

Lost herds of the Highveld: evidence from the written, historical record

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Establishing historical baselines is important for informing present-day conservation and management actions. The historical literature was searched for information on the composition, abundance and distribution of the large ungulate fauna in the grassland-dominated Highveld region of north-central South Africa during the 19th century and early 20th century. The existence of large aggregations (herds comprising one or more taxa) is inferred from the written record, for the early historical period. These aggregations comprised one or more species of eight grazers or mixed feeders. There is weaker evidence of seasonal migratory, or partially migratory, behaviour by some of them. This synthesis highlights the existence of a major, but hitherto unrecognized and unheralded, grazer-grassland system in the region, at least during the early period of colonial expansion. In global terms, this system may have rivalled similar extant migratory systems elsewhere in Africa and globally, if not in the numbers of animals involved then almost certainly in terms of the diversity of ungulates that were present. No records of large ungulate aggregations, or migrations, could be located for the post-1870s period, thus revealing the time of the collapse of this system, mainly as a result of overhunting and loss of habitat. By the end of the 19th century the once widespread and abundant larger ungulate fauna of the Highveld had, barring a few individuals and small and scattered herds, of a few species, been virtually exterminated. Some ecological consequences of this collapse are briefly discussed.

Key words: Highveld, South Africa, historical record, ungulates, large aggregations, migration, grazer-grassland system.

INTRODUCTION

Globally, large aggregations (herds comprising one or more taxa), associated with seasonal migrations, have been recorded for 22 species of medium- to large-sized (c. 30–700 kg) ungulates (Harris, Thirgood, Hopcraft, Cromsigt & Berger, 2009). Of these species, over half (13) live, or lived, on the African continent, whereas three are associated with North America, five with Eurasia and one with both North America and Eurasia. The best studied and best known of these aggregations and migrations include those of the blue wildebeest (*Connochaetes taurinus*), Burchell's (plains) zebra (*Equus burchellii*) and Thompson's gazelle (*Gazella thompsonii*) in the Serengeti-Mara grassland system in East Africa, the pronghorn (*Antilocarpa americana*) and the North American bison (*Bison bison*) of the prairies of North America, and the caribou/reindeer (*Rangifer tarandus*) in parts of North America and Eurasia (Harris, Thirgood, Hopcraft, Cromsigt & Berger, 2009). These systems support aggre-

gated migrations by a single ungulate species (e.g. North American bison, caribou/reindeer) or by several species (e.g. up to six species undertake aggregated migrations in the grasslands of East Africa) (Harris, Thirgood, Hopcraft, Cromsigt & Berger, 2009). These authors note that most of the mass migrants follow, across hundreds of kilometres, the seasonal and shifting patterns of fresh green vegetation over large tracts of savanna, steppe, and grassland, with the numbers of animals involved ranging from several hundred to hundreds of thousands.

Of the 13 species that live, or lived, in Africa, no fewer than eight occurred in the Highveld region (see 'Study area') of north-central South Africa during the early to mid 19th century. These eight species (true quagga, *Equus quagga* (*sensu* Wilson & Reeder, 2005), Burchell's (plains) zebra; eland, *Tragelaphus oryx*; black wildebeest, *Connochaetes gnou*; blue wildebeest; red hartebeest, *Alcelaphus buselaphus*; blesbok, *Damaliscus pygargus phillipsi*; springbok, *Antidorcas marsupialis*) are either grazers or mixed feeders (grazing and browsing).

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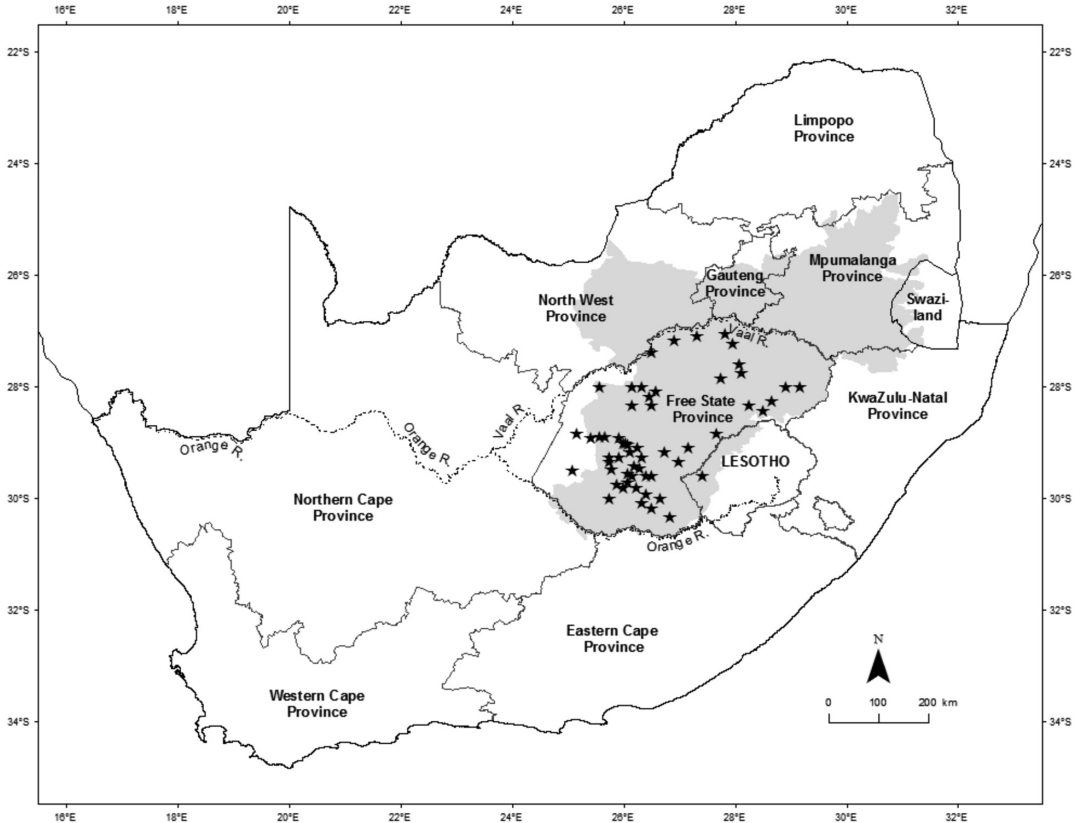


Fig. 1. Localities (stars) of written, historical (19th century) records of large herds of plains-living ungulates in or near to the Highveld region (shaded; as defined in 'Study area') in the study area (Free State Province of South Africa and Lesotho).

While individual literature references with information about large aggregations and mass migrations in savanna-dominated regions far to the north of the Orange River, including the greater Kalahari 'Desert' (actually an arid savanna) in Botswana, exist for these eight species, there is virtually no recognition in the scientific literature of the phenomenon of a formerly existing, extensive, grassland-dominated system in the Highveld region that supported large herds of plains-living ungulates. This may be due to the rapid collapse of this system; there are no published reports of large aggregations after the end of the 1870s. Here we provide the basis for the recognition of this system, together with new insights into its functioning, by presenting and discussing information from the written record. Establishing historical baselines is important for informing present-day conservation and management goals, particularly within the context of setting restoration targets (Roman, Dunphy-Daly, Johnston & Read, 2015).

A detailed review of the written, historical record was conducted and information on the composition, abundance, distribution and migrations of the larger ungulates, in a part of the Highveld region (*i.e.* the study area), was collated, analysed and interpreted.

STUDY AREA

The 119 673 km² study area – comprising the Free State Province of South Africa and the adjacent country of Lesotho (Fig. 1) – incorporates more than half (52%) of the total area (231 167 km²) of the 'Highveld' ('veld' in Dutch/Afrikaans = rangeland), this being a colloquial term for a region of high country to the northeast of the Orange River in north-central South Africa, with small areas occurring in the far western parts of the neighbouring countries of Lesotho and Swaziland. The Highveld is formed by a plateau, which rises to about 2100 m in the east and slopes to about 1200 m in the west (Fig. 1).

The Highveld landscape is characterized by flat or gently undulating plains, typified in places by low mountain ranges, rocky ridges, isolated hills and shallow, river-cut valleys. It has warm to hot (>30°C) summers and cool to cold (<0°C) winters. Annual rainfall, which occurs mainly as summer thunderstorms, varies from ~400 mm in the west to ~1000 mm in the east. Both temperature and rainfall follow a general altitudinal gradient, with the higher country in the east being relatively cool and moist and the lower country in the west being relatively hot and dry.

Ecologically, the Highveld forms part of the Grassland Biome of South Africa, Lesotho and Swaziland; it is dominated by open grassland, comprising Dry Highveld Grassland in the west and southwest, and Mesic Highveld Grassland in the east and northeast (Rutherford, Mucina & Powrie, 2006). The vegetation in the study area is dominated (89.4%) by grassland types, with relatively small areas comprising savanna (5.7%) and karroid (4.9%) types (Rutherford, Mucina & Powrie, 2006).

METHODS

Literature sources were systematically searched for written records of the historical incidence of medium- to large-sized mammals in the study area. These sources comprise mainly the letters, journals, diaries or books written by some of the literate pioneers – notably various European missionaries, explorers, travellers, naturalists, military personnel, big game hunters and pastoralists – who visited or settled in the study area, starting in the 1820s, this being considered as the start of the main colonial period in the region in question. The written record for the period ending with the 1920s was consulted. Notwithstanding certain interpretational challenges, related to the quantity and quality of the information, the use of written, historical accounts is a widely applied research tool to assist in the reconstruction of past faunal assemblages (e.g. Rookmaaker, 1989; Ceballos & Ehrlich, 2002; Zielinski, Truex, Schlexer, Campbell & Carroll, 2005; Skead, 2007, 2011; Burbridge *et al.*, 2009; Harris, Thirgood, Hopcraft, Cromsigt & Berger, 2009; Boshoff & Kerley, 2010, 2013).

Another potential source of information regarding the early incidence of large mammals in a particular area is the oral history record that originated in the pre-colonial period. However, owing to inconsistencies in the quality of this type of information (Boshoff & Kerley, 2013), oral history

records were not considered in this study.

Records that mention the occurrence of large aggregations, and landscape-level movements (migrations), of the larger ungulates in the study area during the 100-year period mentioned above were collated, analysed and interpreted. The species referred to and the localities of the individual observations (to whatever level of precision was possible) were extracted; the latter are shown on a map.

RESULTS

Large aggregations

A total of 66 historical literature passages (in English or translated into English), that make mention of large aggregations of medium- to large-sized ungulates in the study area during the 19th century, were found in the references listed in Appendix 1. The earliest of these records date to the year 1833, and the latest to the decade of the 1870s. Of these 66 passages, 48 identify the ungulates concerned (by common name for a species or for a general taxon, e.g. 'zebra', 'wildebeest') and provide 'precise' (a spot locality or a roughly circular area with a diameter of up to about five km), 'imprecise' (a roughly circular area with a diameter of up to about 50 km) or 'approximate' (in the general area, as deduced from the journey descriptions provided by the respective chroniclers). Seven passages identify the ungulates observed but provide only broad or vague locality information, thereby preventing their depiction on a map. Finally, nine passages do not identify the ungulates observed but provide reasonable locality information, and two passages provide neither ungulate identification nor good or reasonable locality information. Many of these passages refer to more than one taxon.

Of the 55 records for which the taxon is known, 45 mention one or more wildebeest, *Connochaetes* spp. (black wildebeest, blue wildebeest, species indeterminate), 41 mention the blesbok and 35 mention the springbok. Similarly, 27 mention one or more equids, *Equus* spp. (true quagga, Burchell's/plains zebra, species indeterminate), with 10 making mention of the red hartebeest and only three referring to the eland. All eight species are herd-forming and plains-living, with two of these (red hartebeest and eland) also living (apparently in smaller herds) in hilly and mountainous areas (Skinner & Chimimba, 2005).

To convey the essence of the descriptions

provided by the authors of the 66 written records referred to above, a selection of words and phrases used by them, in one or more passages, to describe the large aggregations they observed, is presented in Table 1.

A few prominent examples of extracts that describe large aggregations are listed in Table 2.

In order to show the spatial pattern of records of large aggregations of plains game, the localities of the 48 records that mention large aggregations, and for which good or reasonable locality information (see earlier) is available, and those of the nine records for which the species or group is not identified but similar locality information is available, are mapped in Fig. 1. For the sake of simplicity, no distinction is made between 'precise', imprecise' and 'approximate' localities on this map.

All but two of the 57 records mapped in Fig. 1 fall within areas of Mesic Highveld Grassland or Dry Highveld Grassland. The remaining two fall within areas where the latter grassland type intergrades with Eastern Kalahari Bushveld (a savanna type) and Upper Karoo (a karroid type) vegetation units, in the west (all named vegetation units are bioregions, after Rutherford, Mucina & Powrie, 2006). The Mesic Highveld Grassland and Dry Highveld Grassland types occupy typical plains areas.

Migrations

Seventeen references (listed in Appendix 2) contain passages which mention, or allude to, migrations by one or more of the following ungulate taxa: equids, eland, black wildebeest, blue wildebeest, blesbok, red hartebeest, springbok. The first record refers to the 1820s and the last record to the 1870s, with a record from the 1890s being dealt with under 'Discussion'. A selection of excerpts is provided in Table 3.

DISCUSSION

The issue of how realistic, in terms of the actual numbers of animals observed, the early chroniclers' descriptions are about the relative size of the aggregations of plains game in 19th century South Africa, is unlikely to ever be resolved. It has been contended that even if many of the statements tend towards hyperbole, the actual numbers must indeed have been very high in order to elicit the use of adjectives and phrases such as those listed in Table 1 (Skead, 2007). We agree with this contention. It is noteworthy that trained observers tended to underestimate the true abundance

of ungulates in large herds of plains game by about 30% (Sinclair, 1985). Further, observations of large aggregations come from single locations and therefore do not necessarily provide descriptions of the scale of the regional population.

Wildebeest, blesbok, springbok and equids provide the highest number of records (in order of declining number of literature references), which suggests that these four taxa, representing six species, formed the largest aggregations. The paucity of historical records of large herds of eland may, in large part, result from this easy-to-hunt animal being under heavy pressure from hunters equipped with horses and fire-arms from the early part of the 19th century (Boshoff & Kerley, 2013).

No records of large aggregations specifically involving the six taxa discussed above were found for the Lesotho highlands or lowlands. The Lesotho highlands were the domain of the red hartebeest and the eland but the sizes of these historical herds are not known. Given the harsh climate and the extremely rugged terrain in the Lesotho highlands, it is considered unlikely that these two species exhibited abundances similar to those where they occurred on the plains of the Highveld. While there is evidence from the zoo-archaeological record that equids and wildebeests lived in the wide river valleys of Lesotho (notably the Senqu (Orange) River valley) in pre-colonial times (Plug & Badenhorst, 2001), no written records from the 19th century could be found (Boshoff & Kerley, 2013); it should be noted that these particular parts of Lesotho were rarely visited by literate travelers during the first part of the 19th century (Boshoff & Kerley, 2013). However, the written record confirms that equids, wildebeests, blesbok, springbok, red hartebeest and eland occupied the western lowlands of Lesotho during the 1830s, some of them apparently in large numbers (Arbousset & Daumas, 1846; Casalis, 1861; Kirby, 1939). These western lowlands form an easterly extension (across the Caledon River) of the Highveld system.

Any interpretation of the spatial patterns evident in Fig. 1 must recognize that the written, historical distribution records were made on a non-systematic basis, *i.e.* there was no attempt by any of the early chroniclers to sample the landscape or to record their observations of wildlife in a comprehensive manner. Thus, for example, the cluster pattern of records that is evident in Fig. 1 does not mean that a similar pattern in the distribution of large aggregations existed in the field. Bearing

Table 1. Selection of adjectives and phrases used by some 19th century chroniclers to describe large aggregations of herd-forming, plains-living ungulates observed in and near to the Highveld region in north-central South Africa. Duplicate words or phrases indicate use by more than one author. The sources of this information are listed in Appendix 1.

	Equids*	Wildebeest**	Blesbok	Springbok	Red hartebeest	Eland
Multi-taxon aggregations: taxa not identified			Single taxon (st) or multi-taxon (mt) aggregations: taxa identified *true quagga and/or Burchell's/plains zebra and/or species indeterminate **black wildebeest and/or blue wildebeest and/or species indeterminate			
'thousands'	'plentiful' (mt)	'multitudes' (st)	'hundreds' (st)	'plentiful' (mt)	'plentiful' (mt)	'hordes' (st)
'thousands'	'multitude' (mt)	'teem' (st)	'droves' (st)	'multitude' (mt)	'hordes' (st)	'hundreds of thousands' (mt)
'prodigious number'	'immense troops' (st)	'plentiful' (mt)	'multitude' (mt)	'innumerable multitudes' (mt)	'hundreds of thousands' (mt)	'teemed' (mt)
'game ... in great abundance'	'by no means sparingly dispersed' (st)	'innumerable multitudes' (mt)	'innumerable multitudes' (mt)	'great many' (st)	'teemed' (mt)	
'myriads of antelopes'	'squadrons' (st)	'large herds' (st)	'abundance' (st)	'abundance' (st)	'hundreds' (mt)	
'number ... almost realised fable'	'forty or fifty thousand' (mt)	'immense number' (st)	'incredible herds' (mt)	'numerous' (st)	'immense herd' (mt)	
'large herds of plains game'	'herds ... in numbers which, if approximately hinted at now, with absolute truth, would wrinkle the countenance of the reader with a derisive smile' (mt)	'very large herds' (st)	'astounding herds' (st)	'incredible herds' (mt)	'vast herds, numbering some thousands' (st)	
'vast herds of game'	'thousands and thousands' (mt)	'immense herds' (st)	'herds ... in numbers which, if approximately hinted at now with absolute truth, would wrinkle the countenance of the reader with a derisive smile' (mt)	'countless thousands' (st)	'thousands of head' (mt)	
'appearance of a living ocean ... tumultuous waves formed by various herds'	'myriads' (mt)	'almost incredible' (st)	'About 3 000 [one herd]' (st)	'thousands' (st)		
'any description of the masses of game ... must appear exaggerated'	'hundreds of thousands' (mt)	'troops' (st)	'purple mass ... endless living mass ... countless herd' (st)	'herds ... in numbers which, if approximately hinted at now with absolute truth, would wrinkle the countenance of the reader with a derisive smile' (mt)		
'teemed'	'teemed' (mt)	'forty or fifty thousand' (mt)	'thousands and thousands' (mt)	'thousands and thousands' (mt)		

Continued on p. 292

Table 1 (Continued)

	Equids*	Wildebeest**	Blesbok	Springbok	Red hartebeest	Eland
'troops and droves of from ten to a thousand, and often a thousand together'	'thousands ... a grand and imposing spectacle' (mt)	'herds ... in numbers which, if approximately hinted at now with absolute truth, would wrinkle the countenance of the reader with a derisive smile' (mt)	'innumerable herds' (mt)	'innumerable herds' (mt)	'innumerable herds' (mt)	
'countless herds'	'multitudes' (mt)	'thousands and thousands' (mt)	'endless streams ... several thousand' (st)	'vast herds' (mt)	'vast herds' (mt)	
'a flat literally alive with game'	'hundreds' (mt)	'innumerable herds' (mt)	'vast herds' (mt)	'myriads' (mt)	'myriads' (mt)	
'Detached herds of every kind spread themselves over the plain'	'thousands ... and tens of thousands' (mt)	'vast herds' (mt)	'myriads' (mt)	'hundreds of thousands' (mt)	'hundreds of thousands' (mt)	
'thousands and tens of thousands'	'innumerable herds' (st)	'myriads' (mt)	'hundreds of thousands' (mt)	'teemed' (mt)	'teemed' (mt)	
'masses of game'	'immense herd' (mt)	'no less than half a million [one herd]' (st)	'teemed' (mt)	'abundance' (mt)	'abundance' (mt)	
'literally swarming with countless herds'	'vast troops swarm like locusts' (mt)	'hundreds of thousands' (mt)	'abundance' (mt)	'thousands ... a grand and imposing spectacle' (mt)	'thousands ... a grand and imposing spectacle' (mt)	
'thousands of game'	'thousands of head' (mt)	'teemed' (mt)	'thousands ... a grand and imposing spectacle' (mt)	'multitudes' (mt)	'multitudes' (mt)	
	'innumerable game' (mt)	'abundance' (mt)	'hundreds' (mt)	'hundreds' (mt)	'hundreds' (mt)	
	'myriads' (mt)	'thousands ... a grand and imposing spectacle' (mt)	'thousands ... and tens of thousands' (mt)	'thousands ... and tens of thousands' (mt)	'thousands ... and tens of thousands' (mt)	
	'hundreds' (st)	'multitudes' (mt)	'innumerable herds' (mt)	'innumerable herds' (mt)	'innumerable herds' (mt)	
	'hundreds' (mt)	'One herd ... in an unbroken semi-circle, the radius ... might have been more than half a mile [0.8 km]' (st)	'One herd ... in an unbroken semi-circle, the radius ... might have been more than half a mile [0.8 km]' (st)	'thousands of head' (mt)	'thousands of head' (mt)	
	'innumerable herds' (mt)	'immense herd' (mt)	'immense herd' (mt)	'great many' (mt)	'great many' (mt)	
	'immense herd' (mt)	'troops' (mt)	'troops' (mt)	'innumerable game' (mt)	'innumerable game' (mt)	
	'vast troops ... swarm like locusts' (mt)	'thousands of head' (mt)	'thousands of head' (mt)	'myriads' (st, mt)	'myriads' (st, mt)	
	'troops' (mt)	'great many' (mt)	'great many' (mt)	'immense lot' (st)	'immense lot' (st)	

Continued on p. 293

Table 1 (continued)

Equids*	Wildebeest**	Blesbok	Springbok	Red hartebeest	Eland
	'thousands of head' (mt)	'innumerable game' (mt)	'thousands' (st)		
	'immense herds' (st)	'myriads' (mt)	'almost innumerable quantity' (mt)		
	'great many' (mt)	'thousands and tens of thousands' (mt)	'land fairly overrun with ...' (mt)		
		'innumerable game' (mt)	'the veld rumbled/roared' (mt)		
	'myriads' (mt)	'almost innumerable quantity' (mt)	'immense herds' (st)		
	'thousands and tens of thousands' (mt)	'land fairly overrun with ...' (mt)	'many thousand head' (mt)		
	'almost innumerable quantity' (mt)	'the veld rumbled/roared' (mt)	'thousands upon thousands' (mt)		
	'land fairly overrun with ...' (mt)	'many thousand head' (mt)			
	'the veld rumbled/roared' (mt)				
	'thousands upon thousands' (mt)				

this caveat in mind, Fig. 1 reveals that (a) large ungulate aggregations occurred in that portion of the Highveld region that falls within the Free State Province, (b) a single record refers to mass aggregations in Lesotho; more specifically in the western lowlands of that country, (c) there are no such records from the highlands of central and eastern Lesotho. Additional information (Smith, 1849; Mossop, 1937; Du Plessis, 1969; Carruthers, 1995) indicates that this grazer-grassland system incorporated the 111 494 km² (48%) of the Highveld region that lies to the north and northeast of the Vaal River (Fig. 1).

Unfortunately, the paucity of written records, and the limited amount of detail that they contain (for example, the lack of a day or month of observation, the prevailing climatic conditions (*e.g.* drought)), make it difficult to develop a quantified understanding of the nature, scope, frequency and drivers of the movements undertaken by the grazing, herd-forming, ungulates of the Highveld. Some records certainly suggest that mass migrations did indeed occur, that they were related to season, and that they were both directional (medium- to long-distance, over flat or gently sloping country) and altitudinal (short distance, between high ground and adjacent low ground) in nature, at both landscape and local levels (see the sample of records listed in Table 3). Although none of the historical accounts categorically state that mass migrations were witnessed first-hand, the excerpts in Table 3 and elsewhere clearly indicate that this phenomenon was well-known in and around the Highveld region, at least during the mid- to latter 1800s.

The information in Table 3 and elsewhere (Boshoff & Kerley, 2013) suggests that the large herds migrated away from the sour (*i.e.* unpalatable in winter) grassland in the highest parts of the Highveld region, at the start of winter, and moved to the lower parts, namely the lower fringes of the Highveld and beyond, where sweet grass provided some winter forage; the latter includes karroid and grassland areas to the south and west of the Orange River, grassland to the north of the Vaal River, and the rolling country along the base of the Drakensberg Escarpment, *i.e.* to the east and southeast of the Highveld proper. If these were true migrations then, presumably, the directions were reversed during spring and early summer. The possible migration routes of the Highveld mass migrants are discussed in some detail by Boshoff & Kerley (2013).

Table 2. Some examples of passages in the early literature that refer to large aggregations of ungulates in parts of the Highveld region, north-central South Africa.

Date	Locality	Excerpt
1834	Near Thaba-Nchu, eastern Free State Province.	'There was contained within the circle this day an immense number of gnus, a number of quaggas, one hartebeest [and] a great many springboks' (Smith, in Kirby 1939).
1836	Near the Vet River, west-central Free State Province.	'The number of wild animals congregated on this swampy flat almost realised fable; the roads made by their incessant tramp resembling so many well-travelled high-ways. At every step incredible herds of bonte-boks [blesboks], blesboks and springbucks, with troops of gnoos, and squadrons of the common, or stripeless quagga ...' (Harris 1852).
1845/46	'Orange Free State'.	'In 1845–46 the plains of the Orange Free State were covered with herds of gnus, Burchell's zebras, blesbuck and springbuck in numbers which, if approximately hinted at now with absolute truth, would wrinkle the countenance of the reader with a derisive smile' (Nicholson 1898).
1849	Heilbron district, northern Free State Province.	'The plains abounded in all sorts of game ... But what to us was most remarkable consisted in the myriads of quaggas, blesboks, springboks, and wildebeest or black gnu, which continually crossed our path. I could have formed no conception of the reality of the accounts I had often heard of the vast quantity of game to be met with here. Indeed, at certain times of the day the plains, for miles around, had sometimes the appearance of a living ocean, the tumultuous waves being formed by the various herds crossing and re-crossing each other in every direction' (Chapman, in Tabler 1971).
1849	Northwest of Heilbron, northern Free State Province.	'The flats covered with all sorts of game ... At a moderate computation, it is supposed that within the circumference of 12 miles [19.2 km] no less than half a million wildebeest could be seen, [also] some blesbok, springboks and occasionally a few ostriches' (Chapman, in Tabler 1971).
1850	Top of the Drakensberg Escarpment, Harrismith district, northeastern Free State Province.	'Here are the chief haunts of those countless herds ... The grotesque gnu, the graceful quagga, the light and elegant springbok, the swift blesbok, may be seen here in thousands, aye, and tens of thousands, spread over the plains, or marching in almost endless lines across its surface ...' (Barter 1852).
1850	Vredefort district, northern Free State Province.	'The plains, about two miles [3.2 km] from the river, presented a scene that must be witnessed to be conceived: innumerable herds of quaggas, both of the bonte and half-striped varieties, stood quietly grazing ...' (Baines, in Kennedy 1964)
1850	Viljoenskroon district, northern Free State Province.	'On surmounting a little rising ground, the flats I mentioned before presented a panorama of life and motion that will never be effaced from my memory. As far as we could see before us stretched a line of gnoos, quaggas, blesboks and hartebeestes, and behind, across a valley of six or seven miles [9–11 km] in breadth, the same line was continued more or less dense, it is true, but still unbroken, till the rear of the immense herd was lost behind the rising ground in the distance. Detached herds of every kind spread themselves over the plain... ' (Baines, in Kennedy 1964).
1853	Between Bethlehem and Harrismith, northeastern Free State Province.	'... saw thousands and tens of thousands of blesboks and wildebeest and hundreds of quagga' (St John, in Schoeman 1988).
1850s	Bloemfontein district, south-central Free State Province.	'... almost innumerable quantity of wildebeest, springbucks, and blesbucks, which totally covered our flats' (Schoeman 1980)

Table 3. Some examples of passages in the early literature (see Appendix 2) that mention, or allude to, migratory behaviour by larger ungulates in the study area.

Date	Excerpt
1820s/1830s	'Both species of <i>Gnu</i> inhabit, during a certain period of the year, the extensive grassy plains which exist some considerable distance to the northwards of the Vaal River, and at another period a portion of each, at least, advances to the southward to feed upon the vegetation which occurs in that direction after the fall of the summer rains. Both species advance simultaneously as far as the southern branches of the Orange River, but on reaching those, the species here figured [blue wildebeest] ceases to advance, and the common species (<i>Catoblepas Gnu</i>) [black wildebeest] passes by itself into the [Cape] Colony' (Smith 1849).
1849	'Inspanned at 5 p.m. and ascended the [Drakensberg] mountain by the road east of De Beers and called the Quagga Footpath from the fact of these animals having made a road for themselves in a very passable spot, when the winter is too severe on the mountain' (Chapman, in Tabler 1971).
Late 1840s/1850s	'The <i>imbutumu</i> , gnu, or wilder-beest of the Dutch, and the <i>idube</i> , or quagga, which some call the wild ass, can hardly be said to belong to the fauna of Natal; though they often come down and spend some of the cold winter months on this side of the Kwahlamba [Drakensberg], together with hordes of other wild animals ...' (Grout 1863).
1850s	'During the two or three mid-winter months, the monarch with the big mane [male lion] crosses the Drakensberg into the Klip River country, and the upper districts of the colony [now KwaZulu-Natal Province (KZNP)], with the blesse buck, wilder beest, quagga, and zebra, which migrate so far in search of pasture' and 'The hartebeest is found in the winter season in the upland districts [of 'Natal'], within five hours' ride of Maritzburg ... The eland comes over the Berg into the upland districts of Natal in the months of July and August ... The blesse buck ... the quagga ... the wildebeest (gnu), and the zebra, are found under the Drakensberg, on the Natal side, during the three coldest months of the winter' (Mann 1859).
1850	'...it was the Lesser Draakberg [Drakensberg] which we were now approaching; in fact we were in the neighbourhood of De Beer's pass, though we contemplated making the ascent by another road, a little to the north-east of De Beer's, and known by the name of 'Quaggas Pad', from being the usual track of these animals in their annual migrations between the [Orange River] Sovereignty [Highveld] and the higher parts of Natal' (Barter 1852).
1850	Near the village of Harrismith, northeastern Free State Province: 'Game now began to be more plentiful than we had yet seen it, though the vast herds of which I have spoken had already begun their annual migration to the interior [Highveld]. In the winter, want of pasture drives them from their favourite <i>vlakten</i> [plains] into the mountain districts, which, except in unusually arid seasons like the present, are never entirely dried up, but as soon as the summer rains set in they return to the plains' (Barter 1852).
1860s/early 1870s	'The eland ... is occasionally encountered in the high uplands of the colony [KZNP], in the cool months of July and August, when it comes there from beyond the mountains [the Highveld, north of the Drakensberg] for better grass' (Brooks 1876).

The historical record also reveals that at least for some taxa (notably the black wildebeest) the migration was of a partial nature, *i.e.* not all individuals migrated during the cold, dry season, with some staying on the Highveld during this period (Boshoff & Kerley, 2013). Local, altitudinal, migrations involved seasonal movements of animals from high and exposed plateaux to deep, sheltered, neighbouring valleys; such movements were recorded for eland and red hartebeest in central and eastern Lesotho (Boshoff & Kerley, 2013).

Even though very few of the chroniclers of large aggregations of ungulates in the Highveld region

made a link between these aggregations and migratory behaviour, the possibility that this link occurred exists. Work conducted in the Serengeti grasslands in East Africa (Fryxell, Greever & Sinclair, 1988; Fryxell & Sinclair, 1988) indicates that, for reasons related to resource use, unless herd-forming ungulates migrate they cannot occur in large aggregations all year round, and that migration enables migratory populations to reach higher abundances than resident ones.

As is the case in similar grassland-dominated systems elsewhere in Africa, where migration of larger ungulates is closely linked to the availability

of resources (Fryxell & Sinclair, 1988; Fryxell, 1995), it can probably be safely predicted that the main ecological driver of the Highveld mass migrations was spatial change in the quantity and quality of forage, and that this was influenced mainly by seasonal rainfall and air temperature patterns.

Harris, Thirgood, Hopcraft, Cromsigt & Berger (2009) provide a global summary of information pertaining to historical mass migrations by larger ungulates, and to their ecological drivers and the threats that face them. The findings of the present study will enhance our knowledge about these issues in a part of the southern African sub-region.

The collapse of the system

To the best of our knowledge, no records of large aggregations or mass migrations of any of the eight species of ungulates exist for the post-1870s period in the Highveld region. The end of these phenomena in the Highveld region was brought about principally by overhunting (with firearms) and loss of habitat (to stock farming and crop agriculture) (Carruthers, 1995; Le Roux, 1999; Boshoff & Kerley, 2013). The collapse of the large herds was achieved in the remarkably short space of about 20 years, being the period incorporating the 1860s and 1870s (Boshoff & Kerley, 2013). In a similar scenario, the North American bison, an ungulate that occurred in large herds in the prairie grasslands of North America, had lost 99% of its population by the end of the 1880s, with overhunting and habitat loss listed as prominent reasons for the dramatic population decline (Hornaday, 1889).

For the post-1870s period, a single historical record indicates seasonal, altitudinal migration movements, by a 'few' remaining red hartebeest and eland, between the Drakensberg Escarpment on the southeastern border of Lesotho and lower-lying country in KwaZulu-Natal Province (South Africa), during the 1890s (Henkel, 1903) (Table 3).

There is a relatively recent report of annual movements of springbok in the south and south-western Free State Province, 'probably in search of suitable grazing' (Von Richter, Lynch & Wessels, 1972). A stock farmer in the Bultfontein district of west-central Free State reported (M. Van Loggerenberg, pers. comm., March 2013) that every year during winter small groups of springbok (up to about 50 head) appear on the farm and

remain there for a time (days, weeks) before moving on, with this activity being commonly known to several generations of the farming family. Annual game hunts, targeting, *inter alia*, resident and 'herds of hundreds of migratory springboks [trekbokke in Afrikaans]', take place on farms in the southern Free State between March and October (Steyn, 2013). Notably, such movements, which appear to represent the remains of a springbok migratory system, persist despite the loss (through crop agriculture, urbanization etc.) and alteration (through fencing, roads, irrigation canals, etc.) of the habitat of this antelope. These migratory movements should not be confused with the now extinct springbok 'treks', a phenomenon which saw very large aggregations of springbok forming, in response to prevailing, regional, drought conditions, prior to trekking large distances (100s of km) before dispersing (Roche, 2004).

Some ecological consequences of the collapse of the Highveld grazer-grassland system

Here we briefly discuss what we consider to be some important ecological consequences of the collapse of the Highveld grazer-grassland system.

Moderate intensities of grazing is a key ecological process in grassland systems, where it plays a critical role in stimulating primary productivity, promoting plant species diversity, influencing the spatial distribution of soil nitrogen properties at every scale from individual plants to plant communities, and facilitating the cycling of other soil and plant nutrients (McNaughton, 1993; McNaughton, Banyikwa, & McNaughton, 1997; Olf & Ritchie, 1998; Frank, McNaughton & Tracy, 1998; Augustine & Frank, 2001). It follows that these functions will be lost, or reduced, in areas where the multi-species, natural, grazer/mixed feeder component (*i.e.* wild ungulates) is largely or completely removed or replaced by domestic livestock (involving only one, two or three species – cattle, sheep, goats) which are highly managed, year-round, for commercial (= maximum production) purposes, often leading to overgrazing and unsustainability (Milton, Dean, Du Plessis & Siegfried, 1994; Pringle, Young, Rubenstein & McCauley, 2007). Given the high and increasing levels of anthropogenic land-use change, habitat degradation and fragmentation, by urban development, roads, farms and fences, in the Highveld grasslands (see www.grasslands.org.za), and

their deleterious impacts on the herbivore-based food web, it is evident that any attempts to restore this system back to its natural grazer-grassland status would be presented with major challenges. For example, in order to restore mass aggregations to the Highveld, it is necessary to provide sufficient space for migratory behaviour to take place. This would entail the conversion of vast tracts of land from crop agriculture to grassland, a step which, given the vested interests of the commercial agriculture sector, would be prohibitively expensive. Furthermore, a prominent ungulate – the true quagga – is now extinct (Skinner & Smithers, 1990).

CONCLUSIONS

Written, historical records provide good evidence of the occurrence, during part of the 19th century, of large aggregations of medium- to large-sized, plains-living, ungulates in that part of the grassland-dominated Highveld region of South Africa that lies between the Orange River in the south and the Vaal River in the north. There is some written evidence of mass migratory behaviour by some of these species. Additional information indicates that these large aggregations also occurred in that part of the Highveld lying to the north of the Vaal River.

Owing to the rapid collapse of the grazing component of the Highveld grazer-grassland system, there is a paucity of information on its ecological drivers, characteristics and dynamics. Nonetheless, our contribution helps to establish the scale of the system that existed there prior to the approximate start of the colonial period (c. 1820). The rapid collapse of these populations is consistent with the current understanding of the vulnerability of large herbivores to over-exploitation. Thus, Ripple *et al.* (2015) show that the decline of large herbivores globally is linked to their large body size, which confers high value and slow life histories, resulting in high demand, and slow recovery to over-exploitation.

By all accounts, the Highveld grazer-grassland system, which ceased to exist functionally by the end of the 1870s, owing principally to overhunting and habitat loss, may have rivalled similar large-mammal systems in Africa, and elsewhere on earth, in terms of larger ungulate abundance and diversity. Whilst all the ecological consequences of the collapse of the grazer component of the Highveld system are not understood, they are considered to have triggered significant changes

to ecosystem processes, and witnessed the extinction of one taxon.

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Appendix 1

References that contain information on large aggregations of medium- to large-sized, plains-living, herd-forming, ungulates in the area covered by today's Free State Province (South Africa) and Lesotho (see Table 1).

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- Appendix 2**
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