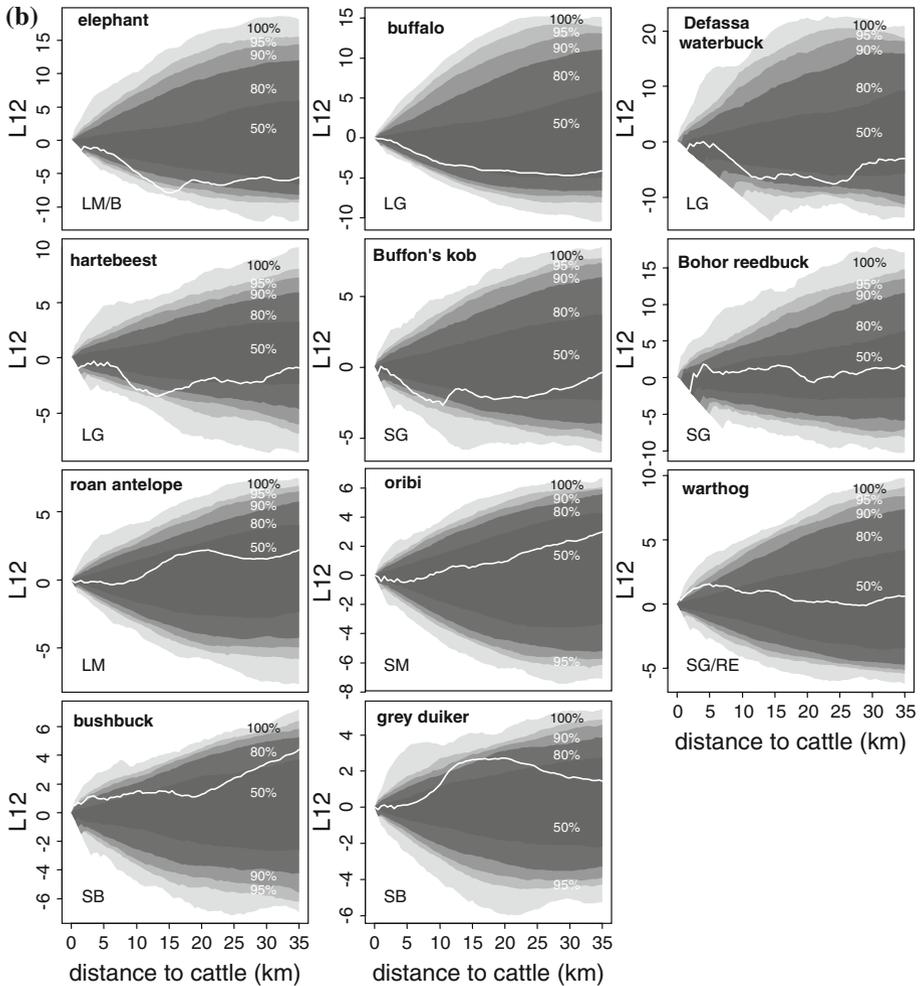
Fig. 4 continued

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