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Large herbivore dynamics in northern Gonarezhou National Park, Zimbabwe

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Abstract: We compared densities and distribution of wild ungulates and domestic livestock based on aerial surveys conducted during 1991 - 2010 in northern parts of Gonarezhou National Park (GNP), Zimbabwe. The sampled area covered approximately 320 km² (Chipinda Pools area) representing ca. 27 % of the GNP, which was colonized by a few herder families along with their cattle in the year 2000. We hypothesized that (1) human and livestock encroachment in the park would lead to decline in densities of native ungulates, and (2) wild ungulates would avoid habitats influenced by humans. The results show that cattle densities significantly increased after the year 2000 whereas the densities of the native ungulates did not differ significantly after 2000. The 'no change' situation in herbivore populations is attributed to strict anti-poaching measures and restriction of human activities within small portion (4 %) of the park. However, the aerial survey does suggest that human and livestock presence in the northern GNP did influence the distribution of wild ungulates. Repeat observations during various seasons would be necessary to understand the spatio-temporal segregation among cattle and wild ungulates.

Resumen: Comparamos las densidades y distribuciones de los ungulados silvestres y el ganado doméstico basado en reconocimientos aéreos realizados durante 1991-2010 en el norte del Parque Nacional Gonarezhou (PNG), Zimbabue. El área de muestreo cubre aproximadamente 320 km² (área de las Pozas Chipinda) que representa aproximadamente 27 % del PNG, que fue colonizado por una pocas familias de pastores junto con su ganado en el año 2000. Nuestras hipótesis fueron: (1) que la invasión humana y la ganadería en el parque llevaría a una disminución en las densidades de ungulados nativos, y (2) que los ungulados silvestres evitarían los hábitats influenciados por los humanos. Los resultados muestran que las densidades de ganado aumentaron significativamente después del año 2000, mientras que las densidades de los ungulados nativos no difirió significativamente después de 2000. La situación sin cambios en las poblaciones de herbívoros se atribuye a las medidas estrictas contra la caza furtiva y la restricción de las actividades humanas en una porción pequeña (4 %) del parque. Sin embargo, el reconocimiento aéreo sugirió que la presencia humana y la ganadería en el norte del PNG sí han influido en la distribución de los ungulados silvestres. Haría falta realizar observaciones repetidas durante varias temporadas para entender la segregación espaciotemporal entre el ganado y los ungulados silvestres.

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Resumo: Compararam-se as densidades e distribuição de ungulados silvestres e animais domésticos com base em levantamentos aéreos realizados durante 1991 - 2010, no norte do Parque Nacional Gonarezhou (PNB), Zimbabwe. A área amostrada cobriu cerca de 320 km2 (área de charcos de Chipinda) representa cerca de 27 % do PNG, que foi colonizada por algumas famílias de pastores junto com o seu gado no ano de 2000. As nossas hipóteses foram: (1) que a invasão humana e de gado no parque levariam a uma diminuição na densidade dos ungulados nativos, e (2) que os ungulados silvestres evitariam habitats influenciados pelos humanos. Os resultados mostram que as densidades de gado aumentaram significativamente depois do ano 2000, enquanto as densidades dos ungulados nativos não diferiram de forma significativa a partir de 2000. A situação sem alterações nas populações de herbívoros é atribuída a estritas medidas contra a caça furtiva e à restrição quanto às atividades humanas a uma pequena parte do parque (4 %). No entanto, o levantamento aéreo sugeriu que a presença humana e da pecuária no norte do PNG influenciaram a distribuição dos ungulados silvestres. Faz falta a realização de observações repetidas durante várias estações entender a segregação espaço-temporal entre o gado e os ungulados silvestres.

Key words: Aerial survey, Africa, conservation, encroachment, habitat, livestock, protected area.

Introduction

Domestic livestock graze more than one third of the world's land area, often sharing space and resources with native ungulates (de Haan *et al.* 1997). Free grazing by livestock in natural areas is known to affect natural vegetation and faunal communities in various ways (Cumming *et al.* 1997; Lambin *et al.* 2003; Shackleton *et al.* 2001; Steinfeld *et al.* 2006). Effects of livestock grazing vary from place to place depending upon their spatio-temporal use of habitat, abundance, niche overlap with wild ungulates and primary productivity. This issue has attracted attention of several researchers around the globe (Acebes *et al.* 2012; Bhatnagar *et al.* 2006; de Boer & Prins 1990; de Iongh *et al.* 2011; du Toit & Cumming 1999; Kittur *et al.* 2010; Odadi *et al.* 2011; Prins & Olff 1998; Walker 1993; Young *et al.* 2005). Direct competition for forage resources between domestic and wild herbivores can lead to changes in foraging behaviour and population dynamics of the latter (de Leeuw *et al.* 2001; Madhusudan 2004).

There has been a steady increase in conflicts for resource use between the local communities and the protected area (PA) managers, especially in developing countries (Lamprey & Reid 2004; Mascia & Pailler 2011; Mworia *et al.* 2008). Human population increase, poverty, land tenure systems, development policies, economic incentives, and political disturbances such as civil wars contribute to encroachment into PAs through expansion of settlements, agriculture, livestock grazing, poaching and even illegal settlements inside legally established PAs (Baudron *et al.* 2011; Kideghesho *et al.* 2006; Newmark 2008; Stephens *et al.* 2001). Human and livestock presence in the wildlife areas often result in elimination of the large mammals, and degradation of habitat (Chaumba *et al.* 2003; Eltringham 1990; Girma *et al.* 2012; Lindsey *et al.* 2011; Mamo & Bekele 2011; Stephens *et al.* 2001). Furthermore, high livestock densities have been reported to have negative effects on wildlife densities, as a result of competition for forage resources between wild herbivores and livestock, given habitat and diet overlap under conditions of resource limitation (du Toit & Cumming 1999; Prins 1992, 2000; Rawat & Sathyakumar 2002).

The Gonarezhou National Park (GNP) in Zimbabwe, like so many of Africa's PAs, has been under anthropogenic pressures including livestock grazing (Gandiwa *et al.* 2011; Mombeshora & Le Bel 2009; Wolmer 2005). Subsequent to the land reforms that occurred in 2000, there were local migration among the herders and encroachment in northern section of the GNP resulting in an increase in livestock, especially cattle (*Bos taurus*) population (Wolmer 2005; Mombeshora & Le Bel 2009). Sudden flux of livestock inside the park is thought to have resulted in competition between domestic and wild herbivores and stress on habitat

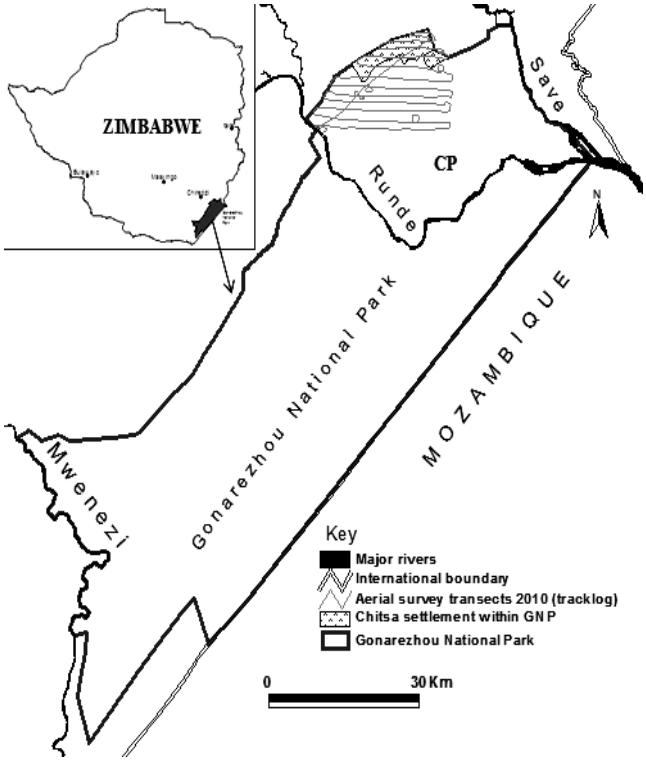


Fig. 1. Location of Gonarezhou National Park, Zimbabwe and transects flown in the September 2010 aerial survey. CP denotes Chipinda Pools aerial survey area bounded by Runde and Save Rivers.

(Gandiwa *et al.* 2011; Muboko 2011;Wolmer 2005). The aim of this study was to investigate the effects of encroachment by the local people and livestock on the native large herbivore densities and distribution in the northern part of the GNP. We hypothesized that: (1) human and livestock encroachment into a protected area would lead to a decline in native herbivore densities, and (2) native large herbivore species would avoid habitats close to human settlements.

Materials and methods

Study area

This study was carried out in the northern parts of GNP covering Chipinda Pools area and Chitsa settlements. Located in southeastern Zimbabwe, this park is spread over an area of 5,000 km^2 (Fig. 1), with bearings between 21° 00' - 22° 15' S and 30° 15' - 32° 30' E, bordering Mozambique and South Africa. Established in the early 1930s as a Game Reserve, GNP was upgraded to a national park under the Parks and Wildlife Act of 1975. Mean annual precipitation for the GNP based on data recorded between 1972 and 2010 is 501 mm (SE = 35). Three seasons can be recognized: hot and wet (November to April), cool and dry (May to August) and hot and dry (September to October). The vegetation of the park is predominantly dry deciduous savanna woodland, characteristic species being mopane (*Colophospermum mopane*), and short grasses (Gandiwa *et al.* 2012). GNP is rich in wild ungulates, notably African buffalo (*Syncerus caffer*), African elephant (*Loxodonta africana*), blue wildebeest (*Connochaetes taurinus*), eland (*Taurotragus oryx*), giraffe (*Giraffa camelopardalis*), hippopotamus (*Hippopotamus amphibius*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), plains zebra (*Equus quagga*), roan antelope (*Hippotragus equinus*), sable antelope (*Hippotragus niger*) and waterbuck (*Kobus ellipsiprymnus*). The large carnivores in the park include cheetah (*Acinonyx jubatus*), lion (*Panthera leo*), and spotted hyena (*Crocuta crocuta*).

Data collection

Data on ungulate density and distribution are based on aerial surveys (Norton-Griffiths 1978). The park management had conducted aerial surveys during 1991 and 2009 which have been kept at Chipinda Pools Research Centre in GNP. The park is divisible into six discrete strata demarcated by well-defined features such as a railway line, roads, rivers, and the park boundary that allows estimation of densities for various areas. For the present study, we only extracted data for the northern stratum of GNP, namely Chipinda Pools, which lies between the Runde and Save Rivers (Fig. 1). Chipinda Pools stratum is an open area allowing animals to move in and out of the stratum when the Runde and Save Rivers have low volumes of water and through the northern park boundary which is unfenced in some sections. A total of seven aerial surveys were conducted between 1991 and 2009 in GNP. Four surveys, conducted in 1991, 1995, 1996 and 1998 had a mean survey area of 1,202 ± 54 km^2 with a mean sampling intensity of 13.25 ± 0.01 % whereas three aerial surveys conducted in 2001, 2007 and 2009 had a survey area of 1,167 km^2 with a mean sampling intensity of 16.77 ± 0.02 %. Previous aerial surveys gave evidence that there were no livestock in the park prior to 2000. We compared densities and distribution of nine large herbivores species, viz., giraffe, buffalo, waterbuck, zebra, eland, elephant, impala, kudu, and cattle (Table 1).

Table 1. Densities of wild ungulates, and cattle (number km^{-2}) based on aerial surveys during 1991 - 2009 in northern Gonarezhou NP, Zimbabwe, and estimates of respective home range sizes. Dash (–) denotes data not available/not applicable.

Year	Month	Cattle	Buffalo	Eland	Elephant	Giraffe	Impala	Kudu	Waterbuck	Zebra	Sampling intensity (%)	Survey area (km^2)	Source
1991	September	–	1.73	–	0.92	0.01	–	–	–	0.25	11.70	1361	Jones (1991)
1995	July	0.00	0.00	0.17	0.98	0.02	0.46	0.10	0.03	0.30	12.70	1137	Davies *et al.* (1995)
1996	August	0.00	0.01	0.02	0.74	0.03	1.24	0.23	0.00	0.07	12.80	1174	Davies (1996)
1998	August	0.00	0.13	0.10	0.90	0.03	0.88	0.27	0.004	0.18	15.80	1137	Mackie (1999)
2001	August	0.04	0.17	0.06	1.48	0.02	1.05	0.53	0.13	0.23	14.90	1167	Dunham (2002)
2007	October	2.70	0.44	0.16	0.71	0.03	1.75	0.38	0.06	0.12	14.50	1167	Dunham *et al.* (2007)
2009	September	2.45	0.004	0.22	2.18	0.02	1.80	0.99	0.28	0.25	20.90	1167	Dunham *et al.* (2010)
Home range size (km^2)	–	–	601.00	34.00	864.00	113.00	0.37	8.00	1.05	160.00	–	–	Grant *et al.* (1992)

Table 2. Mean densities (number km^{-2}) of wild ungulates, and cattle before and after 2000 in Chipinda Pools area of GNP, Zimbabwe. Values are mean ± standard errors; median and range in parenthesis. Independent samples two-tailed *t*-tests, df = degrees of freedom; Mann-Whitney *U* test, one-tailed; * = $P < 0.05$; dash (–) denotes not applicable.

Common name	1991-1998	2001-2009	*t*-value	df	*U* statistic	*P*-value
Buffalo	0.074 (1.73)	0.170 (0.44)	–	–	7.00	0.362
Cattle	0.00 (0.00)	2.45 (2.66)	–	–	9.00	0.025*
Eland	0.10 ± 0.04	0.15 ± 0.05	–0.76	4	–	0.487
Elephant	0.89 ± 0.05	1.46 ± 0.42	–1.58	5	–	0.174
Giraffe	0.025 (0.02)	0.020 (0.01)	–	–	7.00	0.362
Impala	0.86 ± 0.23	1.53 ± 0.24	–2.05	4	–	0.110
Kudu	0.20 ± 0.05	0.63 ± 0.18	–2.27	4	–	0.086
Waterbuck	0.01 ± 0.01	0.16 ± 0.06	–2.23	4	–	0.089
Zebra	0.20 ± 0.05	0.20 ± 0.04	0.01	5	–	0.990

Repeat aerial surveys of ungulates were conducted during September 2010, within Chitsa and Chipinda Pools covering approximately 320 km^2 area, i.e., 27 % of Chipinda Pools and 6 % of the entire GNP area, using a Cessna 185 aircraft. The aerial survey methods were similar to those used in previous years in the GNP. A total of 11 transects which were 1.5 km apart ranging from 6.5 to 21.1 km length were flown (Fig. 1). Transects primarily covered the areas where cattle were known to graze (Gandiwa *et al.* 2011). All transects were covered in one survey flight on 17 September 2010 between 11:20 and 13:00 hours and we searched for both domestic and wild ungulates. The aerial survey was flown at an average speed of 160 km/hour and at a height of approximately 90 m above the ground with one pilot, one recorder and two observers. Animals sighted were recorded and their position marked into a Garmin Geographic Positioning System (GPS) 60 receiver unit.

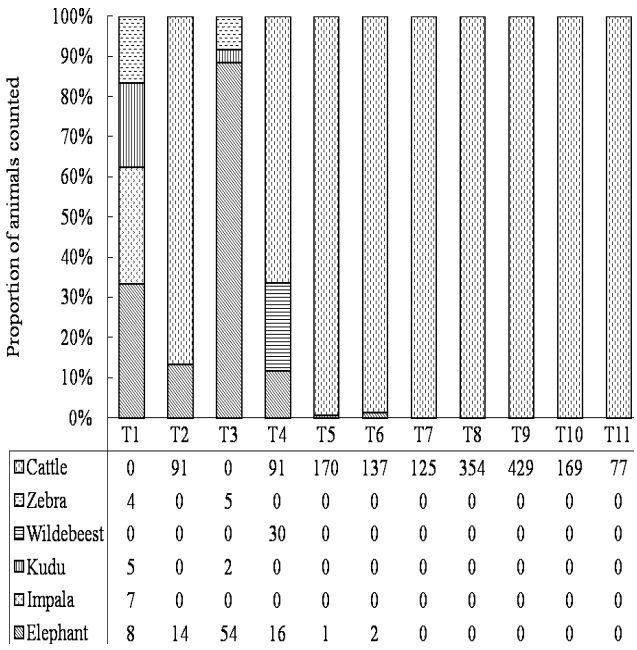
Data analysis

Data from past aerial surveys were divided into two periods, i.e. 1991 - 1998 and 2001 - 2009, in order to cover the periods before and after the human and livestock encroachment into the northern parts of GNP. We used SPSS version 19 (SPSS Inc., Chicago, Illinois) for data analysis. The data were tested for normality using the Shapiro-Wilk test and we found buffalo, cattle and giraffe density data to be non-normal. We tested whether densities of these species differed before and after 2000 in Chipinda Pools using independent samples two-tailed t-tests with unequal sizes for animal species with normally distributed density data and Mann-Whitney *U* tests.

We also evaluated the spatial distribution of animal sightings in relation to human settlements from the September 2010 aerial survey in northern GNP using ArcView 3.2 software in a Geographic Information Systems (GIS) environment. Vector GIS data including location of rivers, boundaries of the park and Chitsa settlement within the northern GNP were obtained from the GNP database. Data on animal sightings in the September 2010 aerial survey were captured into a Microsoft Excel spreadsheet and converted into a GIS shapefile in ArcView GIS. The tracklog file for the flown survey transects was similarly converted into a GIS shapefile. With these data layers, we related the animal sightings to the layers representing the flown tracklog, Chitsa settlement and the northern GNP using the overlay function in order to establish the distribution of large herbivores in relation to the human settlements.

Results

There were no significant differences in the densities of buffalo, eland, elephant, giraffe, impala, kudu, waterbuck and zebra in northern GNP between 1991 - 1998 and 2001 - 2009 (all, $P > 0.05$; Table 2). As expected, there was a significant increase in the density of cattle between 1991-1998 and 2001-2009 in northern GNP (Mann-Whitney $U = 9.00$, one-tailed $P = 0.025$; Table 2). However, during the aerial survey of September 2010, only



	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11
Cattle	0	91	0	91	170	137	125	354	429	169	77
Zebra	4	0	5	0	0	0	0	0	0	0	0
Wildebeest	0	0	0	30	0	0	0	0	0	0	0
Kudu	5	0	2	0	0	0	0	0	0	0	0
Impala	7	0	0	0	0	0	0	0	0	0	0
Elephant	8	14	54	16	1	2	0	0	0	0	0

Fig. 2. Number of large herbivores recorded in 11 transects (T1 - T11) during aerial survey of GNP, in September 2010.

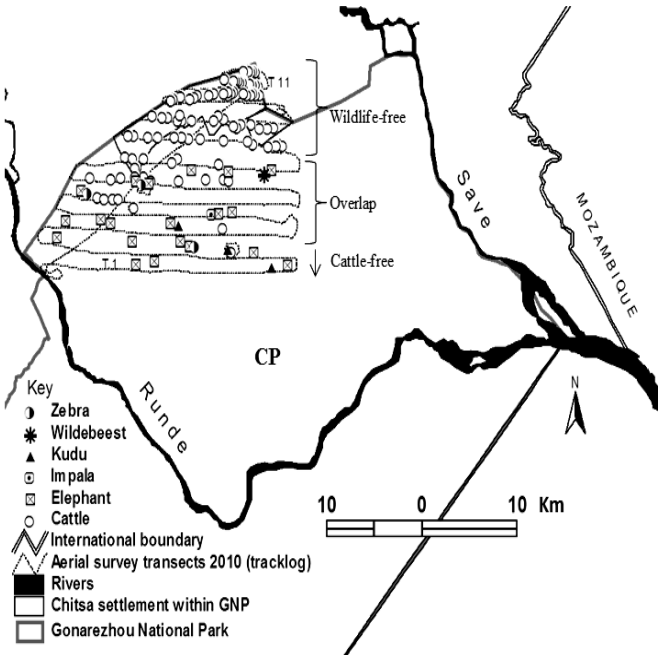


Fig. 3. Spatial distribution of large herbivores recorded during aerial survey along 11 transects (T1 to T11) in September 2010. CP denotes Chipinda Pools aerial survey area bounded by Runde and Save Rivers.

six species of large herbivores were sighted (a total of 1,791 individuals) in northern GNP (Fig. 2). Cattle (n = 1,643) were the most common species in the survey area. About 32 % (n = 526) of the total sighted cattle were recorded outside the human settlements but within the park boundary. Cattle were spread as far as 8 kms from the human settlement (Fig. 3). Elephant and wildebeest were the most abundant large wild herbivores. Elephant, wildebeest and zebra were sighted approximately 1 - 2 km from the human settlements whereas impala and kudu were sighted ≥ 5 km from the human settlements. Kudu and elephants were sighted closer to cattle (< 0.1 km), zebra were slightly away (0.5 - 1 km), while impala and wildebeest were sighted farthest (>1 km). No large wild herbivores were sighted within the human settlement area during the September 2010 survey.

Discussion

Data used in the present analysis were collected using systematic reconnaissance flight methods over the study period (Norton-Griffiths 1978). Despite the limitations of aerial surveys such as observer biases and sample errors (Ferreira & Van Aarde 2009; Redfern *et al.* 2002), there is a validity and consistency in the results. The results show that though the cattle density increased significantly after 2000 in northern GNP, densities of all eight large wild herbivore species remained the same between 1991 - 1998 and 2001 - 2009. Contrary to our hypothesis, none of the eight wild herbivores showed decline in densities following the human and livestock encroachments into the northern GNP in 2000. However, giraffe and zebra showed a slight non-significant decline. In contrast, other authors have reported a steady reduction in large wild herbivore abundances over the past 20 years in many PAs across the African continent (e.g. Craigie *et al.* 2010; Ogutu *et al.* 2011; Ottichilo *et al.* 2001). The reasons for the decline of herbivore populations in other PAs have been attributed largely to anthropogenic pressures including livestock grazing, poaching, disease outbreaks, habitat loss and destruction (Biru & Bekele 2012; Newmark 2008; Ogutu & Owen-Smith 2003; Scholte 2011).

The results partly support our second hypothesis that native large herbivores would avoid habitats close to human settlements. All wild ungulates were sighted outside the human habitation which had the highest concentration of cattle. However, there was a partial range overlap

between wild and domestic ungulates. Cattle in the northern GNP are commonly herded and also, there is restriction of free grazing from the park management. It has been suggested that introduction of domestic livestock in areas of low primary productivity would eventually lead to competitive exclusion of native ungulates which have similar body size and niche (Acebes *et al.* 2012; Mishra *et al.* 2004; Voeten & Prins 1999). Though, overall densities within the reserve were same, at a local scale we did find evidence of spatial segregation between domestic and wild ungulates.

Interactions between livestock and native large wild herbivores are complex, and can vary under different ecological conditions (Dave & Jhala 2011). Earlier studies have suggested that interactions between livestock and wild herbivores may be competitive (Mishra *et al.* 2004; Mishra *et al.* 2002; Odadi *et al.* 2011; Shrestha & Wegge 2008), facilitative (Odadi *et al.* 2011; Rannestad *et al.* 2006) or without much effect especially on large wild herbivores (Sitters *et al.* 2009). Human presence and disturbances have been reported to influence native herbivore distribution. For instance, large wild herbivores avoided livestock areas with high human disturbance in other similar ecosystems (Ogutu *et al.* 2010; Stephens *et al.* 2001; Wallgren *et al.* 2009). In northern GNP, most households keep domestic dogs (*Canis familiaris*) to protect livestock from predators. Inadequately provisioned and loosely controlled dogs could have also influenced distribution of small to medium native herbivores in the park (Gandiwa 2011). Repeat observations during various seasons would be necessary to understand the spatio-temporal segregation among cattle and wild ungulates.

Remote sensing data reveals that the total area under human encroachment in northern GNP has remained fairly low i.e., 4 % of Chipinda Pools area since 2000 (Gandiwa *et al.* 2011). Similarly, the negative effects of illegal hunting on native large herbivores densities seem to have been low due to a stringent law enforcement in GNP during 2004 and 2010 (Gandiwa *et al.* 2013). However, with increase in cattle and human populations it would be extremely challenging to maintain multi-species assemblages and integrity of PAs in the long run.

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References

Acebes, P., J. Traba & J. E. Malo. 2012. Co-occurrence and potential for competition between wild and domestic large herbivores in a South American desert. *Journal of Arid Environments* **77**: 39-44.

Baudron, F., M. Corbeels, J. A. Andersson, M. Sibanda & K. E. Giller. 2011. Delineating the drivers of waning wildlife habitat: The predominance of cotton farming on the fringe of protected areas in the Mid-Zambezi Valley, Zimbabwe. *Biological Conservation* **144**: 1481-1493.

Bhatnagar, Y. V., R. Wangchuk, H. H. T. Prins, S. E. Van Wieren & C. Mishra. 2006. Perceived conflicts between pastoralism and conservation of the kiang *Equus kiang* in the Ladakh Trans-Himalaya, India. *Environmental Management* **38**: 934-941.

Biru, Y. & A. Bekele. 2012. Food habits of African elephant (*Loxodonta africana*) in Babile Elephant Sanctuary, Ethiopia. *Tropical Ecology* **53**: 43-52.

Chaumba, J., I. Scoones & W. Wolmer. 2003. From Jambanja to planning: the reassertion of technocracy in land reform in southeastern Zimbabwe? *Journal of Modern African Studies* **41**: 533-554.

Craigie, I. D., J. E. M. Baillie, A. Balmford, C. Carbone, B. Collen, R. E. Green & J. M. Hutton. 2010. Large mammal population declines in Africa's protected areas. *Biological Conservation* **143**: 2221-2228.

Cumming, D. H. M., M. B. Fenton, I. L. Rautenbach, R. D. Taylor, G. S. Cumming, M. S. Cumming, J. M. Dunlop, A. G. Ford, M. D. Hovorka & D. S. Johnston. 1997. Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science* **93**: 231-236.

Dave, C. & Y. Jhala. 2011. Is competition with livestock detrimental for native wild ungulates? A case study of chital (*Axis axis*) in Gir Forest, India. *Journal of Tropical Ecology* **27**: 239-247.

Davies, C. 1996. *Aerial Census of Elephants and Other Mammals in the North-West Matebeleland and Gonarezhou Regions of Zimbabwe: August-September 1996*. Department of National Parks and Wildlife Management, Harare.

Davies, C., C. Craig, C. Mackie, T. Chimuti & D. S. C. Gibson. 1995. *Aerial Census of Elephants and Other Large Mammals in the Gonarezhou, Zambezi Valley, North-West Matebeleland, Sebungwe, Dande and Communal Land Regions of Zimbabwe: July-November 1995*. Department of National Parks and Wildlife Management, Harare.

de Boer, W. F. & H. H. T. Prins. 1990. Large herbivores that strive mightily but eat and drink as friends. *Oecologia* **82**: 264-274.

de Haan, C., H. Steinfeld & H. Blackburn. 1997. *Livestock and the Environment: Finding a Balance*. Report of study by the Commission of the European Communities, the World Bank and the Governments of Denmark, France, Germany, The Netherlands, UK and USA. Wren Media, Eye, Suffolk.

de Iongh, H. H., C. B. de Jong, J. van Goethem, E. Klop, A. M. H. Brunsting, P. E. Loth & H. H. T. Prins. 2011. Resource partitioning among African savanna herbivores in North Cameroon: the importance of diet composition, food quality and body mass. *Journal of Tropical Ecology* **27**: 503-513.

de Leeuw, J., M. N. Waweru, O. O. Okello, M. Maloba, P. Nguru, M. Y. Said, M. A. Hesbon, I. M. A. Heitkönig & R. S. Reid. 2001. Distribution and diversity of wildlife in northern Kenya in relation to livestock and permanent water points. *Biological Conservation* **100**: 297-306.

du Toit, J. T. & D. H. M. Cumming. 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation* **8**: 1643-1661.

Dunham, K. M. 2002. *Aerial Survey of Elephants and Other Large Herbivores in Gonarezhou National Park and Some Bordering Lands, Zimbabwe: 2001*. WWF-SARPO Occasional Paper 4. Department of National Parks and Wildlife Management, Harare.

Dunham, K. M., C. S. Mackie, O. C. Musemburi, C. Zhuwau, G. H. Nyaguse, R. D. Taylor & T. Chimuti. 2007. *Aerial Survey of Elephants and Other Large Herbivores in Gonarezhou National Park, Zimbabwe: 2007*. WWF-SARPO Occasional Paper 18. Department of National Parks and Wildlife Management, Harare.

Dunham, K. M., E. Van Der Westhuizen, H. F. Van Der Westhuizen & E. Gandiwa. 2010. *Aerial Survey of Elephants and Other Large Herbivores in Gonarezhou National Park (Zimbabwe), Zinave National Park (Mozambique) and Surrounds: 2009*. Zimbabwe Parks and Wildlife Management Authority, Harare.

Eltringham, S. K. 1990. Wildlife carrying capacities in relation to human settlements. *Koedoe* **33**: 87-97.

Ferreira, S. M. & R. J. Van Aarde. 2009. Aerial survey intensity as a determinant of estimates of African elephant population sizes and trends. *South African Journal of Wildlife Research* **39**: 181-191.

Gandiwa, E. 2011. Preliminary assessment of illegal hunting by communities adjacent to the northern Gonarezhou National Park, Zimbabwe. *Tropical Conservation Science* **4**: 445-467.

Gandiwa, E., I. M. A. Heitkönig, A. M. Lokhorst, H. H. T. Prins & C. Leeuwis. 2013. Illegal hunting and law enforcement during a period of economic decline in Zimbabwe: A case study of northern Gonarezhou National Park and adjacent areas. *Journal for Nature Conservation*: http://dx.doi.org/10.1016/j.jnc.2012.1011.1009.

Gandiwa, E., N. Tupulu, P. Zisadza-Gandiwa & J. Muvengwi. 2012. Structure and composition of woody vegetation around permanent-artificial and ephemeral-natural water points in northern Gonarezhou National Park, Zimbabwe. *Tropical Ecology* **53**: 169-175.

Gandiwa, P., M. Matsvayi, M. M. Ngwenya & E. Gandiwa. 2011. Assessment of livestock and human settlement encroachment into northern Gonarezhou National Park, Zimbabwe. *Journal of Sustainable Development in Africa* **13**: 19-33.

Girma, Z., A. Bekele & H. Graham. 2012. Large mammals and mountain encroachments on Mount Kaka and Hunkolo Fragments, southeast Ethiopia. *Asian Journal of Applied Sciences* **5**: 279-289.

Grant, J. W. A., C. A. Chapman & K. S. Richardson. 1992. Defended versus undefended home range size of carnivores, ungulates and primates. *Behavioral Ecology and Sociobiology* **31**: 149-161.

Jones, M. A. 1991. *Aerial Census of Elephants and Other Large Mammals in the Gonarezhou National Park and Adjacent Areas: September 1991*. Department of National Parks and Wildlife Management, Harare.

Kideghesho, J. R., J. W. Nyahongo, S. N. Hassan, T. C. Tarimo & N. E. Mbije. 2006. Factors and ecological impacts of wildlife habitat destruction in the Serengeti Ecosystem in Northern Tanzania. *African Journal of Environmental Assessment and Management* **11**: 17-32.

Kittur, S., S. Sathyakumar & G. S. Rawat. 2010. Assessment of spatial and habitat use overlap between Himalayan tahr and livestock in Kedarnath Wildlife Sanctuary, India. *European Journal of Wildlife Research* **56**: 195-204.

Lambin, E. F., H. J. Geist & E. Lepers. 2003. Dynamics of land-use and land-cover change in tropical regions. *Annual Review of Environment and Resources* **28**: 205-241.

Lamprey, R. H. & R. S. Reid. 2004. Expansion of human settlement in Kenya's Maasai Mara: what future for pastoralism and wildlife? *Journal of Biogeography* **31**: 997-1032.

Lindsey, P. A., S. S. Romanãch, S. Matema, C. Matema, I. Mupamhadzi & J. Muvengwi. 2011. Dynamics and underlying causes of illegal bushmeat trade in Zimbabwe. *Oryx* **45**: 84-95.

Mackie, C. 1999. *Aerial Census of Elephants and Other Large Herbivores in the Sebungwe Region and Gonarezhou National Park 1998*. USAID NRMP II-WWF Multispecies Project. WWF Project No. ZW0025, Harare.

Madhusudan, M. D. 2004. Recovery of wild large herbivores following livestock decline in a tropical Indian Wildlife Reserve. *Journal of Applied Ecology* **41**: 858-869.

Mamo, Y. & A. Bekele. 2011. Human and livestock encroachments into the habitat of Mountain Nyala (*Tragelaphus buxtoni*) in the Bale Mountains National Park, Ethiopia. *Tropical Ecology* 52: 265-273.

Mascia, M. B. & S. Pailler. 2011. Protected area downgrading, downsizing, and degazettement (PADDD) and its conservation implications. *Conservation Letters* **4**: 9-20.

Mishra, C., S. E. Van Wieren, P. Ketner, I. M. A. Heitkönig & H. H. T. Prins. 2004. Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. *Journal of Applied Ecology* **41**: 344-354.

Mishra, C., S. E. Wieren, I. Heitkönig & H. H. T. Prins. 2002. A theoretical analysis of competitive exclusion in a Trans-Himalayan large-herbivore assemblage. *Animal Conservation* **5**: 251-258.

Mombeshora, S. & S. Le Bel. 2009. Parks-people conflicts: the case of Gonarezhou National Park and the Chitsa community in south-east Zimbabwe. *Biodiversity and Conservation* **18**: 2601-2623.

Muboko, N. 2011. *Conflict and Sustainable Development: the Case of the Great Limpopo Transfrontier Park (GLTP); Southern Africa.* D.Phil. Thesis. Nelson Mandela Metropolitan University, Port Elizabeth.

Mworia, J. K., J. I. Kinyamario & J. M. Githaiga. 2008. Influence of cultivation, settlements and water sources on wildlife distribution and habitat selection in south-east Kajiado, Kenya. *Environmental Conservation* **35**: 117-124.

Newmark, W. D. 2008. Isolation of African protected areas. *Frontiers in Ecology and the Environment* **6**: 321-328.

Norton-Griffiths, M. 1978. *Counting Animals: Techniques Currently Used in African Wildlife Ecology No. 1*. African Wildlife Foundation, Nairobi.

Odadi, W. O., M. K. Karachi, S. A. Abdulrazak & T. P. Young. 2011. African wild ungulates compete with or facilitate cattle depending on season. *Science* **333**: 1753-1755.

Ogutu, J. & N. Owen-Smith. 2003. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecology Letters* **6**: 412-419.

Ogutu, J. O., N. Owen-Smith, H. P. Piepho & M. Y. Said. 2011. Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977-2009. *Journal of Zoology* **285**: 99-109.

Ogutu, J. O., H.-P. Piepho, R. S. Reid, M. E. Rainy, R. L. Kruska, J. S. Worden, M. Nyabenge & N. T. Hobbs. 2010. Large herbivore responses to water and settlements in savannas. *Ecological Monographs* **80**: 241-266.

Ottichilo, W. K., J. De Leeuw & H. H. T. Prins. 2001. Population trends of resident wildebeest [*Connochaetes taurinus hecki* (Neumann)] and factors influencing them in the Masai Mara ecosystem, Kenya. *Biological Conservation* **97**: 271-282.

Prins, H. H. T. 1992. The pastoral road to extinction: Competition between wildlife and traditional pastoralism in East Africa. *Environmental Conservation* **19**: 117-123.

Prins, H. H. T. 2000. Competition between livestock and wildlife in Africa. pp. 51-80. *In:* H. H. T. Prins, J. G. Grootenhuis & T. T. Dolan (eds.) *Wildlife Conservation by Sustainable Use*. Kluwer Academic, Boston MA.

Prins, H. H. T. & H. Olff. 1998. Species-richness of African grazer assemblages: towards a functional explanation. pp. 449-490. *In:* D. M. Newbery, H. H. T. Prins & N. Brown (eds.) *Dynamics of Tropical Communities*. Blackwell Science, Oxford.

Rannestad, O. H., T. Danielsen, S. R. Moe & S. R. Stokke. 2006. Adjacent pastoral areas support higher densities of wild ungulates during the wet season. *Journal of Tropical Ecology* **22**: 675-683.

Rawat, G. S. & S. Sathyakumar. 2002. Conservation issues in the Himalayan region of India. *Envis Bulletin, Wildlife and Protected Areas* **1**: 50-56.

Redfern, J. V., P. C. Viljoen, J. M. Kruger & W. M. Getz. 2002. Biases in estimating population size from an aerial census: a case study in the Kruger National Park, South Africa. *South African Journal of Science* **98**: 455-461.

Scholte, P. 2011. Towards understanding large mammal population declines in Africa's protected areas: A

West-Central African perspective. *Tropical Conservation Science* **4**: 1-11.

Shackleton, C. M., S. E. Shackleton & B. Cousins. 2001. The role of land-based strategies in rural livelihoods: the contribution of arable production, animal husbandry and natural resource harvesting in communal areas in South Africa. *Development Southern Africa* **18**: 581-604.

Shrestha, R. & P. Wegge. 2008. Wild sheep and livestock in Nepal Trans-Himalaya: coexistence or competition? *Environmental Conservation* **35**: 125-136.

Sitters, J., I. M. A. Heitkönig, M. Holmgren & G. S. O. Ojwang'. 2009. Herded cattle and wild grazers partition water but share forage resources during dry years in East African savannas. *Biological Conservation* **142**: 738-750.

Steinfeld, H., P. Gerber, T. Wassenaar, V. Castel, M. Rosales & C. de Haan. 2006. *Livestock's Long Shadow: Environmental Issues and Options*. Food and Agricultural Organisation, Rome.

Stephens, P. A., C. A. d'Sa, C. Sillero-Zubiri & N. Leader-Williams. 2001. Impact of livestock and settlement on the large mammalian wildlife of Bale Mountains National Park, southern Ethiopia. *Biological Conservation* **100**: 307-322.

Voeten, M. M. & H. H. T. Prins. 1999. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* **120**: 287-294.

Walker, B. 1993. Rangeland ecology: Understanding and managing change. *Ambio* **22**: 80-87.

Wallgren, M., C. Skarpe, R. Bergström, K. Danell, A. Bergström, T. Jakobsson, K. Karlsson & T. Strand. 2009. Influence of land use on the abundance of wildlife and livestock in the Kalahari, Botswana. *Journal of Arid Environments* **73**: 314-321.

Wolmer, W. 2005. Wilderness gained, wilderness lost: wildlife management and land occupations in Zimbabwe's southeast lowveld. *Journal of Historical Geography* **31**: 260-280.

Young, T. P., T. M. Palmer & M. E. Gadd. 2005. Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biological Conservation* **122**: 351-359.

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