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Filling the gaps on the maps: historical distribution patterns of some larger mammals in part of southern Africa

André Boshoff*, Marietjie Landman & Graham Kerley

Centre for African Conservation Ecology, PO Box 77000, Port Elizabeth, Nelson Mandela Metropolitan University, Port Elizabeth 6031, South Africa

*Corresponding author E-mail: andre.boshoff@nmmu.ac.za

Distribution data form the basis of the study of zoo-geography, which has applications in, *inter alia*, ecology and conservation. Written records were used to estimate the distribution patterns of some of the medium- to large-sized terrestrial mammals in central, southern and western South Africa, and neighbouring Lesotho, during the early historical period (late 1400 s to the 1920s). The sources of these records comprise mainly published or unpublished letters, journals, diaries or books written by literate pioneers – notably various missionaries, explorers, travellers, naturalists, military personnel, big game hunters and agro-pastoralists. The classification (according to record type) of the written records in key publications was standardised, and records overlooked by them are taken into account. Interpretation of the spatial patterns provided by the written records was aided by reference to supporting information, in the form of qualifying palaeontological, zoo-archaeological and museum records. Written records of acceptable quality are shown, together with supporting records (where applicable), on a series of species occurrence maps, which also depict the biomes that are represented in the study area. The information on these maps is interpreted, together with relevant information in the source texts and a map of the bioregions that constitute the biomes in question, to estimate distribution patterns that prevailed during the period under study. Data are presented for 27 genera, 36 species and 2 subspecies, comprising 7 carnivores and 30 herbivores. Despite the limitations associated with the use of written records, the information provided is considered to offer a realistic distribution pattern for most of the taxa covered. The use of supporting records is justified, since the majority of these corroborate the ranges derived from the written records. The present study enhances our knowledge of distribution patterns for these larger mammal species in a large part of the southern African sub-region during the early historical period. It also provides a first attempt to describe the sub-regional scale, historical, distribution patterns within the context of the broad biogeographical characteristics of the area in question. There is a need to extend the coverage achieved by this study to include the remaining approx. 30% of “South Africa”, i.e. the region incorporating South Africa, Lesotho and Swaziland, and also the area incorporated by the countries of Namibia, Botswana, Zimbabwe and Mozambique. This level of coverage will permit enhanced definition of historical distribution patterns for some larger mammals in the southern African sub-region. There is also a need to better understand the drivers, as well as the implications, of the observed changes in the distribution of the larger mammals since the start of the historical period.

Keywords: historical distribution; mammals; southern Africa; biogeographical regions

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INTRODUCTION

Distribution data are the basis of the study of zoo-geography, which has applications in, *inter alia*, ecology and conservation. These data are essential for establishing the link between the occurrence of a species on a landscape and its habitat requirements. They are also important for investigating the presence, absence or nature of spatial and temporal patterns and trends of a species across a landscape, as well as guiding the restoration of species to areas from which they have been extirpated (IUCN, 2001). The benefits of combining the (usually) parallel disciplines of environmental history (being primarily an interpretation of the past) and conservation biology (which primarily seeks to shape the future) are largely the increased confidence in the understanding of distribution information, and hence implementation and sustainability of any management actions (Boshoff & Kerley, 2010). Such management actions would include the development of conservation targets and strategies and the drawing up of policies, legislation and regulations appropriate to the management of populations, especially those in the threatened or near-threatened categories, and to protect the ecosystems and evolutionary processes that sustain them. Distribution data are also a key component of taxonomic studies (Roberts, 1951).

The above statements are relevant to initiatives that involve the researching and conservation of mammals, and for which knowledge of their natural distribution patterns is required, i.e. their distribution prior to significant changes in their status (ranges and numbers) as a direct or indirect consequence of mans' activities. For example, research has shown that species range shifts have occurred in response to climate change (Peters & Lovejoy, 1992; Hughes, 2000) and this provides challenges for conserving biodiversity in the face of such change (Hannah *et al.*, 2002). Robust information on species' historical distribution assists our understanding of the nature of the impacts of such changes on, *inter alia*, mammals, and also the compilation of detailed strategies and plans to mitigate these. Published estimates of historical distribution ranges are also widely used to inform mammal stocking programmes for protected areas, private nature reserves and game farms (e.g. Kerley *et al.*, 2003a; Cowell & Ferreira, 2015).

In southern Africa the larger terrestrial mammals have been highly impacted by mans' activities, especially since the start of the colonial period. Consequently, over the past 250–300 years the populations of several species in this sub-region have become locally, regionally or globally extinct, or have undergone marked fragmentation of their ranges, or a decline in

numbers (Du Plessis, 1969; Smithers, 1983, 1986; Friedmann & Daly, 2004; Skinner & Chimimba, 2005; Skead, 2007, 2011; Boshoff & Kerley, 2013; Kingdon *et al.*, 2013). Critically, in all cases, these changes took place before their natural distributions could be comprehensively studied and recorded.

The 20th century saw a number of initiatives to publish summaries of the life-histories, or aspects thereof, of the larger mammal taxa in southern Africa (Sclater, 1900; FitzSimons, 1919, 1920; Haagner, 1920; Roberts, 1951; Sidney, 1965; Dorst & Dandelot, 1970; Smithers, 1983; Skinner & Smithers, 1990; Apps, 1996), with this trend continuing into the early 21st century (Skinner & Chimimba, 2005; Kingdon *et al.*, 2013). While all of these works make some reference to the historical distribution of the species covered, none attempts to deal with this topic in a comprehensive (systematic) manner. In certain cases, some localities and dates of early distribution records of some species are mentioned but, for the greater part, this issue is dealt with through a series of short statements of a generalised nature, with a complete absence of supporting data, and localities are usually described only in geopolitical terms (e.g. countries, provinces, magisterial districts), rather than in biogeographical ones. While some authors (e.g. Dorst & Dandelot, 1970; Smithers, 1983; Skinner & Smithers, 1990; Skinner & Chimimba, 2005) do state that their distribution maps show current ranges, for others it is not always clear whether they pertain to a species' historical or current distributions. Furthermore, it is seldom clear whether the statements on historical ranges are based on actual records (sightings, signs or specimens), or on hearsay, opinions, unsubstantiated extrapolations, or on a combination thereof. This situation makes it difficult to obtain reliable estimates of the natural distribution ranges, and to conduct spatial assessments of species richness and diversity, of the larger mammals in southern Africa.

Historical distribution maps need to be as comprehensive as possible in order to, *inter alia*:

- (a) develop an understanding of how distribution patterns have been impacted by anthropogenic activities, not least in the form of global change (e.g. Hannah *et al.*, 2002; Kerley & Boshoff, 2014),
- (b) provide a basis for studies that use modern statistical techniques to investigate how populations, communities and species have shifted, spatially, over long temporal scales, (e.g. Tingley & Beissinger, 2009),
- (c) assist attempts to mitigate the "shifting baseline syndrome" (Pauly, 1995) in the conservation field by, for example, contributing to the creation of historical baselines for use in Red Data Book revisions, and to set baselines for measuring conservation success (Roman *et al.*, 2015), and also to
- (d) explore invasive species biology and theory, focusing on areas where species did not occur naturally and have been introduced (e.g. Matthee *et al.*, 2013).

Notwithstanding interpretational challenges related to the quantity and quality of the information, the use of written, historical accounts and physical specimens is a widely applied research tool to assist in the reconstruction of past faunal assemblages (e.g. Rookmaaker, 1989, 2007; Shaffer *et al.*, 1998; Ceballos & Ehrlich, 2002; Ray *et al.*, 2005; Zielinski *et al.*, 2005; Skead, 2007, 2011; Matthews & Heath, 2008; Burbridge *et al.*,

2009; Harris *et al.*, 2009; Boshoff & Kerley, 2010, 2013; Ripple *et al.* 2015).

The post-1965 period has witnessed a number of attempts to use written, historical records to investigate the early distributions of various larger mammal species in southern Africa. Notable studies in this regard are listed and briefly discussed below.

Du Plessis (1969): This study covers the species in the orders Perissodactyla (rhinoceroses and zebras) and Artiodactyla (hippopotamus, pigs, giraffe, African buffalo and antelopes), for the southern African sub-region. However, full details of how the "presence polygons" on the distribution maps were derived are not provided; it can only be assumed that these represent some kind of "broadbrush" approach that is akin to determining the "extent of occurrence" of a species (a convex polygon created by joining the outermost distribution records, as defined in IUCN, 2015). If so, it introduces the problem of the possible existence of "false positives"; here a species may be considered to occur everywhere within its "extent of occurrence" but no data or information exist to confirm this (Laliberte & Ripple, 2004; Habib *et al.*, 2006). A further limitation of the Du Plessis study is that it uses "rock paintings" and "place names" as sources of distribution information; both of these are considered to be unreliable for this purpose (Skead, 2007, 2011; Boshoff & Kerley, 2013). Thus, while the Du Plessis study provides a basis for zoo-geographical studies in the sub-region, the limitations briefly discussed above detract somewhat from its usefulness for this purpose. Finally, this work (an MSc dissertation) was never published and is consequently difficult to access by researchers.

Rookmaaker (1989): This study presents information for the southern and western parts of the sub-region, and the Karoo.

Roche (2004): This autecological study records springbok 'treks' in the Karoo (1774–1908).

Rookmaaker (2007): This study, which covers the entire sub-region, deals with the two rhinoceros species that occur there.

Skead (2007, 2011) and Boshoff & Kerley (2013): These studies cover one or more provinces of South Africa, and the small country of Lesotho. While the spatial focus of these individual studies offers tantalising glimpses into historical mammal distributions within their respective areas (largely geopolitical units), individually they cannot be used to identify the broader (sub-regional) zoo-geographical patterns.

Notwithstanding the fact that the studies by Rookmaaker (1989, 2007), Roche (2004), Skead (2007, 2011) and Boshoff & Kerley (2013) are geographically and/or taxon limited, by virtue of their subject matter and design, they contain the bulk of the written distribution records used for the present study, and therefore they provide the foundation for the present study.

To address the issues discussed above, we provide a compilation of written distribution records from a range of key literature sources, boosted by records overlooked by them, and appropriate supporting records (in the form of palaeontological, zoo-archaeological and museum records) and use this information to estimate the distribution patterns of selected larger mammals in 70% of the area incorporated by the southern African countries of South Africa, Lesotho and Swaziland.

Importantly, the area covered by the present study includes the entire areas of the Fynbos, Succulent Karoo, Nama-Karoo, and Desert biomes in South Africa, most of the area of the Albany Thicket Biome, and large parts of the Grassland,

Savanna and Indian Ocean Coastal Belt biomes. Accordingly, the present study has substantial biome-scale coverage, which was not achieved by some of the previous studies, listed above. Hence, the present study provides a first attempt to describe the distribution patterns, referred to above, within the context of the key biogeographical characteristics of the study area.

STUDY AREA

The study area incorporates the present-day, political, territories formed by the Western Cape, Eastern Cape, Northern Cape and Free State provinces, and the far western part of the North West Province, of the Republic of South Africa, and the independent country of the Kingdom of Lesotho (Figure 1). Their combined areas constitute some 70% of the total area of "South Africa" (881 377 km²), i.e. South Africa and the countries of Lesotho and Swaziland. For practical reasons, the boundary of the study area follows the areas covered by the three main sources of information, namely Skead (2007, 2011) and Boshoff & Kerley (2013), which in turn are based on the provincial boundaries of South Africa prior to its rebirth as a democratic country in 1994. Skead

(2007, 2011) represent revised editions of these works, originally published in 1980 and 1987, respectively.

The broad rainfall pattern in the study area, as delineated by selected rainfall classes, shows a marked east-west gradient, and a somewhat lesser north-south gradient, to the west of about 23° E (Figure 2).

The Orange River to the west of its confluence with the Vaal River is also known as the Gariep River, and its upper section, which flows in Lesotho, is known as the Senqu River. The upper section of the Vaal River is also known as the Likwa (Liqua) River.

METHODS

The early historical distribution of 27 genera, 36 species and 2 subspecies (comprising 7 carnivores and 30 herbivores) is investigated by mapping qualifying, known, written records and supporting records, and by consulting unmappable, written records in the literature (see below).

For the purposes of the present study, the "early historical period" is defined as that starting in the late 1400s (i.e. when the first written records were made, by European visitors) and ending with the 1920s (i.e. prior to the start of an era of wide-scale translocation of some of the larger mammal

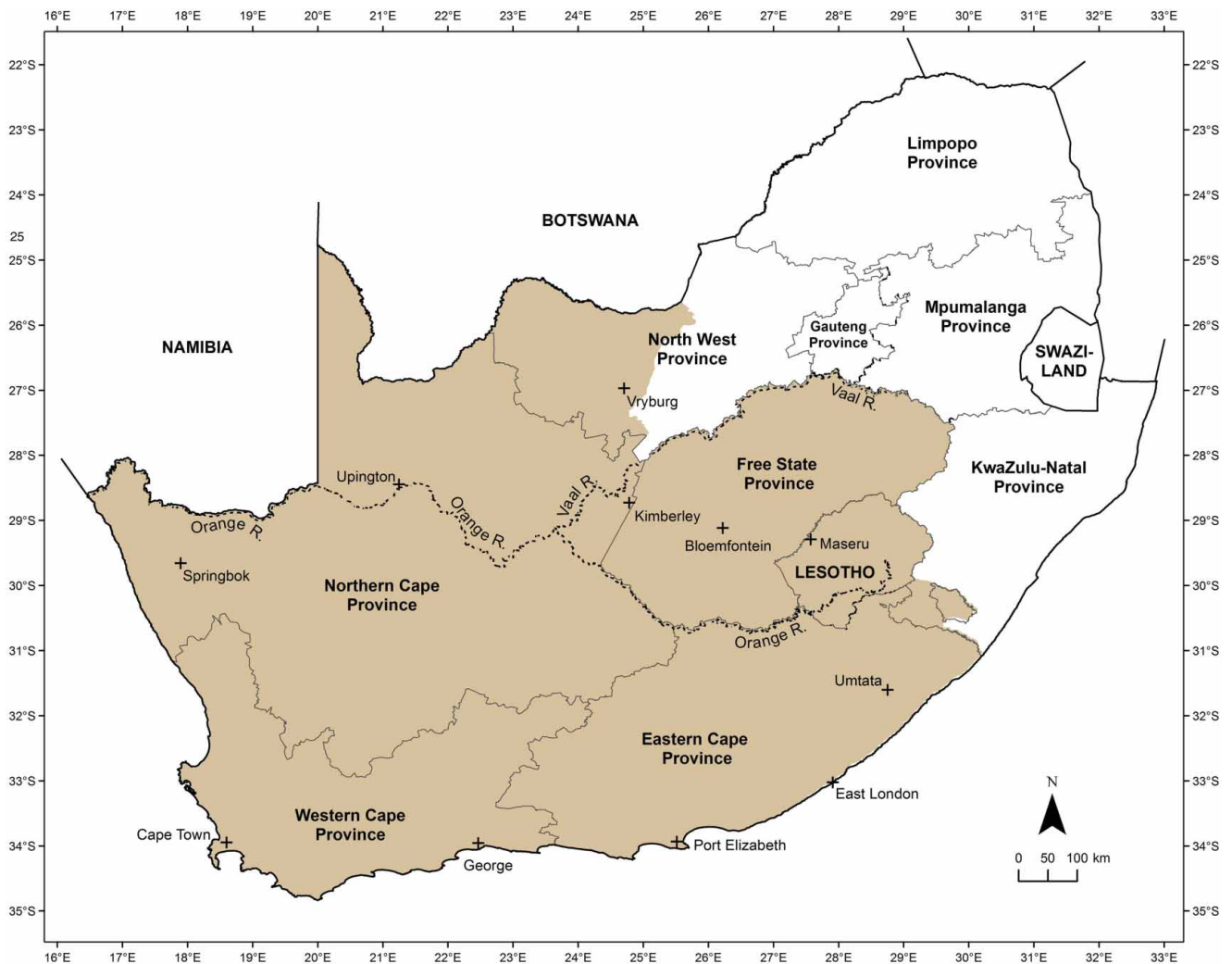


Figure 1. The nine provinces of the Republic of South Africa and the kingdoms of Lesotho and Swaziland. The study area is shaded.

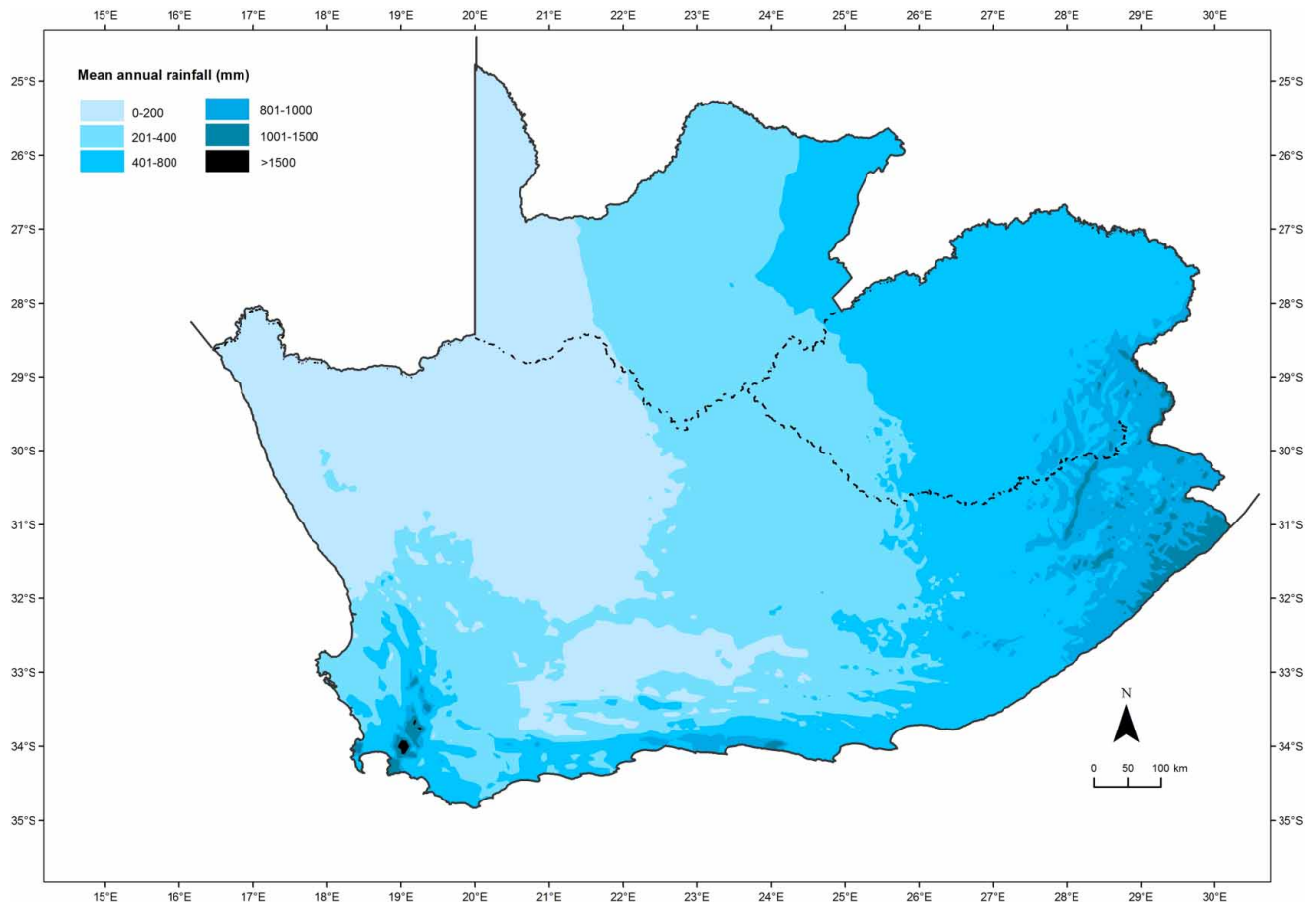


Figure 2. The broad rainfall pattern in the study area, as delineated by selected rainfall classes, shows east-west and north-south gradients.

species by man). However, this specific period varies across the study area; in the south-western part it commenced in the late 1400s, whereas in the far north-eastern part it only commenced when the first literate people started to visit this region during the early 1800s, i.e. around 300 years later.

Owing to inherent limits on the quality of the data and information, an empirical approach is followed, i.e. no attempt at modelling, however simple, has been made. Thus, the descriptions of apparent distribution patterns are heavily biased towards “presence” records. In this approach, it is emphasised that the absence of a record for a species from a particular place or area does not necessarily mean that it did not occur there. The bias referred to is, to some extent, mitigated by reference to broad habitat surrogates, in this case biomes and bioregions (see later), and the ecological requirements of the species in question, when inferring general distributions within the area under consideration.

The written and supporting records are mapped using a system similar to that used in Skead (2007, 2011) and Boshoff & Kerley (2013). Sightings, vocalisations and signs (e.g. tracks/spoor) form the basis for most of the written records. In the legends on the species distribution maps the following definitions apply:

Identification (ID)

The identification categories listed below mainly apply to written records; the identification of supporting records is usually based on specimens and is considered to be accurate (but see later):

Acceptable ID: there is certainty, or, occasionally, reasonable certainty about the animals’ identity (taxon).

Questionable ID: there is some doubt about the animals’ identity, or a reasonable possibility that the identification is accurate.

Locality

“Precise” locality: located at an identifiable place, or within a roughly circular area with a diameter of approximately 5 km; this qualifies as a “mappable” record.

“Imprecise” locality: located within a roughly circular area with a diameter of approximately 50 km; this qualifies as a “mappable” record.

“Unmappable” record: some historical records are not considered spatially specific enough to be represented on maps, and are hence classified as “unmappable”. Examples include general, regional, references to the occurrence of a species, such as “species X was observed between two distant points [named]”. Such records do, however, still provide value, in terms of distribution information at a regional scale, and they are used accordingly.

Broad record categories

Written records

Three published works (namely Skead, 2007, 2011 and Boshoff & Kerley, 2013), which collate and attempt to interpret early distribution records from a wide range of sources, form the main sources of the written records used in this study. These three volumes include important information from the

studies conducted by Rookmaaker (1989, 2007). Space restrictions prevent repetition, in the species accounts, of the details of the numerous individual records (and associated literature references), from the various source documents, that are used to estimate broad, historical, distribution patterns.

“Written records” broadly applies to information captured in published and unpublished documents, notably books, journal articles, popular articles, reports, catalogues, diaries, journals and letters. The 37 taxa selected for the present study are those for which distribution data and information are provided in all three publications listed above. In order to meet the criteria for the present study, the data-sets used for the species maps in the three publications were edited to (a) remove post-1920s records, (b) achieve standardisation in terms of the categorisation of records (i.e. “record type”), and (c) incorporate additional records that were omitted or overlooked; in this regard, 64 records have been added to the data-sets used by Skead (2007, 2011) and Boshoff & Kerley (2013). The criteria used for allocating a written record to a particular “record type” (see the legends on the species distribution maps) are discussed in Skead (2007, 2011) and Boshoff & Kerley (2013).

Literature sources other than Skead (2007, 2011) and Boshoff & Kerley (2013) were consulted for historical distribution information from areas adjacent to the study area.

Supporting records

Three types of supporting records (all shown on the species distribution maps) are used to support the written records. A total of 202 of these records have been added to the datasets used by Skead (2007, 2011) and Boshoff & Kerley (2013). Aspects relating to the use of the supporting records are briefly discussed below.

Palaeontological records

Fossilised, semi-fossilised and non-fossilised skeletal remains of mammals provide a potential source of information to assist in estimating the historical incidence of the larger mammals (Boshoff & Kerley, 2013). This information usually derives from tusks, teeth, skulls or large bones that are uncovered by soil erosion or by human activities (e.g. building, tilling). Skead (2007, 2011) cautions against the possibility that some palaeontological material may represent items that were discarded, intentionally or unintentionally, along the way by early hunting expeditions returning from the interior. Thus, single bones should be treated with caution, while a partial or complete skeleton provides a more reliable record. Similarly, some such material may represent trade or tribute items moved over considerable distances (Mitchell, 2009).

Given that it is often difficult to accurately date palaeontological material, such records are used in a broadly supportive, rather than a primary, role, i.e. to enhance the findings from the written record. Bearing its limitations in mind, palaeontological information for the period up to about 3000 years BP (Before Present, defined by international consensus as 1 January 1950) has been used in the present study.

Zoo-archaeological records

Specimens (usually teeth and bones) of larger mammals found in archaeological deposits can be useful for reconstructing the distribution patterns of these animals in early historical times.

In fact, zoo-archaeological information has been shown to provide useful insights into animal behaviour, distribution and habitat use, and its value in wildlife and heritage conservation has also been highlighted (e.g. Badenhorst & Plug, 2004; Plug & Lauwerier, 2004; other papers in Lauwerier & Plug, 2004).

Numerous archaeological sites in rock shelters and in the open have been excavated in the study area and the results provide a useful source of information. However, a study of the literature clearly indicates that archaeological samples, insofar as their mammalian content is concerned, must be interpreted with caution. Two particular problems are those of misidentification of specimens (taxa) (especially when a single, small fragment is used to attempt an identification) and the transport of material through transhumance. In addition, the absence of remains, of a mammal that potentially occurred in a particular area, in archaeological samples must not be interpreted to mean that it did not occur in the area or region (Plug & Badenhorst, 2001). Zoo-archaeological information is usually complex and provides analytical and interpretational challenges – this is discussed in more detail by Boshoff & Kerley (2013).

Our use of zoo-archaeological information from the later Holocene (about 4000 years to present) to support early written historical records is considered appropriate. Climatic conditions have been moderately stable over the past 5000 years in Africa (Deacon & Lancaster, 1988) and there is evidence that modern biomes were well established during the Quaternary, and that from c. 7000 years BP, and probably before, they began to reflect modern conditions, although small fluctuations occurred until recently (Scott *et al.*, 1997). It has also been shown that modern mammal communities in Africa, including the larger mammal assemblages, have prevailed since the mid-Holocene (de Vivo & Carmignotto, 2004).

Owing to interpretational pitfalls associated with zoo-archaeological data and information (discussed by, *inter alia*, Boshoff & Kerley, 2013), they are used in a broadly supportive, rather than a primary, role, i.e. they are selectively used as a guideline to assist in the interpretation of the findings from the written record.

Museum records

A source of historical, distribution information is provided by the mammal collections in South African natural history museums. These comprise skins or whole or partial skeletons from mammals donated by members of the public, or collected during field excursions by museum-based scientists. Like the palaeontological and archaeological records, information from museum collections is used in the present study to support that from the written records. Museum records that are discussed in unpublished and published reports and articles are sometimes included as “written records”.

Supporting records from the Free State Province and Lesotho are referenced in Boshoff and Kerley (2013), and are therefore not re-referenced in the various species accounts.

General

Distribution patterns are broadly described in relation to major ecological units or zones, rather than geo-political ones (e.g. countries, provinces). To enable this, the maps depicting the written and supporting records for each species also show the biome (from Rutherford *et al.*, 2006)

coverage and, to facilitate a deeper investigation of these relationships in the individual species texts, a map showing the bioregions that are represented in the study area, is included (Figure 3). Although the biome and bioregional units are strongly biased towards plant communities, they nevertheless represent the influence of various biophysical features, processes and patterns and therefore provide a convenient basis for attempts to describe the indicated historical

distribution patterns of some of the larger mammals on the landscapes of that part of the sub-region covered by the present study (Turpie & Crowe, 1994; Rutherford *et al.*, 2006).

The point locations for the written and supporting records, and the polygons depicting the biome and bioregional zones (after Rutherford *et al.*, 2006), are mapped using ArcGIS Ver. 10.2. Other aspects of the mapping system used are already explained under “Methods”.

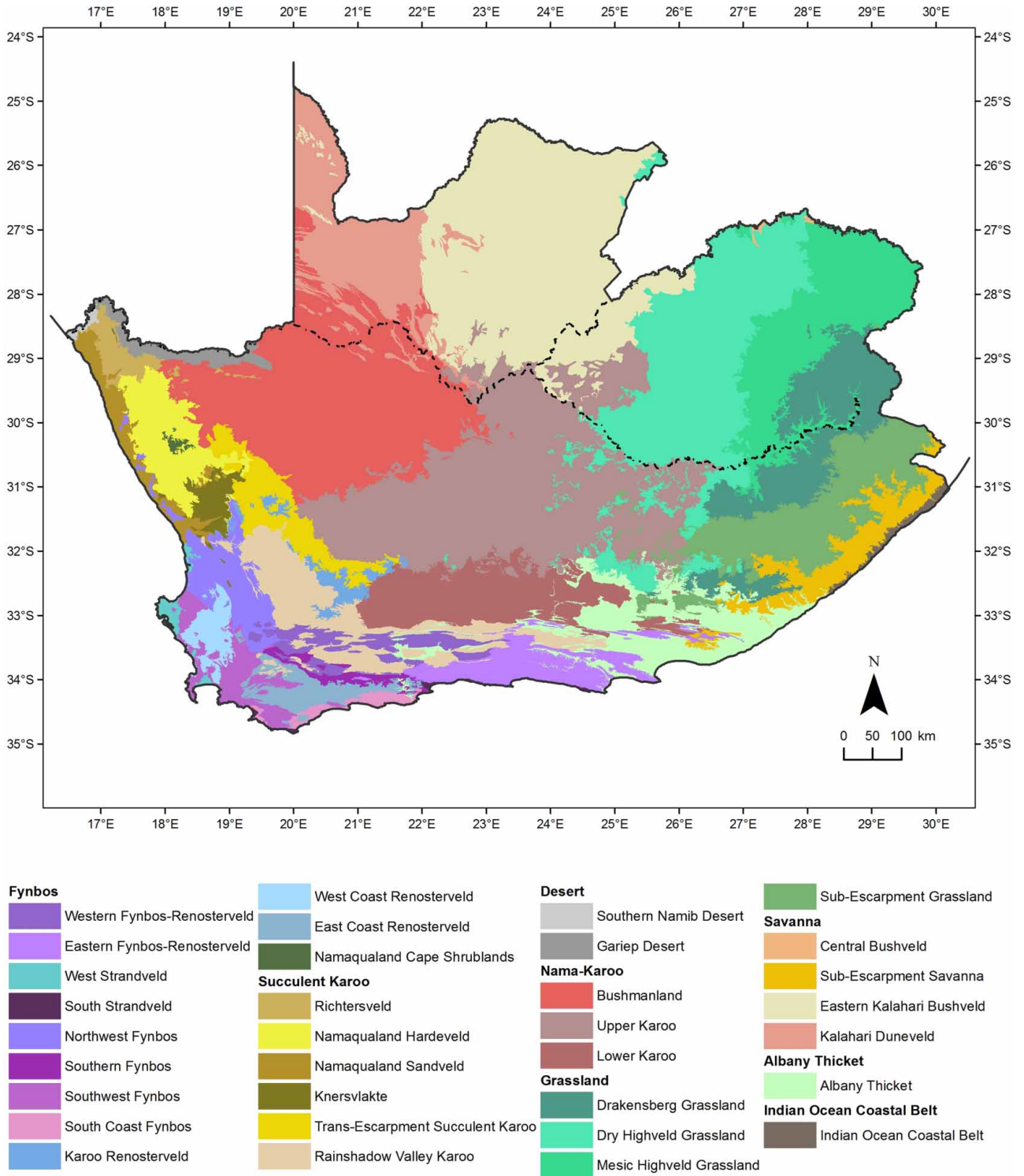


Figure 3. The bioregions, listed according to parent biome, that fall within the study area. Adapted from Rutherford *et al.* (2006).

In order to assess the degree of spatial coverage obtained by the study, all the written and supporting records are plotted on a single (“all records”) map. However, when interpreting the information on this map the reader must bear in mind the constraints associated with the quality of these records (discussed earlier), and what they actually represent. With regard to the latter it is important to note that each written record locality on this map does not represent, on the part of the chronicler (s) in question, the same amount and quality of effort, in terms of observing or hunting, correctly identifying and recording one or more of the larger mammals that occurred at a particular locality. Thus, the written record loci plotted on this map do not represent the outcome of a systematic sampling exercise but rather a general picture of where some, literate, early travellers infrequently or frequently recorded some of the larger mammals that they encountered, usually in the form of sightings, signs, vocalisations and hunting spoils. It follows that the non-systematic manner in which the written records were made must be taken into account when using this information to interpret the broad patterns of historical distribution.

To assist in the interpretation of the patterns of the written records on the species distribution maps, a simple categorisation of early chronicler coverage is used, with broad categories (“poor”, “reasonable”, “good”) selected according to a visual assessment of the relative density of records in the geographical area of interest.

The text that accompanies each species distribution map includes an overview of the broad distribution patterns discerned for that taxon, for the defined historical period. Although, in the compilation of each overview, cognisance was taken of the general habitat characteristics and key ecological requirements of the species concerned, this aspect was not the focus of the study and is therefore dealt with in a relatively cursory manner.

Owing to the non-systematic nature of the data and information used to compile the species distribution maps, no attempt is made to model the “extent of occurrence” or “area of occupancy” (following the definitions in IUCN, 2015) or any other mathematical distribution parameter(s).

Scientific names follow Skinner & Chimimba (2005), who in turn follow Bronner *et al.* (2003). An exception is provided by the equids, where the extinct true quagga is treated here as a distinct species – *Equus quagga* – and Burchell’s (plains) zebra as *E. burchellii*. Trinomials are introduced only in cases where this is deemed necessary, i.e. in the case of the two *Damaliscus* subspecies (bontebok and blesbok), and the two mountain zebras.

The biological and ecological characteristics of the taxa covered are well summarised in Skinner & Chimimba (2005), Kingdon & Hoffmann (2013a,b) and Kingdon *et al.* (2013).

RESULTS

The taxa dealt with in this study are listed according to English common name and scientific name under Contents. Afrikaans common names are provided in the individual species accounts.

Other larger mammals that were (and still are) present in the study area (Skinner & Chimimba, 2005), but were not included in this study owing mainly to a paucity of early written records, which prevents the drawing of meaningful conclusions about their historical distributions, include the caracal *Caracal caracal*, black-backed jackal *Canis mesomelas*,

bushbuck *Tragelaphus scriptus*, blue duiker *Philantomba monticola*, common duiker *Sylvicapra grimmia*, steenbok *Raphicerus campestris* and Cape grysbok *R. melanotis*. The possible reasons for the paucity of records for these taxa are discussed in Skead (2007, 2011) and Boshoff & Kerley (2013).

Chronicler coverage

The spatial pattern of the written records of all taxa (Figure 4) shows that, overall, the coverage in the study area varies, locally, from poor to reasonable to good. Prominent gaps in this coverage are in the Kalahari Duneveld, Bushmanland and Drakensberg Grassland bioregions, and in parts of the Eastern Kalahari Bushveld Bioregion (see Figures 3 and 4). The reasons for this are probably varied and include factors such as distance from early tracks and main wagon-routes, availability of surface water and forage for draught animals, and the presence of rugged terrain. Notwithstanding the incomplete spatial coverage obtained, the spread of the written records is considered to be such that all the taxa covered had reasonable potential to be recorded, where they naturally occurred, within the study area. The distribution pattern of the supporting records mapped in Figure 4 reflects a rather different set of factors, for example, the results of highly area- or site-specific archaeological investigations, and opportunistic (chance) discoveries, usually by lay members of the public.

AFRICAN ELEPHANT

Loxodonta africana (Blumenbach, 1797)

OLIFANT

DISTRIBUTION RECORDS

Written records in Cowan (1808), Moodie (1838), Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Klein & Cruz-Urbe (2000), Plug & Badenhorst (2001), Skead (2007, 2011) and Boshoff & Kerley (2013), and a 1904 specimen in the South African Museum (Iziko Museums, Cape Town) mammal collection, indicate that within the study area African elephant occurred in parts of eight biomes – Fynbos, Succulent Karoo, Desert, Nama-Karoo, Grassland, Savanna, Albany Thicket, Forest. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 5.

Fynbos Biome

A number of written records, supported by six palaeontological and three zoo-archaeological records, and one museum record, indicate the presence of African elephant in a number of bioregions within this biome.

Apart from a few records between 32°30' S and 33° S, and some way inland, in the western part of this biome, all the record localities are at or near the coast. The inland records in the west are from the mountainous Cedarberg area, where a number of wide-bottomed, well-watered valleys provide suitable habitat.

A number of records reveal the occurrence of African elephant on the incised plateau between the Outeniqua-Tsitsikamma mountain ranges and the coast, between 22° and 24° E, an area characterised by a matrix of forest and moderately grassy fynbos.

Succulent Karoo Biome

A few written records suggest that African elephant were present in the sub-coastal zone of the west coast, and close

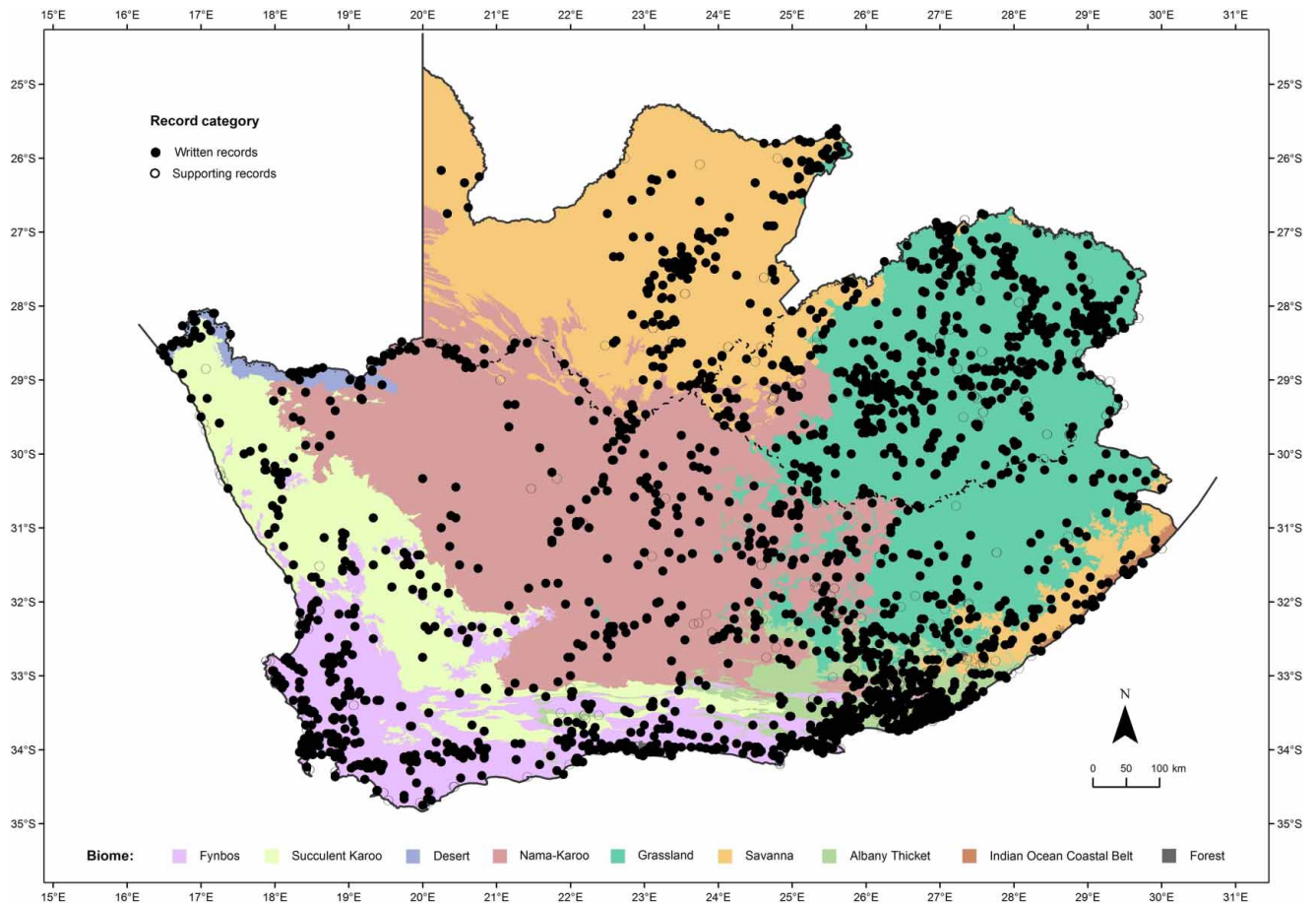


Figure 4. Localities of all written and supporting records (see text), and biomes, in the study area.

to the interface between the Namaqualand Sandveld and Namaqualand Hardeveld bioregions. This region is traversed by seasonal, west-flowing rivers that drain the western flank of the Namaqualand Plateau. A general lack of surface water in this arid biome is considered to have rendered most of it unsuitable for this megaherbivore.

Desert Biome

A number of written records reveal the occurrence of African elephant in the Southern Namib Desert and Gariiep Desert bioregions. However, the localities of these records are at or close to the course of the Orange River, which would have provided a year-round supply of water and forage (in the riparian zone).

Nama-Karoo Biome

The handful of written records of African elephant from the Bushmanland Bioregion is all along the course of the Orange River, which provided a year-round supply of water, and forage (in the riparian zone).

A number of palaeontological records indicate their presence in the south-eastern part of the Upper Karoo Bioregion, and the eastern part of the Lower Karoo Bioregion. Both regions are associated with the Great Escarpment and are relatively well-watered and grassy, compared to the remaining parts of these bioregions (Mucina *et al.*, 2006a). The absence of written records from these areas, despite relatively good early chronicle coverage (Figure 4), suggests that African

elephant had disappeared from there prior to their penetration and settlement by European hunters and colonists (1700s onwards).

Grassland Biome

A cluster of palaeontological records from the western part of the Sub-Escarpment Grassland Bioregion, together with an outlying record to the east, and the absence of written records, from these areas, despite relatively good early chronicle coverage (Figure 4), suggests that African elephant had disappeared from there prior to their penetration and settlement by European hunters and colonists (latter 1700s onwards).

Since the rugged terrain that dominates the Drakensberg Grassland Bioregion is unlikely to have offered suitable African elephant habitat, the handful of palaeontological records from the southern part of this bioregion may represent animals moving along wide valley bottoms. All the records in this bioregion are palaeontological records, and no written records could be located, despite relatively good early chronicle coverage (Figure 4). This suggests that African elephant no longer occupied these landscapes by the time (1700s) the first chroniclers arrived.

No reliable records could be located for the open grasslands to the north-east of the Orange River. An African elephant “cheek-tooth” was discovered when a dam wall on a farm near the Modder River to the north-east of the present-day city of Bloemfontein washed away (in 1976). This record, the

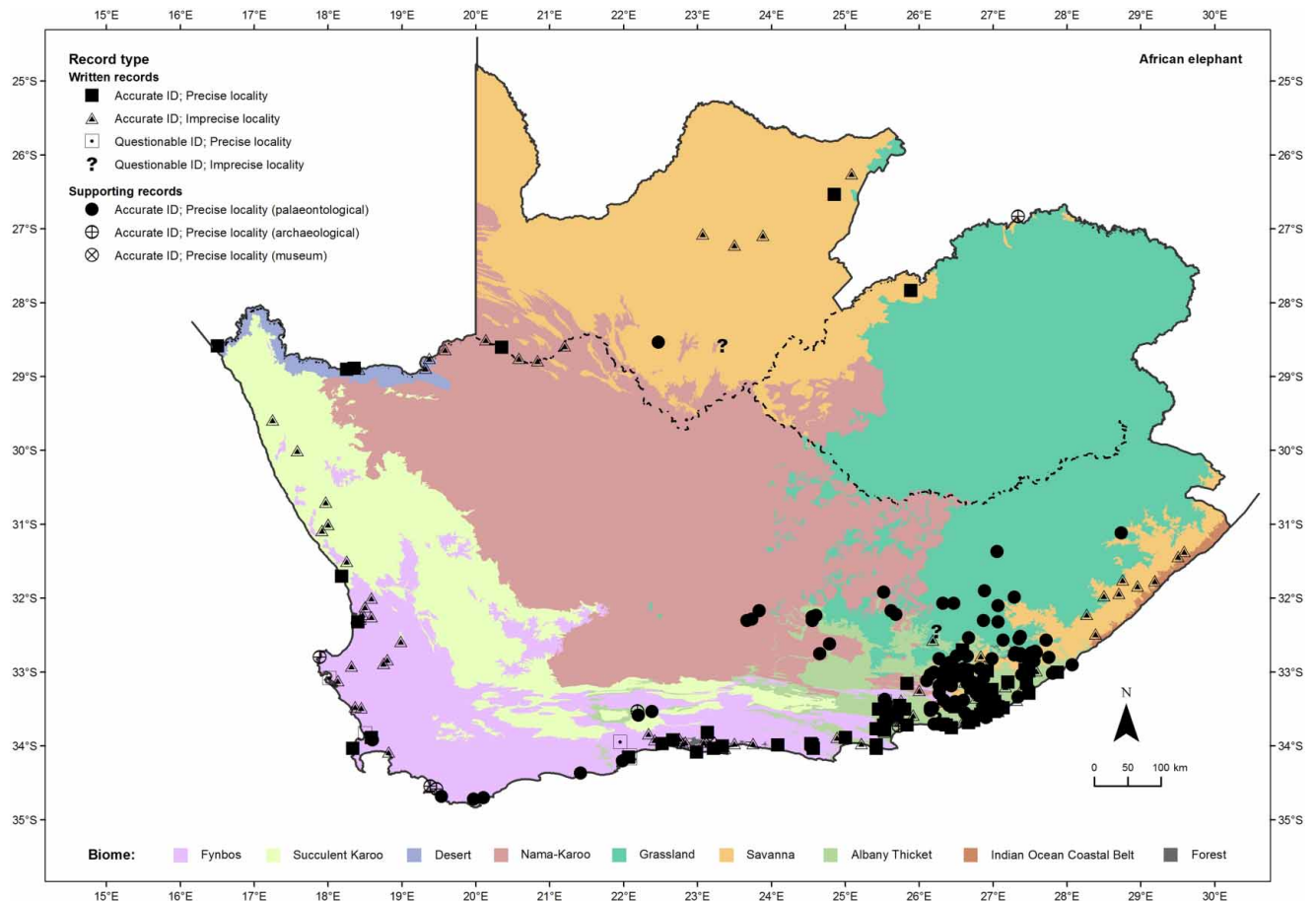


Figure 5. Early historical incidence of the African elephant: mappable written and supporting distribution records (see the text), and biomes.

locality of which falls within the Dry Highveld Grassland Bioregion, is treated with circumspection, owing to uncertainty regarding the provenance of the specimen (Boshoff & Kerley, 2013); it is not shown in Figure 5.

Savanna Biome

A number of written records and a single palaeontological record reveal the former presence of African elephant in the relatively well-watered Eastern Kalahari Bushveld Bioregion, to the north-east of the Orange River. Given that early chronicler coverage in this bioregion, which contains fine African elephant habitat, was reasonable to good in places (Figure 4), the paucity of written records for this easy to detect and identify animal is noteworthy. Could this perhaps be a reflection of the fact that by the 1830s this area had been visited or traversed, and exploited, by several early European and Griqua ivory hunters?

A number of written and palaeontological records show that African elephant occurred in the Sub-Escarpment Savanna Bioregion, in the south-eastern part of the study area.

Albany Thicket Biome

Numerous written records, supported by several palaeontological records and a single zoo-archaeological record, confirm the incidence of African elephant in this biome. Sub-tropical thicket vegetation, with interspersed grassy patches, provides prime African elephant habitat (Kerley & Landman, 2006). The lack of records from the north-western part of this biome is

considered to be due mainly to the dearth of early chroniclers in that area (Figure 4).

Two palaeontological records and a single zoo-archaeological record (Plug & Badenhorst, 2001) indicate the presence of African elephant in the Little Karoo, this being a broad east-west running valley bordered by the Swartberg mountains in the north and the Outeniqua mountains in the south. Patches or areas of thicket vegetation that occur in and near this valley, and which form western outliers of the biome under consideration, would have supported African elephant that lived in, or visited, the valley. Although no eyewitness accounts could be found, there is anecdotal evidence that suggests that African elephant may have moved between the Little Karoo and the coastal plain to the south, for example via the Attakwaskloof (pass) to the north-west of today's town of Mossel Bay (Skead, 2011).

Forest Biome

Loxodonta africana is not a true forest species and its association with stands of Southern Coastal Forest and Southern Afrotemperate Forest in the coastal and sub-coastal areas (see Mucina & Geldenhuys, 2006) is related to its use of open, grassy habitats in the close vicinity of these forest types (the scale of Figure 5 does not allow this to be illustrated). The records of African elephant in tracts of Southern Afrotemperate Forest, south of the Outeniqua-Tsitsikamma mountains and between 22° and 24° E (Skead, 2011), are

Table 1. The density, status and habitats of elephants in three likely zones of occurrence in the broader Eastern Cape (after Boshoff *et al.*, 2002).

	Coastal zone	Sub-coastal zone (south of the Great Escarpment)	Inland zone (north of the Great Escarpment)
Density	Relatively high.	Relatively low.	Largely absent, or at a very low density.
Status	Mainly resident, but local movements undertaken.	Some may have been resident but most were local migrants or nomads.	Present only as occasional migrants or nomads, mainly as travellers between the coastal and sub-coastal zones and [possibly] the Orange River.
Habitats occupied	Present throughout most of the mosaics of forest, thicket and savanna.	Present mainly in the wide river valleys, vegetated with riverine forest and thicket. Interfluves also used.	In transit through karroid vegetation. The riparian and kloof vegetation was most likely also utilised.

believed reflect their use of these forests as a refuge, following direct persecution by humans (Kerley *et al.*, 2012).

Indian Ocean Coastal Belt Biome

The reasons for the absence of records from this biome are not known, as African elephant may be expected to have occurred there. It is speculated that most of this biome (within the study area) did not provide suitable African elephant habitat during the early historical period. This is because it comprised highly dissected, hilly, country, with many steep sided valleys, with an original cover of dense bush and forest (which has been replaced over time by secondary grassland, through clearing by humans for crops and grazing land) (Mucina *et al.*, 2006b).

DISTRIBUTION PATTERNS

- (1) There are no qualifying records, of any kind, of African elephant from the arid or semi-arid hinterland in the south, south-west and west. This presumably reflects a general lack of suitable habitat – caused by the absence or paucity of year-round forage and surface water – in these areas. These requirements seem to have been met in the coastal and sub-coastal zones, albeit probably mainly on a seasonal basis in the arid western and north-western parts, where the winter rainfall pattern would have been critical in creating a suitable habitat for part of the year.
- (2) The fact that only paleontological records were located for the coastal zone between 19° and 22° E suggests that living African elephant no longer existed there when the written history of the area commenced (1700s).
- (3) Although the relatively large number of written records associated with the Albany Thicket Biome, which occurs mainly in the south-eastern part of the study area, is doubtless partly a reflection of the good early chronicle coverage in the region (Figure 4), these records, supported by numerous paleontological records, confirm that this biome provides prime African elephant habitat.
- (4) The absence of written records, and the presence of only paleontological records, in the hinterland to the north-west and north of the Albany Thicket Biome is intriguing. The reasons for this pattern are unknown. It does, however, suggest that African elephant had ceased to exist there by the start of the colonial period in this region (early 1800s), i.e. when the first written records were made. If so, the reasons can only be guessed at. Perhaps African elephant penetrated inland from the Albany Thicket Biome during a period of relative wetness, and following the general scenario proposed by Boshoff *et al.* (2002) (Table 1).
- (5) The African elephant is seemingly not resident in areas of extensive, open, grassland, or even a regular visitor to strips of riparian vegetation that penetrate deep into such grassland, particularly in the region to the north-east of the Orange River. It could be speculated that the lack of records, of any type, from this region may reflect excessive hunting with fire-arms, by White and Griqua hunters, during the latter 1700s and early 1800s (i.e. before the start of the known written record), leading to local extinction. However, even though it is known that African elephant were hunted, with fire-arms, in the interior as far back as the latter 1700s (Carruthers *et al.*, 2008), no evidence has been found to support this supposition.
- (6) The overall pattern of the records suggests that the African elephant population in the south-eastern part of the study area was linked to that in the north-eastern part via a long-distance “corridor”, in which the coastal and sub-coastal areas and the Orange River are important components. However, it is not known whether all sections of this “corridor” were active at the same time.
No good evidence could be found to show that African elephant travelled through the arid Nama-Karoo Biome to link the population in the southern and south-south-eastern parts of the study area with that to the north-east of the Orange River, during the early historical period at least, i.e. as proposed by Boshoff *et al.* (2002) (Table 1).
- (7) African elephant are known to undertake landscape-scale emigration and immigration behaviour, as well as nomadic, migratory or partially migratory movements, in response to spatial changes in the quality and availability of forage and water (Skinner & Chimimba, 2005; Van Aarde *et al.*, 2008). Any such movements are masked in the overall distribution pattern for the study area, which has the effect of “telescoping” time, and which therefore effectively represents the animals’ potential historical distribution.

BROWN HYAENA

Parahyaena brunnea (Thunberg, 1820)

BRUINHÏENA/STRANDWOLF

DISTRIBUTION RECORDS

Written records in Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Plug & Badenhorst (2001) and Boshoff & Kerley (2013), indicate that within the study area the brown hyaena occurred in at least seven biomes – Fynbos, Succulent Karoo, Desert, Nama-Karoo, Grassland, Savanna, Albany Thicket. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 6.

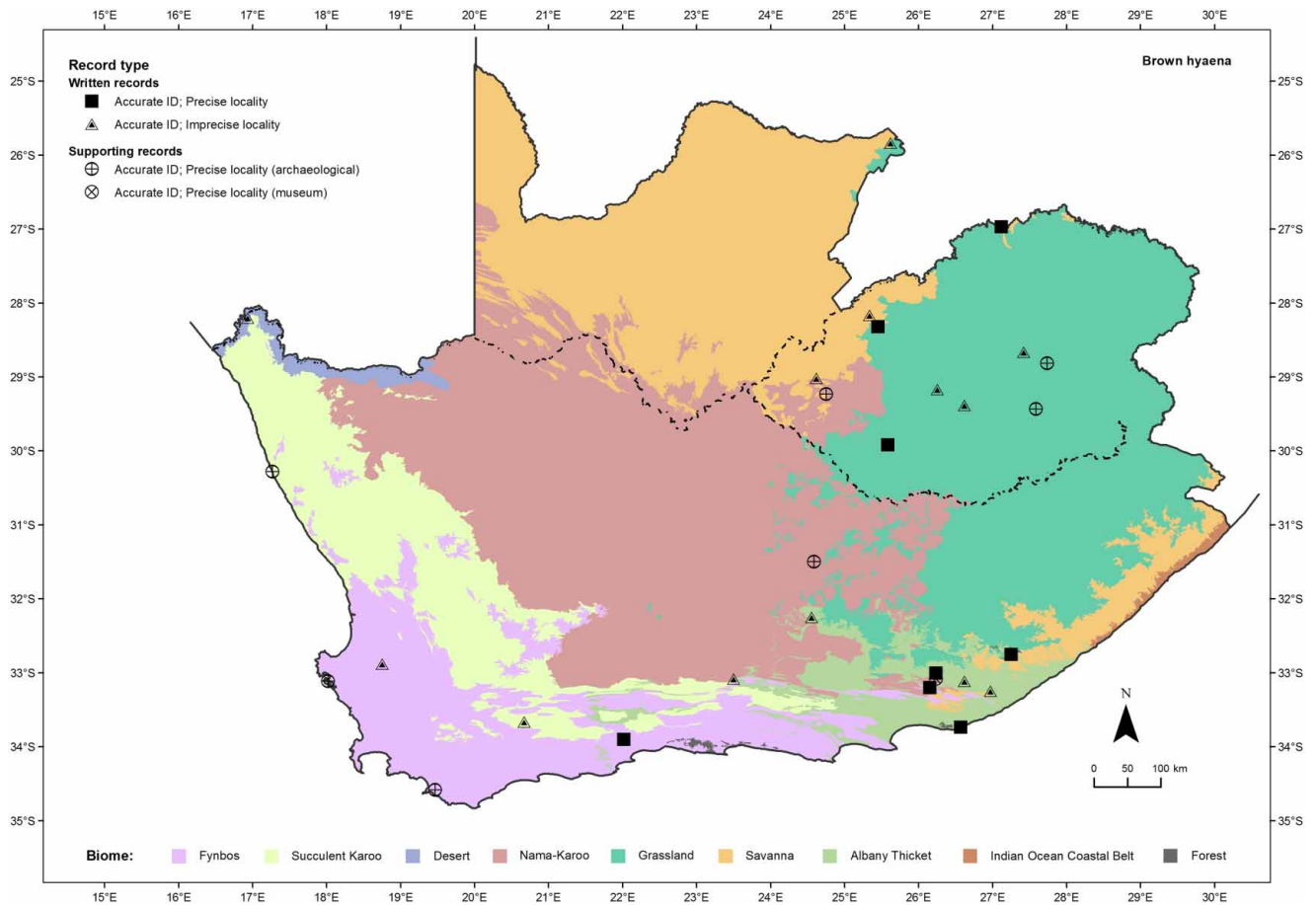


Figure 6. Early historical incidence of the brown hyaena: mappable written and supporting distribution records (see the text), and biomes.

DISTRIBUTION PATTERNS

(1) The relatively low number of written records, and their patchy distribution, are considered to reflect a combination of a number of factors, of which the following are considered to be important:

- (a) There are a number of prominent gaps in the early chronicler coverage, especially in the dry north-western sector of the study area (Figure 4).
- (b) Its secretive nature, and predominantly nocturnal activity pattern, would have counted against it being observed, and identified, by chroniclers journeying during the day, as did most 17th, 18th and 19th century travellers.
- (c) This hyaenas' relative quietness at night (in contrast to the more vocal spotted hyaena *Crocuta crocuta*) would have helped to conceal its presence.
- (d) It probably occurred at a low density in the semi-arid to arid areas, where the amount of potential carrion and prey would have been relatively limited.
- (e) Unfortunately, many of the early chroniclers could not, or did not, offer clues as to which of the two possible species of hyaena (brown or spotted) they encountered during their travels. Consequently, many of the early, written records can only be listed as "hyaena- species indeterminate" (Skead, 2007, 2011; Boshoff & Kerley, 2013). At best, these records indicate that "hyaenas" occurred widely in the study area.

These and other possible reasons for the paucity of early written records for this carnivore are discussed in Skead (2007, 2011) and Boshoff & Kerley (2013).

- (2) The general paucity of early records makes it difficult to compile a general statement regarding the distribution pattern of the brown hyaena in the study area during the early historical period. At best, the information at hand hints at a potentially widespread occurrence in some parts of it. The virtual absence of records from large parts, especially from the arid or semi-arid central, western and northern parts cannot easily be explained, especially since this animal is commonly associated with arid areas (Mills, 2013). That it probably did occur widely in these parts is suggested by the distribution information obtained from relatively recent surveys (Stuart, 1981; Lloyd & Millar, 1983).
- (3) The reasons for the absence of records from country to the south of 30°50' S and east of 28° E, despite reasonable earlier chronicler coverage there (Figure 4), are not known but may be linked to the relatively high annual rainfall of this region (Figure 2). According to FitzSimons (1919), the brown hyaena is unknown historically from the region to the immediate south-east of the study area (i.e. the midlands-lowlands of today's KwaZulu-Natal Province).
- (4) It is concluded that a number of factors, and particularly those mentioned above, generally mitigated against the

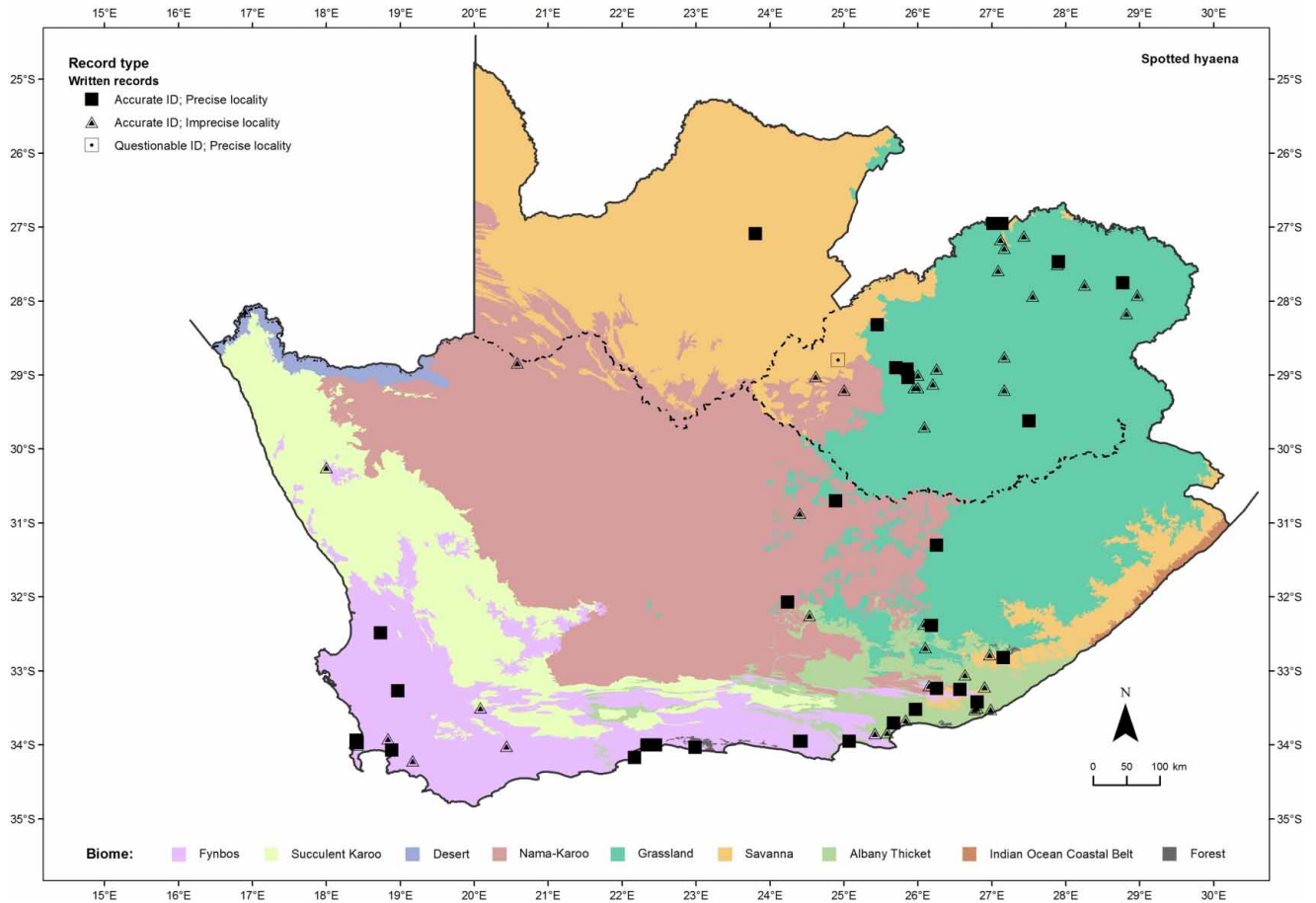


Figure 7. Early historical incidence of the spotted hyaena: mappable written and supporting distribution records (see the text), and biomes.

detection of this animal by the early chroniclers, and that the relatively few records, of any type, that could be located belie its early historical distribution, i.e. it is considered to have been more widespread than is shown.

SPOTTED HYAENA

Crocuta crocuta (Erxleben, 1777)

GEVLEKTE HIËNA

DISTRIBUTION RECORDS

Written records in Glyn (1863), Blaine (1868), Skead (2007, 2011) and Boshoff & Kerley (2013) indicate that within the study area the spotted hyaena occurred in parts of six biomes – Fynbos, Desert, Nama-Karoo, Grassland, Savanna, Albany Thicket. Mappable written records, and the biomes within the study area, are shown in Figure 7.

DISTRIBUTION PATTERNS

(1) This hyaena was recorded by early chroniclers rather more frequently than was the brown hyaena *Parahyaena brunnea* (compare figures 6 and 7). The reasons for this are considered to include the following:

(a) While brown hyaena usually hunt as singletons, spotted hyaena often hunt in small groups (Mills, 2013; East & Hofer, 2013), including during the day, making the latter easier to detect; several early, written, accounts mention group sightings (Boshoff & Kerley, 2013).

(b) Although predominantly nocturnal, the spotted hyaena's loud and characteristic vocalisations (in contrast to the relatively quiet brown hyaena) commonly drew the attention of the early chroniclers. Their eerie calls scared many of the early travellers, who also saw this animal as a threat to their livelihood-critical larger livestock, thus prompting many of them to record their fear of, and interactions with, these potent hunter-scavengers.

(c) Unfortunately, many of the early chroniclers could not, or did not, offer clues as to which of the two possible species of hyaena (brown or spotted) they encountered during their travels. Consequently, many of the early, written records can only be listed as "hyaena- species indeterminate" (Skead, 2007, 2011; Boshoff & Kerley, 2013). At best, these records indicate that "hyaenas" occurred widely in the study area.

Other factors affecting its chances of being recorded in the wild by early chroniclers are discussed in Skead (2007, 2011) and Boshoff & Kerley (2013).

(2) The patchy nature of the written records for the spotted hyaena in Figure 7 is considered to derive from a combination of various factors, notably several gaps in the early chronicler coverage (Figure 4), and the fact that it probably occurred at a low density in the arid areas (East & Hofer, 2013). These factors are believed to be largely

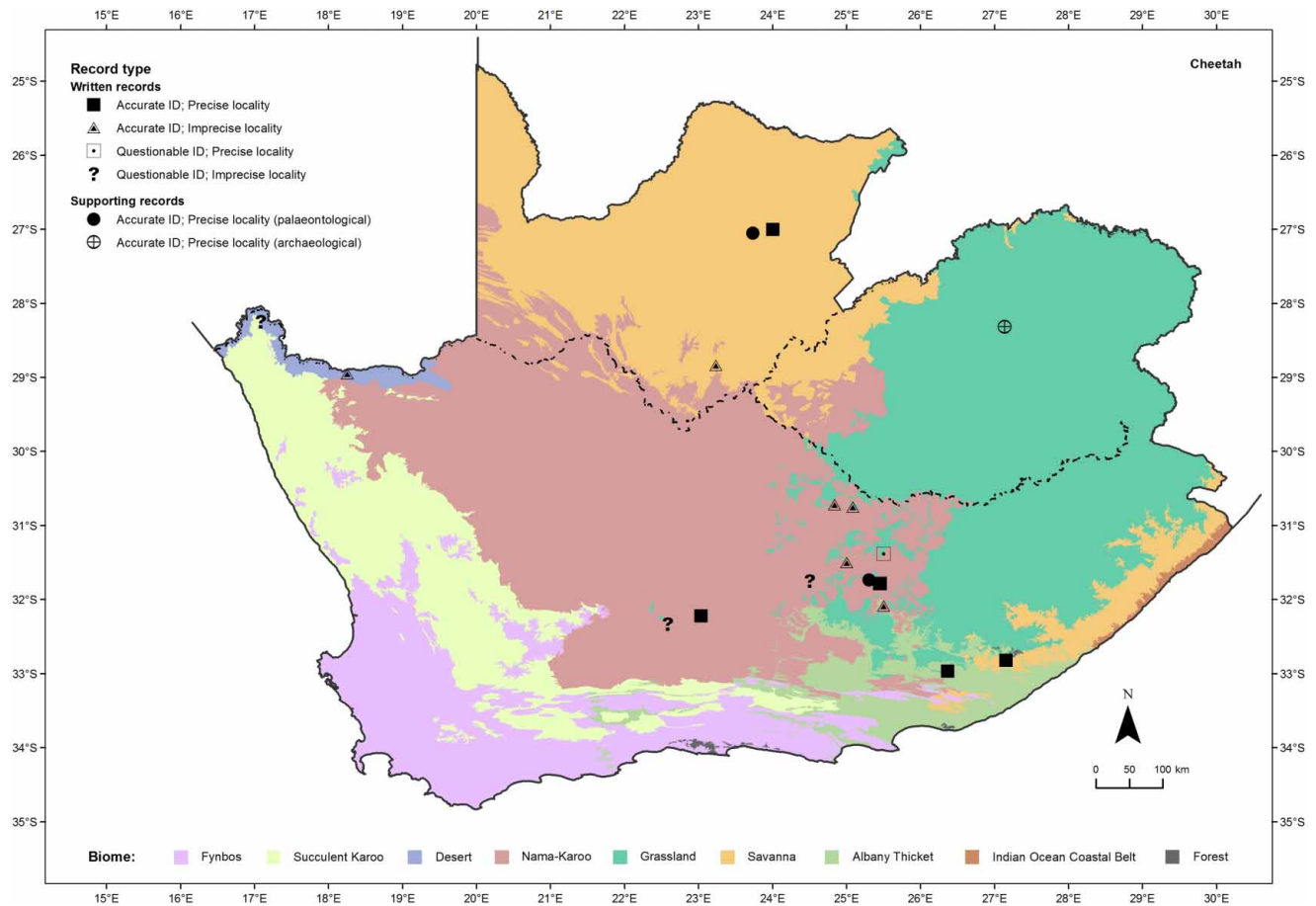


Figure 8. Early historical incidence of the cheetah: mappable written and supporting distribution records (see the text), and biomes.

responsible for the absence or paucity of records from the semi-arid to arid western, central and north-north-western parts. More recent studies have indicated its incidence in these parts (Stuart, 1981; Skinner & Chimimba, 2005).

- (3) It is concluded that the distribution pattern for this animal probably belies the true extent of its distribution in the study area, and that this carnivore is likely to have been more widespread than is shown. The absence of records from most of the grasslands and savanna in the south-eastern part of the study area is intriguing.

CHEETAH

Acinonyx jubatus (Von Schreber, 1775)

DISTRIBUTION RECORDS

Written and selected supporting records in Skead (2007, 2011) and Boshoff & Kerley (2013) indicate that within the study area the cheetah occurred in at least four biomes – Desert, Nama-Karoo, Grassland, Savanna. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 8.

DISTRIBUTION PATTERNS

The relatively few, generally widespread, written and supporting records make it difficult to compile a definitive statement on the estimated distribution of the cheetah in the study area during the early historical period, this despite reasonable to good early chronicler coverage in many places

(Figure 4). Any attempt to interpret the records in Figure 8 should take into consideration the following factors, the combination of which would have influenced the potential of early chroniclers to observe cheetahs and possibly write about them:

- (1) Cheetah generally occur at a very low, natural, density, often occupying huge home ranges (Caro, 2013); a lack or paucity of shade trees and shrubs in places and domination by larger predators and scavengers would have contributed to this situation.
- (2) This cat does not vocalise much, and its calls are not loud (Caro, 2013).
- (3) Its size and low-slung frame render it difficult to detect in the field, especially in savanna woodland and medium-tall grassland, and it may also have been confused with other spotted cats.
- (4) Its local incidence relies on a year-round supply of suitable prey; thus, it may have been absent or ephemeral in arid areas where a lack of grazing and surface water mitigated against a sustained (year-round) supply of prey.
- (5) This carnivore apparently did not represent a personal threat, or any sporting value, to early European travellers, colonists and hunters and this is believed to have contributed to its general lack of mention in the early literature (Boshoff & Kerley, 2013). Furthermore, that cheetah apparently did not present a threat to large domestic stock (horses, cattle) may also have contributed to the lack of mention in early texts. However, they were destructive to

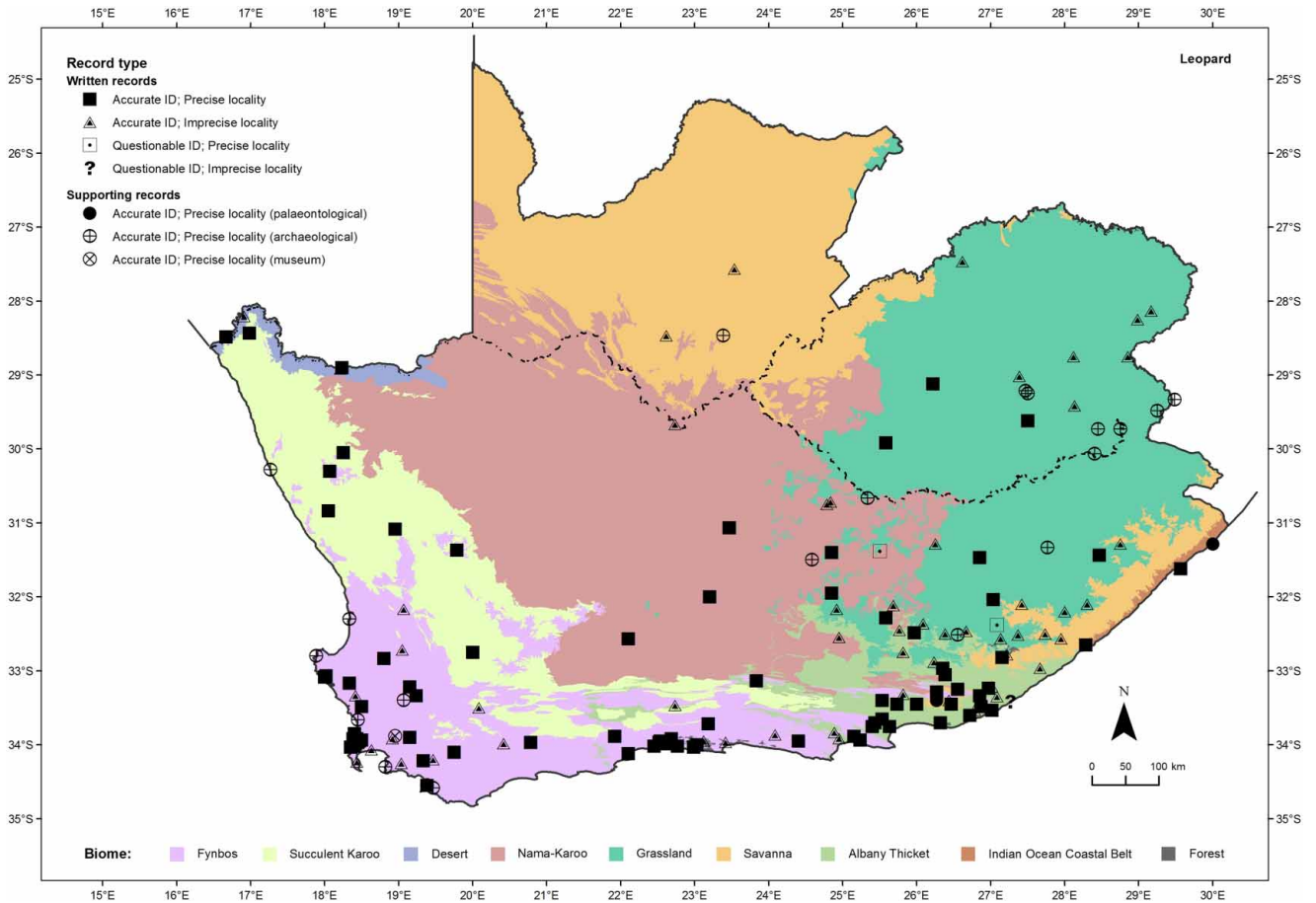


Figure 9. Early historical incidence of the leopard: mappable written and supporting distribution records (see the text), and biomes.

smaller domestic livestock and were consequently persecuted by 19th century farmers, mainly by poisoning and by mounted hunters with fire-arms, with these predators being particularly vulnerable to the latter, possibly leading to early local extinctions, leading in turn to a reduced possibility of being recorded (Skead, 2011; Boshoff & Kerley, 2013).

- (6) It is contended that the pattern of records in Figure 8, and other distribution information in Skead (2007, 2011) and Boshoff & Kerley (2013), belie the true distribution of the cheetah in the study area during the early historical period, and that it was more widespread than is indicated. This view is supported by, for example, the results of a recent survey (reported by Stuart, 1981) which revealed its presence in a large part of the Savanna Biome where it occurs to the north of the Orange River.

LEOPARD

Panthera pardus (Linnaeus, 1758)

DISTRIBUTION RECORDS

Written records in Cowan (1808), Bryden (1897), Rookmaaker (1989), Skead (2007, 2011), Boshoff & Kerley (2013) and Crampton *et al.* (2013), together with selected supporting records in Plug & Badenhorst (2001), Klein & Cruz-Uribe (2000), Skead (2007, 2011) and Boshoff & Kerley (2013), indicate that the leopard occurred in all nine biomes that are represented in the study area – Fynbos, Succulent Karoo,

Desert, Nama-Karoo, Grassland, Savanna, Albany Thicket, Indian Ocean Coastal Belt, Forest. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 9.

DISTRIBUTION PATTERNS

- (1) Despite a number of gaps in the early chronicler coverage (Figure 4), and its secretive nature, largely nocturnal activity pattern and relative quietness, the leopard was recorded surprisingly frequently. One reason appears to be the fear that many of the early European travellers and colonists had for the large cats, including the leopard, and the issue of predation by them on their livelihood-critical domestic livestock, leading to regular mention in the early literature. Other possible reasons can be gleaned from Skead (2007, 2011) and Boshoff & Kerley (2013).
- (2) The written record, together with numerous zoo-archaeological records that exist, indicates that this cat was widespread in the greater part of the study area. That it was probably more widespread in the semi-arid to arid central, northern and north-western regions than is indicated in Figure 9 is suggested by records of its incidence there during a more recent survey (Stuart, 1981).
- (3) The leopard is likely to have occurred patchily and at a low density in extensive, flat, open areas where suitable shelter was scarce, and also where the amount of potential prey

LUIPERD

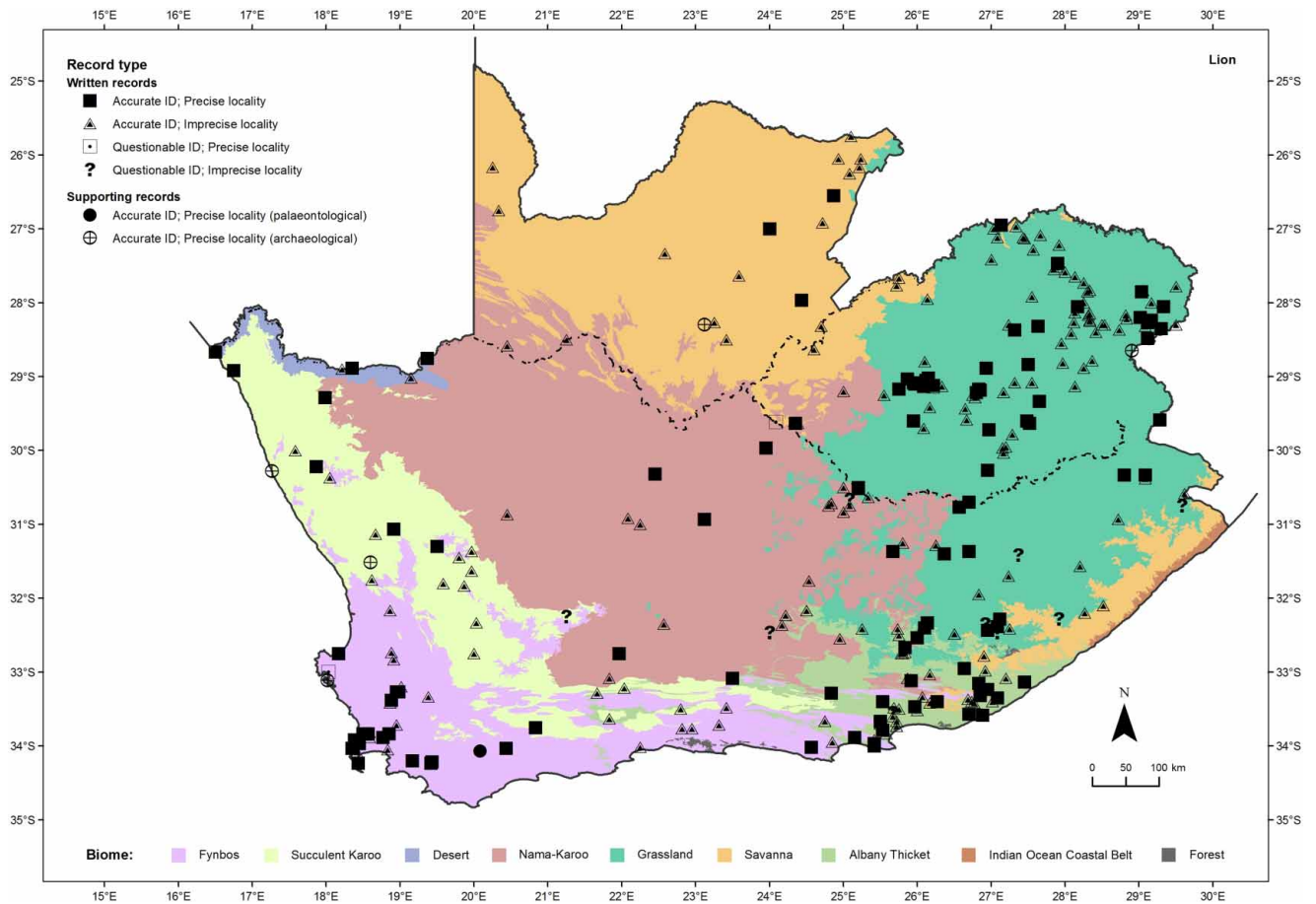


Figure 10. Early historical incidence of the lion: mappable written and supporting distribution records (see the text), and biomes.

was relatively limited, e.g. in the arid regions where ungulate numbers would have been low or highly variable, owing to the lack of a year-round supply of forage and surface water.

(4) It is concluded that the leopard was widely distributed within the study area during the early historical period, potentially occurring wherever its ecological requirements were met.

LION

LEEU

Panthera leo (Linnaeus, 1758)

DISTRIBUTION RECORDS

Written records in Cowan (1808), Skead (2007, 2011), Boshoff & Kerley (2013) and Crampton *et al.* (2013), together with selected supporting records in Plug & Badenhorst (2001), Orton *et al.* (2011), Skead (2011) and Boshoff & Kerley (2013), indicate that within the study area the lion occurred in seven biomes – Fynbos, Succulent Karoo, Desert, Nama-Karoo, Grassland, Savanna, Albany Thicket. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 10.

DISTRIBUTION PATTERNS

(1) The large number of written records in Figure 10 shows that the lion was frequently and widely recorded by the early chroniclers. The reasons for this are considered to include the following (Skead, 2007, 2011; Boshoff & Kerley, 2013):

- (a) The lion, with its reputation as the “King of Beasts”, was greatly admired by early European visitors and settlers in the study area.
 - (b) Lion were greatly feared by many early European travellers and colonists, in terms of both their personal safety and the likelihood of predation on their livelihood-critical large livestock (cattle, oxen, horses).
 - (c) Their large size, and habit of roaring loudly at night, drew attention to their presence, and also enabled accurate identification.
 - (d) Lion were highly sought after by the imperial British hunters, many of whom recorded their travelling and hunting experiences in diaries, journals and books.
- (2) The paucity or absence of records from the arid north-central parts of the study area (Figure 10) may reflect both the generally poor early chronicler coverage in these regions (Figure 4) and the lack of a year-round supply of suitable prey. No records could be located for the Indian Ocean Coastal Belt and Forest biomes, despite reasonable to good early chronicler coverage; this is considered to reflect the generally unsuitable habitat (forest and dense woodland) that characterise them.
- (3) It is concluded that the combination of written and supporting records show the lion to have been widespread in the study area during the early historical period.

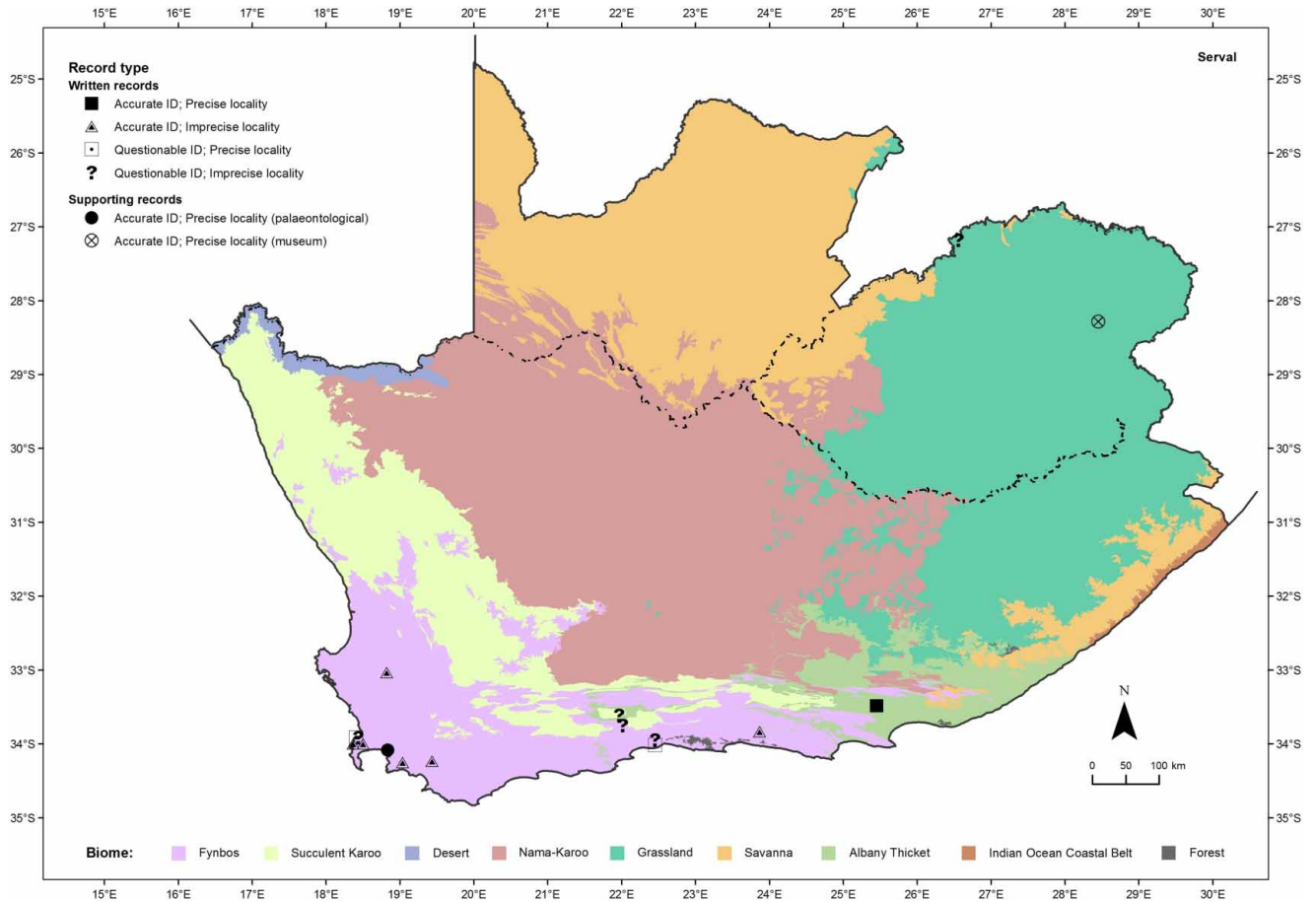


Figure 11. Early historical incidence of the serval: mappable written and supporting distribution records (see the text), and biomes.

SERVAL

Leptailurus serval (Von Schreber, 1776)

DISTRIBUTION RECORDS

Written records in Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Skead (2011) and Boshoff & Kerley (2013), suggest that within the study area the serval occurred in at least three biomes – Fynbos, Grassland, Albany Thicket. However, the occurrence of this long-legged cat is not primarily linked to the various, broad, biophysical factors that define the biomes, but rather to individual, localised, areas of suitable habitat, available year-round, within certain biomes. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 11.

DISTRIBUTION PATTERNS

- (1) The relative paucity of serval records, of any type, is considered to reflect, *inter alia*, the following:
 - (a) Its relatively small size, general silence, solitary nature, habitat characteristics (rank vegetation), and predominantly nocturnal activity pattern and habit of lying up for much of the day, would have strongly counted against it being observed, and identified, by early chroniclers.
 - (b) Its specialised wetland habitat would have resulted in a highly patchy distribution, and consequently a low

TIERBOSKAT

density; these factors are likely to have reduced its chances of detection, identification and possible recording by early chroniclers.

- (c) It posed no threat to large livestock (cattle, oxen, horses).

- (2) The paucity of records, of any type, in Figure 10 and in the literature (Skead, 2007, 2011; Boshoff & Kerley, 2013) make it difficult to offer a reliable statement on the distribution of this cat in the study area during the early historical period. Given its rather specialised habitat requirements, it is considered unlikely to have occurred in the semi-arid to arid northern, central and western parts of the study area. Thus, at best the records suggest that it was confined to the moister parts, more specifically in the far south-western, southern and eastern regions where annual rainfall exceeds 400 mm (Figure 2), where its distribution is likely to have been patchy.

AFRICAN WILD DOG

Lycaon pictus (Temminck, 1820)

DISTRIBUTION RECORDS

Written records in Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Plug & Badenhorst (2001) and Boshoff & Kerley (2013), indicate that within the study area the African wild dog occurred in six, possibly seven, biomes – Fynbos, Succulent Karoo, Nama-Karoo, Grassland, Savanna, Albany Thicket, Indian Ocean

WILDEHOND

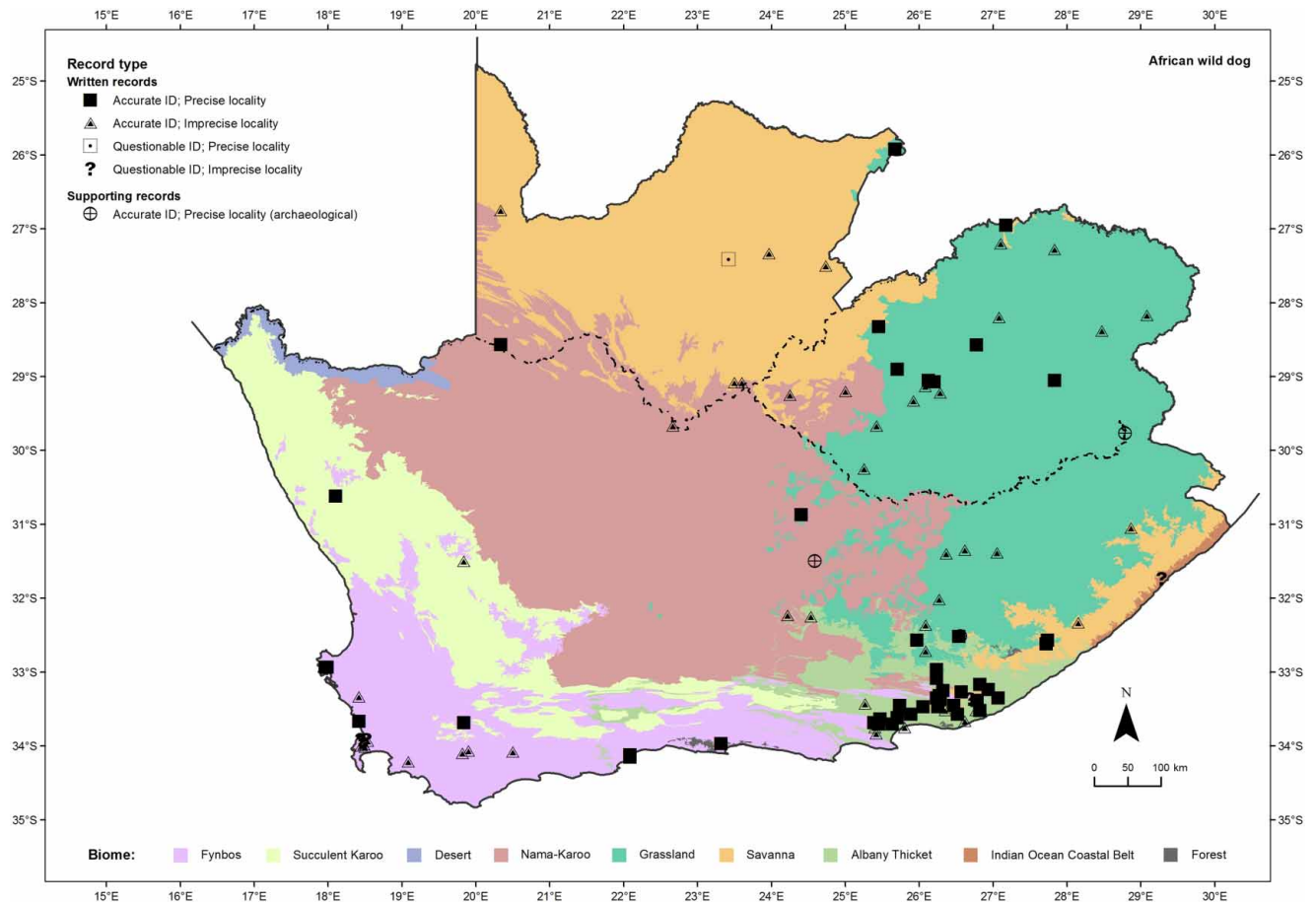


Figure 12. Early historical incidence of the African wild dog: mappable written and supporting distribution records (see the text), and biomes.

Coastal Belt (possibly). Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 12.

DISTRIBUTION PATTERNS

- (1) The African wild dog was recorded relatively frequently by the early chroniclers. The reasons for this are considered to include its diurnal activity pattern, occurrence in (often very large) packs, presence in flat and rolling terrain (preferred by ox-wagon travellers), making it relatively easy to observe. In addition, the threat of predation by African wild dog on the livelihood-critical livestock (horses, oxen, cattle) of the early travellers and colonists contributed to its frequent mention in the early literature.
- (2) Notably, no records could be located for the rugged Maloti-Drakensberg massif in the mid-eastern part of the study area. The cluster of written records in the southern part of the Albany Thicket Biome is considered to be a direct result of good chronicler coverage in this region (Figure 4). Its historical presence in the Indian Ocean Coastal Belt Biome cannot be confirmed.
- (3) The distribution pattern suggested by the records mapped in Figure 12 and from elsewhere in the literature (Skead, 2007, 2011; Boshoff & Kerley, 2013) indicate that the African wild dog was potentially widespread in the study area, occurring wherever suitable habitat existed. Reasons for the sometimes patchy distribution of the

records are believed to include gaps in early chronicler coverage in places (Figure 4), especially in the semi-arid to arid north-central parts, and possibly a relatively limited amount of potential prey in the arid regions where ungulate numbers would have been low or highly variable.

WHITE RHINOCEROS

Ceratotherium simum (Burchell, 1817)

DISTRIBUTION RECORDS

Written records and additional information in Cowan (1808), Rookmaaker (2007), Skead (2011) and Boshoff & Kerley (2013), together with selected supporting records in Skead (2011), indicate that in the study area the white rhino occurred in a single biome – Savanna. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 13.

Savanna Biome

A handful of written records indicate that the white rhino occurred in the far northern part (north of 27°30' S) of the Eastern Kalahari Bushveld Bioregion, i.e. to the north-east of the Orange River, within the study area. Early chronicler coverage in this bioregion was reasonable to good in parts of it (Figure 4). This cluster of records incorporates a single palaeontological record.

Two written records within this cluster fall on or close to the boundary between the Eastern Kalahari Bushveld Bioregion

WITRENOSTER

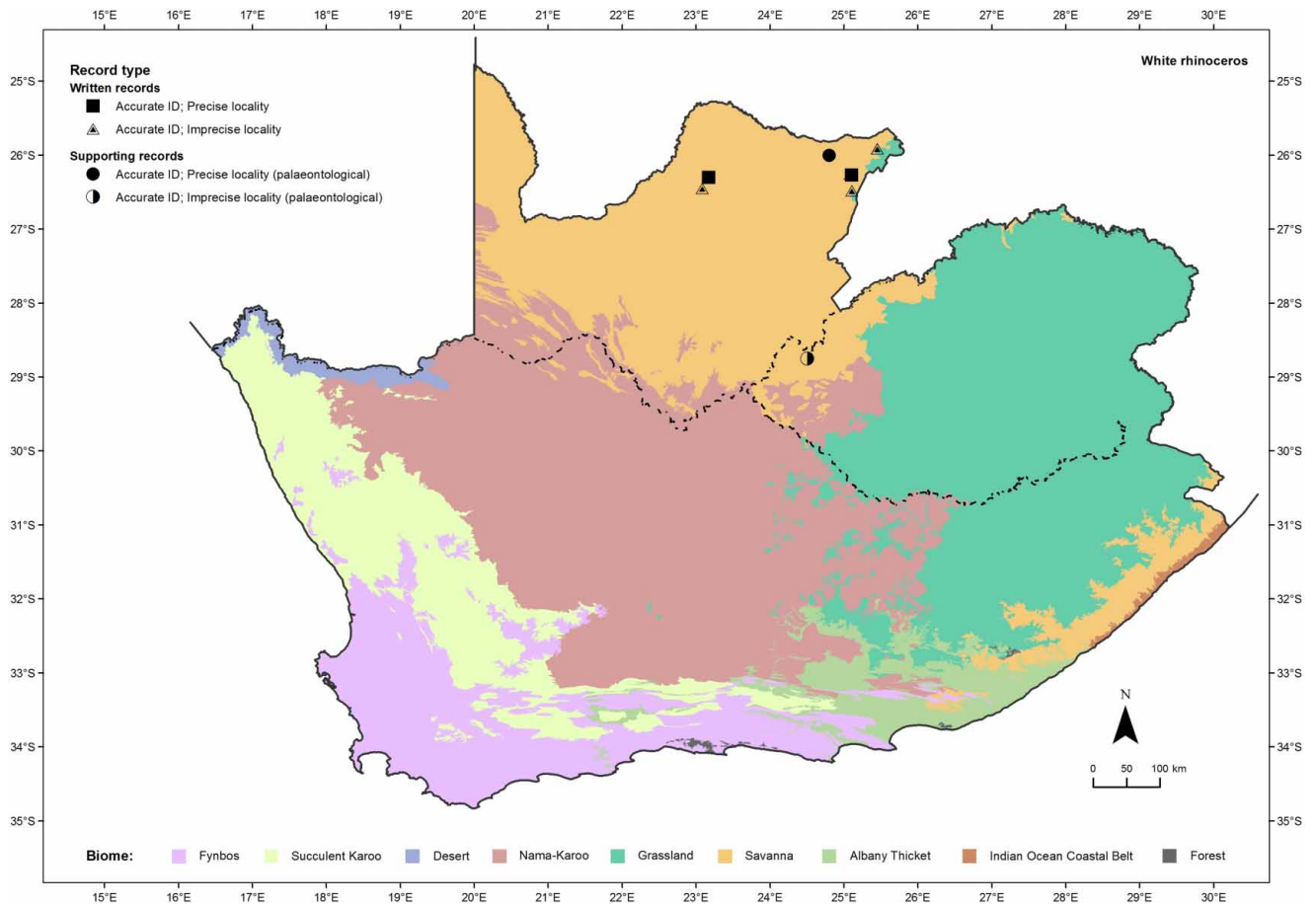


Figure 13. Early historical incidence of the white rhinoceros: mappable written and supporting distribution records (see the text), and biomes.

and the Dry Highveld Grassland Bioregion, in the north-north-east of the study area. Unfortunately, the “imprecise” locality status of these two records makes it impossible to confidently place them in one or the other of these two bioregions. Given that this megaherbivore is known to have occurred in the Eastern Kalahari Bushveld Bioregion, and is not considered to be an animal of extensive open grassland, it is suggested that these two records are more likely to have come from the Eastern Kalahari Bushveld Bioregion rather than from the Dry Highveld Grassland Bioregion, or from the ecotonal area between them.

That this rhino also occurred further south in the Eastern Kalahari Bushveld Bioregion is indicated by the unearthing of a specimen (incomplete skull) from a depth of about 2.4 m at a site just west of Kimberley in 1893 (Sclater, 1900; Bigalke, 1963) (the “record type” for this record has been changed from that given in Figure 4.17 in Skead, 2011).

Two “rhinoceros– species indeterminate” records are associated with a small area of Central Bushveld Bioregion, a savanna type, and outliers thereof, in the east-north-eastern part of the study area (Boshoff & Kerley, 2013). Consequently, the possibility exists that these records refer to white rhino.

DISTRIBUTION PATTERNS

(1) Despite reasonable to good early chronicler coverage in most of the study area (Figure 4), the only confirmed, written, white rhino records come from the Eastern Kalahari Bushveld Bioregion (a constituent bioregion of the

Savanna Biome, within the study area). The only supporting records (both palaeontological) that could be found also come from this bioregion.

(2) The only known record of the white rhino in the region south of the Orange River involves a partial mandible with teeth that was exposed in a river bank located at 31° 46' S; 25°05' E on the farm “Grassridge”, which is some 45 km north of the modern town of Cradock. This site falls in a region where fragments of Dry Highveld Grassland Bioregion occur within a matrix of Upper Karoo Bioregion. The provenance of this material, apparently collected in the early 1960s, and which was confirmed as belonging to a white rhino, is discussed at length by Skead (2007). Owing to lingering doubts about its provenance, not least the possibility that it comes from a skull transported to the farm by earlier owners thereof (who are known to have “hunted big game to the north”), the general unsuitability of the habitat in the Cradock district, and the complete absence of other records (of any type) in the region to the south of the Orange River (despite relatively good early chronicler coverage), we do not accept the validity of this record.

BLACK RHINOCEROS

Diceros bicornis (Linnaeus, 1758)

SWARTRENOSTER

DISTRIBUTION RECORDS

Written records and additional information in Cowan (1808), Rookmaaker (2007), Skead (2007, 2011) and Boshoff & Kerley

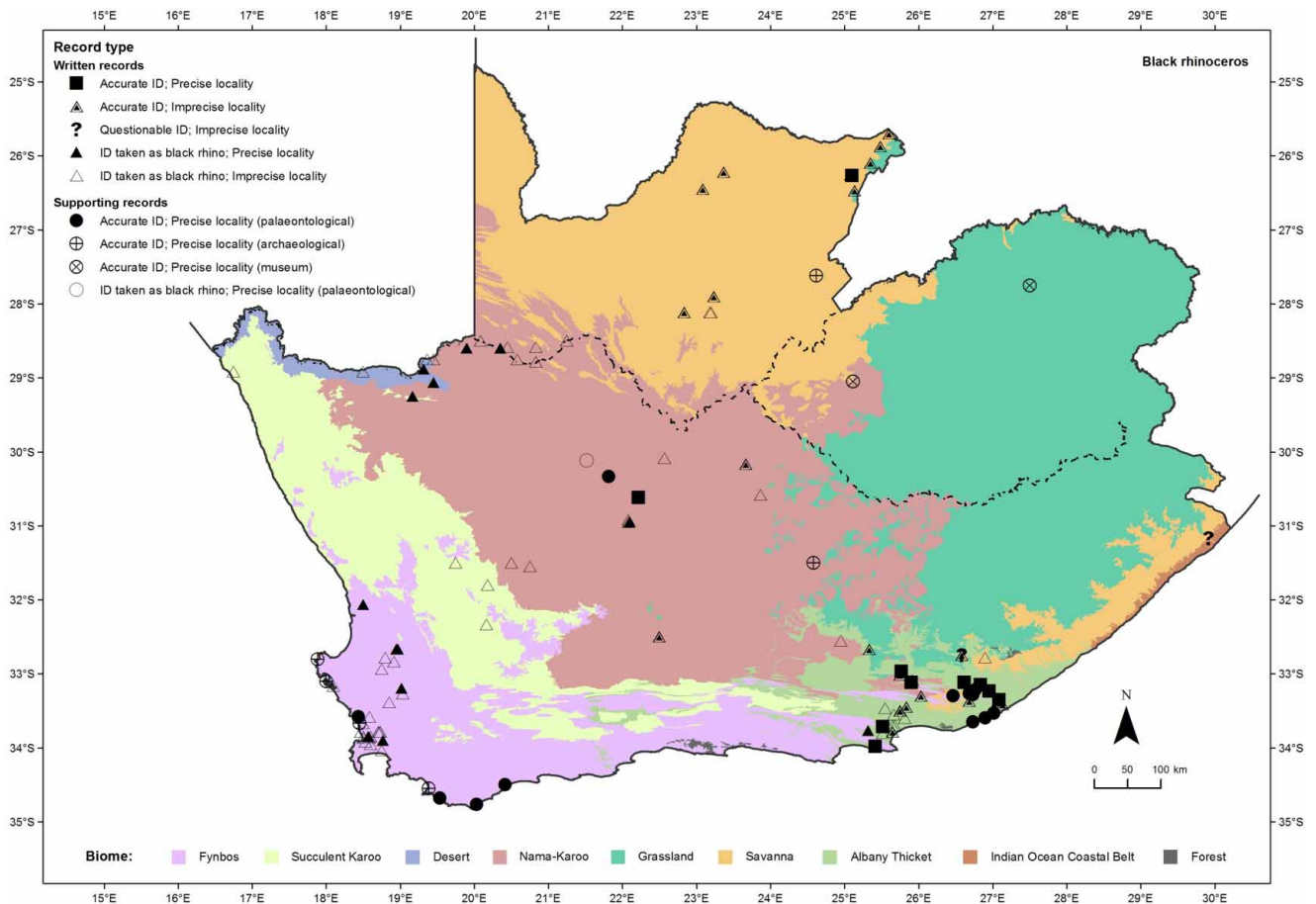


Figure 14. Early historical incidence of the black rhinoceros: mappable written and supporting distribution records (see the text), and biomes. Owing to the absence of confirmed records of white rhino to the south of the Orange River, all “rhinoceros – species indeterminate” records from that region are taken as referring to the black rhinoceros (see Skead, 2011).

(2013), together with selected supporting records in Klein & Cruz-Urbe (2000), Plug and Badenhorst (2001), Skead (2007, 2011), van der Merwe (1979) and Boshoff & Kerley (2013), indicate that within the study area the black rhino occurred in six biomes – Fynbos, Succulent Karoo, Desert, Nama-Karoo, Savanna, Albany Thicket.

Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 14. Owing to the absence of confirmed records of the white rhino *Ceratotherium simum* from the region south of the Orange River, all the “rhinoceros – species indeterminate” records from there (van der Merwe, 1979; Skead, 2007, 2011) are taken as referring to the black rhino, and mapped as such.

Fynbos Biome

The incidence of this megaherbivore in this biome is indicated by a single written record from the Eastern Fynbos-Renosterveld Bioregion, and by supporting records from the South Coast Fynbos Bioregion. In addition, a number of written records and supporting records indicate its presence in the West Strandveld, West Coast Renosterveld and South West Fynbos bioregions.

Succulent Karoo Biome

One or more written records from the Namaqualand Sandveld, Trans-Escarpment Succulent Karoo and

Rainshadow Valley Karoo bioregions reveal its occurrence in this biome.

Desert Biome

A handful of written records indicate its presence in or close to the narrow strip of Gariiep Desert Bioregion to the south of the Orange River, in the far north-western part of the study area. Some of these records may fall within adjacent areas of the Bushmanland Bioregion (Nama-Karoo Biome).

Nama-Karoo Biome

Despite several gaps in the early chronicler coverage (Figure 4), a number of written records indicate the presence of black rhino in all three bioregions within this biome, namely Bushmanland, Upper Karoo and Lower Karoo. In addition, supporting records suggest its presence in the Bushmanland and Upper Karoo bioregions.

Most of the written records from the Bushmanland Bioregion are from the vicinity of the Orange River, which would have provided a year-round source of surface water. This record pattern is, however, considered to partially reflect increased early chronicler coverage along this river (Figure 4).

Savanna Biome

A number of written records, supported by a zoo-archaeological record, show its existence in the relatively well-watered

Eastern Kalahari Bushveld Bioregion, to the north of the Orange River.

Four written records fall on or close to the boundary between the Eastern Kalahari Bushveld Bioregion and the Dry Highveld Grassland Bioregion, in the north-north-east of the study area. Unfortunately, the “imprecise” locality status of these records makes it impossible to confidently place them in one or the other of these two bioregions. Given that this rhino is known to have occurred in the Eastern Kalahari Bushveld Bioregion, and is not known to be an animal of extensive open grassland, it is suggested that these four records are more likely to have come from the Eastern Kalahari Bushveld Bioregion, rather than from the Dry Highveld Grassland Bioregion, or from the ecotonal area between them.

In the south-eastern part of the study area there is a written record that mentions unidentified “rhinoceros” from the area where the Sub-Escarpment Savanna Bioregion intergrades with the **Indian Ocean Belt Biome**; although the identity of the animal(s) observed will never be known it is considered more likely to be black rhino than white rhino as the nearest rhino records (to the south-west) are of the former (Rookmaaker, 2007).

Albany Thicket Biome

Numerous written records, supported by several palaeontological records, confirm the presence of this rhino in this biome. Areas dominated by subtropical thicket vegetation, both xeric and mesic, provide prime black rhino habitat (Kerley *et al.*, 1995).

The only record, of any type, from the **Grassland Biome** is a museum record (specimen), from the Dry Highveld Grassland Biome, north of the Orange River. However, there are no clues as to the provenance of this record. There is an early written record of an unidentified rhino, considered by one later zoologist (W.L. Sclater; see Sclater, 1900) to be a black rhino, from the same area (Boshoff & Kerley, 2013). Since the wide grassy plains in this region are deeply penetrated in places by river courses fringed by trees and shrubs, and isolated hills (koppies) found there are clad in grassy shrubland, it is possible that black rhino may have occurred there, perhaps ephemerally and at a very low density.

DISTRIBUTION PATTERNS

- (1) The general spread of records suggests that the black rhino was widespread in a large part of the study area, being absent, or possibly so, from certain areas (below).
- (2) The absence of written records from country to the south of the Cape Fold Belt, between about 19°15' E and 25° E, despite reasonable to good early chronicler coverage in this region (Figure 4), is intriguing and deserves further investigation. The generally low nutrient status of the fynbos vegetation in this region may be a factor.
- (3) No records could be located for country to the north-west of the Orange River, a region characterised mainly by the Kalahari Duneveld Bioregion (a savanna type). Even though early chronicler coverage was poor there (Figure 4), it is considered that a lack of permanent surface water would have rendered this area largely unsuitable for this highly water-dependent species. For the same reason its incidence in the other arid biomes (Succulent Karoo and Desert) and bioregions (Bushmanland) in the study area was likely to have been spatially limited.

- (4) The absence of records (of any type), with the single exception of a specimen record from the northern part of the Grassland Biome (which includes patches of temperate thicket vegetation), indicates that the black rhino is not an animal of extensive, open, grassland.
- (5) Despite reasonable early chronicler coverage (Figure 4), the lack of confirmed written records from the coastal and sub-coastal regions between the Great Fish River in the west and the Umtamvuna River in the east (approx. 27° to 30° E, and including the former Transkei), is noteworthy, given that suitable black rhino habitat was present there in places. Skead (2007) lists two written records that allude to the presence of the black rhino in Pondoland but these contain no detail. The lack of rhino records – by inference black rhino – from this region, and from the region to the east of the south-eastern boundary of the present study area, led Skead (2007) to propose the existence of a zoo-geographical “gap” in the distribution of the black rhino in south-eastern South Africa; this “gap”, spanning about 700 km, lies between the Great Kei River in the west and Zululand (east of the Thukela River) in the east.

MOUNTAIN ZEBRA

Equus zebra (Linnaeus, 1758)

BERGSEBRA

Taxonomy

Two forms of mountain zebra occurred historically in southern Africa – the Cape mountain zebra *Equus zebra zebra* and the Hartmann’s mountain zebra *E. z. hartmannae* (Penzhorn, 2013). Observers have claimed to see zebras crossing the Orange River in the far north-western part of the study area (Skead, 2011), and therefore the animals seen at or near this river in that region (Figure 15) were probably Hartmann’s mountain zebras, which are known to have been present in neighbouring southern Namibia (Novellie *et al.*, 2002; Penzhorn, 2013).

It has been postulated that Hartmann’s mountain zebra extended as far south as the Kamiesberg (some 200 km south of the Orange) (Novellie *et al.*, 2002). However, no records that confirm this view have been located, to date (Skead 2011). Thus, while all the records of mountain zebras in the study area south of 31° S can probably safely be taken as referring to the Cape mountain zebra, the identities of those observed in the Kamiesberg area (between 30° and 31° S) remain a matter of conjecture.

DISTRIBUTION RECORDS

Written records in Skead (2007, 2011), together with selected supporting records in Plug & Badenhorst (2001), indicate that in the study area the mountain zebra occurred in five biomes – Fynbos, Succulent Karoo, Desert, Nama-Karoo, Grassland. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 15.

Fynbos Biome

Numerous written records, from various bioregions, indicate the presence of the mountain zebra in this biome. The widespread localities of the records reveal that this zebra potentially occurred throughout the area of this biome. This includes the outliers formed by the Namaqualand Cape Shrublands Bioregion (in the Kamiesberg area in the north-west) and the Karoo Renosterveld Bioregion in the north-eastern hinterland. The fact that only a handful of records could be located in the

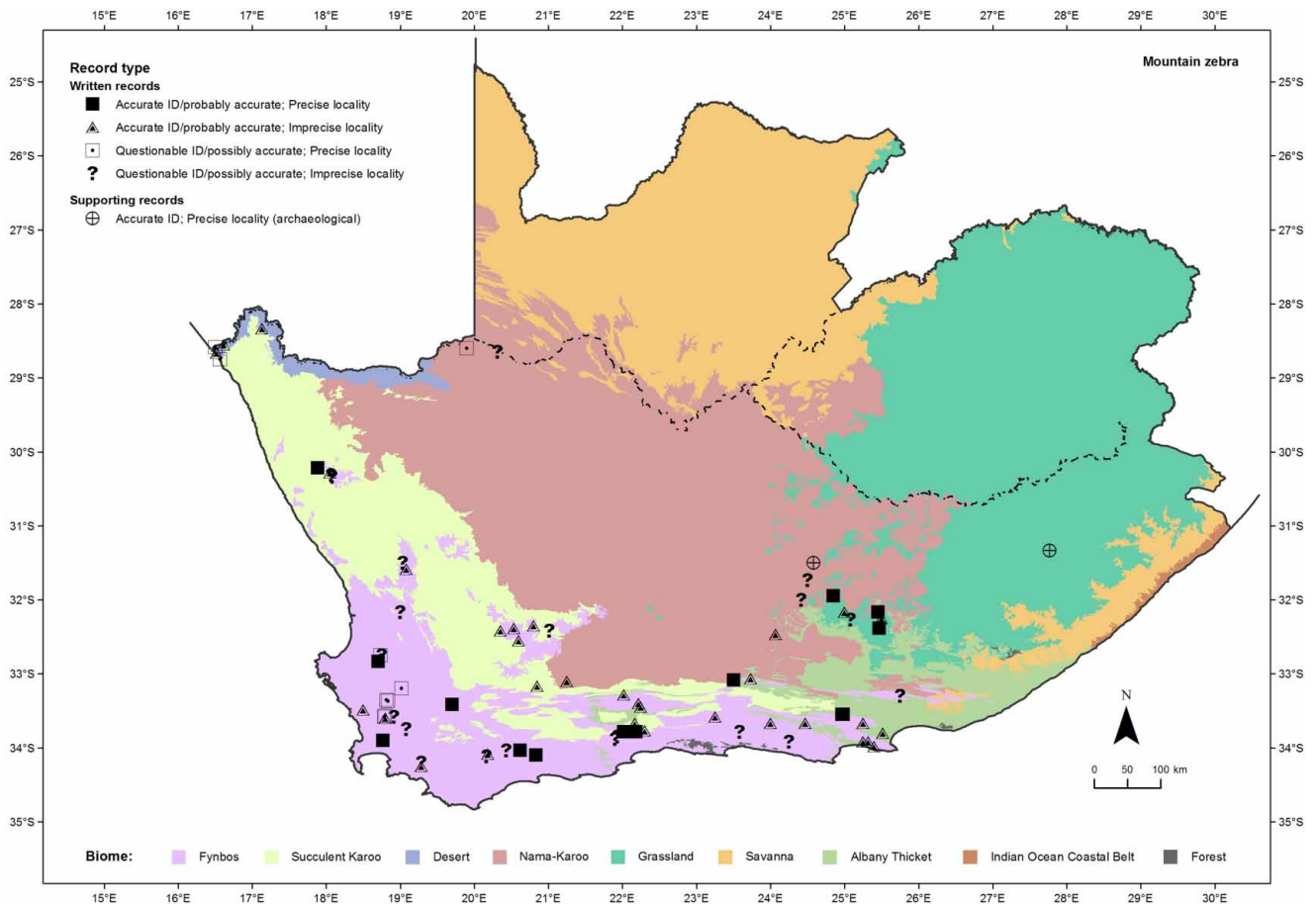


Figure 15. Early historical incidence of the mountain zebra: mappable written and supporting distribution records (see the text), and biomes.

areas of other biomes clearly indicates that the Fynbos Biome was the stronghold for this equid.

Succulent Karoo

Only a single (written) record, from the Rainshadow Valley Karoo Bioregion, could be located.

Desert Biome

Three written records from the Southern Namib Desert Bioregion and one written record from the Gariiep Bioregion reveal its incidence in this biome. All of these records are close, or relatively close, to the Orange River.

Nama-Karoo Biome

The written record for this biome is extremely poor, with only a handful of written records from the rugged southern and eastern fringes of the Lower Karoo Bioregion, two possible written records and a single supporting zoo-archaeological record from the grassy eastern part of the Upper Karoo Bioregion, and two possible written records from just south of the Orange River, in the northern part of the Bushmanland Bioregion.

Grassland Biome

A handful of written records indicates or suggests the presence of mountain zebra in the most southerly outliers of the Dry Highveld Grassland Bioregion, far to the south of the Orange River.

A single zoo-archaeological record, from a site in the Sub-Escarpment Grassland Bioregion, and some way east of the small cluster of records in the Dry Highveld Grassland Bioregion (above), is intriguing. The fact that mountain zebra remains from this same site date from three consecutive time periods – 12 000–8000, 8000–6000 and 4000–2000 years BP (Plug & Badenhorst, 2001), suggests that the pre-Recent range of this zebra once extended somewhat further eastwards than is indicated by the written records (Figure 15).

DISTRIBUTION PATTERNS

- (1) The distribution of this equid in the study area is closely associated with that of the Fynbos Biome, within which it appears to have been restricted to grassy areas (e.g. grassy plateaux) in hilly or mountainous areas. Outside of this biome there is evidence of a population in similar terrain in a matrix formed by part of the grassy eastern Nama-Karoo Biome and by the south-western parts of the Grassland Biome.
- (2) Despite the presence of suitable habitat there, no written records could be located for country south of 31° S and east of 26° E, a region where its former presence is hinted at only by a single supporting (zoo-archaeological) record. The reason, or reasons, for this apparent north-south, zoo-geographical boundary (coinciding roughly with the course of the Great Fish River) are not understood.

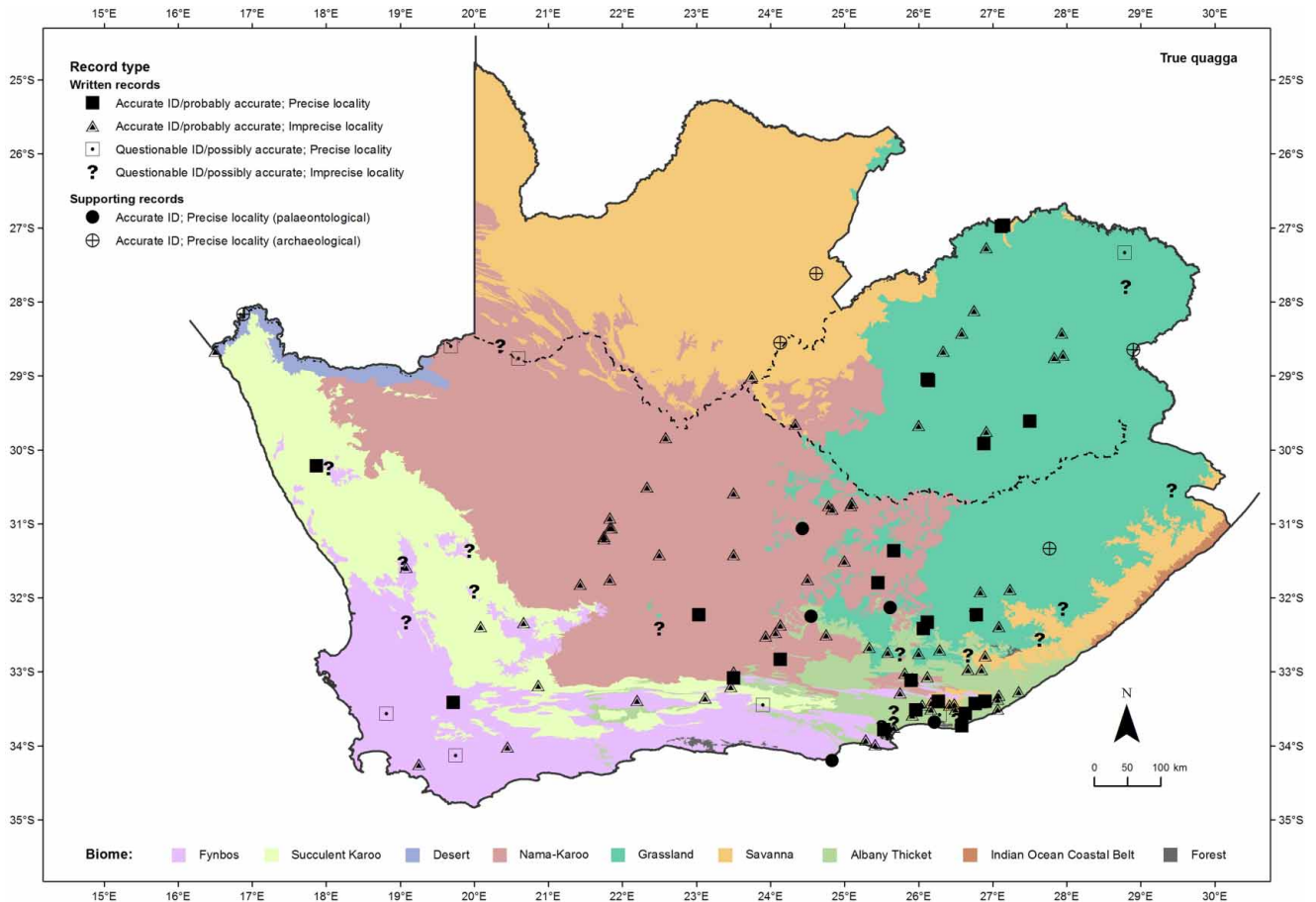


Figure 16. Early historical incidence of the true quagga: mappable written and supporting distribution records (see the text), and biomes.

(3) The most northerly records, all at or near the Orange River, may represent a different taxon to those further to the south (see Taxonomy).

supporting records, and the biomes within the study area, are shown in Figure 16.

TRUE QUAGGA

Equus quagga (Boddaert, 1785)

KWAGGA

Taxonomy

Bronner *et al.* (2003), Skinner & Chimimba (2005) (who follow Bronner *et al.* 2003) and Klingel (2013) consider the true quagga to be conspecific with the Burchell's (plains) zebra, under the scientific name *E. quagga*. However, for reasons elaborated in Skead (2011) and, particularly, in Boshoff & Kerley (2013), the true quagga is taken here to be a separate species – *E. quagga* (*sensu* Wilson & Reeder, 2005), with the Burchell's (plains) zebra resorting under *E. burchellii*. It is believed that the true quagga was extinct in the wild by the end of the 1870s (Boshoff & Kerley, 2013).

DISTRIBUTION RECORDS

Written records in Cowan (1808), Glyn (1863), Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Plug & Badenhorst (2001), Skead (2007, 2011) and Boshoff & Kerley (2013), indicate that in the study area the true quagga occurred in seven biomes – Fynbos, Succulent Karoo, Desert, Nama-Karoo, Grassland, Savanna, Albany Thicket. Mappable written records and qualifying

Fynbos Biome

Although early chronicler coverage is good in parts of this biome (Figure 4), few records relating to this zebra could be located. Nevertheless, the spread of these records suggests that this animal may have occurred fairly widely within the biome. Curiously, it was not recorded from the coastal and sub-coastal zone to the south of the Cape Fold Belt and between 21° and 25° E, a region well frequented by early chroniclers (Figure 4). The poorly developed grass layer in most of the Fynbos Biome is likely to have limited numbers.

Succulent Karoo Biome

A handful of records suggest that this equid occurred, or possibly occurred, in certain bioregions within this biome. The generally poor, and highly seasonal grass cover, along with a general shortage of surface water, would have rendered it unattractive for year-round occupation by large herds of true quaggas.

Desert Biome

A single written record and a single supporting (zoo-archaeological) record, both from the Southern Namib Desert Bioregion, suggest the presence of the true quagga in this narrow biome, which tracks the lower reaches of the Orange River.

Nama-Karoo Biome

A number of written records indicate the incidence of this zebra in, at least, the eastern part of the Lower Karoo Bioregion. A number of written records, and two supporting (palaeontological) records, confirm that it occurred widely in the Upper Karoo Bioregion.

Its occurrence, or potential occurrence, in the Bushmanland Bioregion is indicated or suggested by a single written record from the far eastern part, and from three written records at or near the Orange River in the northern part. Early chronicle coverage in the Bushmanland Bioregion was, overall, poor (Figure 4) and this no doubt influenced the reporting pattern. As with the Succulent Karoo Biome, the generally poor, and highly seasonal, grass cover, together with a lack of surface water, in this arid bioregion would have rendered it unattractive for year-round occupation by large herds of this equid.

Grassland Biome

A number of written records reveal the occurrence of the true quagga in the Dry Highveld Grassland and Mesic Highveld Grassland bioregions, where they occur to the north of the Orange River. A few records are located in or close to fragments of the Dry Highveld Grassland Bioregion, where these occur to the south of this river, in a matrix of Upper Karoo vegetation units.

No records, of any type, were located for the Drakensberg Grassland Bioregion, which is dominated by the Maloti-Drakensberg massif; this is to be expected, given that the mountainous terrain that characterises this bioregion does not provide suitable habitat for the plains-living true quagga.

A number of written records and a single supporting (zoo-archaeological) record suggest its incidence in the Sub-Escarpment Grassland Bioregion, in the south-eastern part of the study area. Nearly all these records are from country to the west of 28° E. Skead (2007) speculates that the outlying written record south of 30° S and east of 29° E may refer to a Burchell's zebra on migration from north of the Lower Drakensberg Escarpment, to the north-east.

Savanna Biome

Despite reasonable to good early chronicle coverage, only a single written record could be located for the Eastern Kalahari Bushveld Bioregion, to the north of the Orange River (see Figures 3 and 4). This record, which appears to come from within, or close to, the ecotonal zone between this bioregion and that to the south (i.e. Upper Karoo Bioregion), is supported by two zoo-archaeological records.

Its presence in the western part of the Sub-Escarpment Savanna Bioregion, in the south-eastern part of the study area, is hinted at by the existence of a few written records but their "imprecise" locality status makes it difficult to confidently assign them to this bioregion; at least some of them may have been located in, particularly, grassy areas within the adjacent Albany Thicket Biome.

Albany Thicket Biome

Numerous written records, associated with two supporting (paleontological records) records, reveal the presence of this equid in this biome. However, the true quagga is not a typical "thicket" species and its presence in this biome is considered to have been related to the existence, in places, of areas of open or relatively open grassland.

DISTRIBUTION PATTERNS

- (1) The true quagga appears to have been widespread in a large part of the study area. The paucity or absence of written records from the arid western and north-western parts of the study area (notably the Bushmanland Bioregion of the Nama-Karoo Biome) is believed to reflect poor early chronicle coverage (Figure 4) and a paucity of grass forage in these areas.
- (2) The reasons for the lack of records, of any type, from country to the south of 30° S and east of 28° E, despite the existence in places of areas of apparently suitable habitat and reasonable early chronicle coverage (Figure 4), require investigation.
- (3) Whereas this equid was sympatric with Burchell's (plains) zebra in grassland to the north of the Orange River, in the Kalahari bushveld, a savanna type to the north of this river, this zebra appears to have been absent or scarce while the Burchell's (plains) zebra was seemingly widespread.
- (4) Despite reasonable to good early chronicle coverage there (Figure 4), very few records could be located for country to the south of the west-east axis of the Cape Fold Belt.

BURCHELL'S (PLAINS) ZEBRA

BONTKWAGGA/BONTSEBRA

Equus burchellii (Boddaert, 1785)

Taxonomy

See the true quagga account.

DISTRIBUTION RECORDS

Written records in Cowan (1808), Skead (2011) and Boshoff & Kerley (2013), together with selected supporting records in Plug & Badenhorst (2001) and Boshoff & Kerley (2013), indicate that in the study area Burchell's zebra occurred principally in two biomes – Grassland, Savanna. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 17.

Grassland Biome

A number of written records, and three supporting (zoo-archaeological) records, indicate its occurrence in that part of the Dry Highveld Grassland Bioregion that lies to the north of the Orange River.

Similarly, its presence in the adjacent Mesic Highveld Grassland Bioregion is revealed by a number of written records, and two supporting (zoo-archaeological) records; one of the latter is from the head valley of the Orange (Senqu) River in today's Lesotho.

Savanna Biome

A number of written records, and two supporting (zoo-archaeological) records, confirm, or suggest, its presence in the Eastern Kalahari Bushveld Bioregion, to the north-east of the Orange River.

The absence of written records from the Kalahari Duneveld Bioregion, to the north-west of the Orange River, may reflect a combination of poor chronicle coverage (Figure 4) and unsuitable habitat, caused by a lack of year-round surface water and forage.

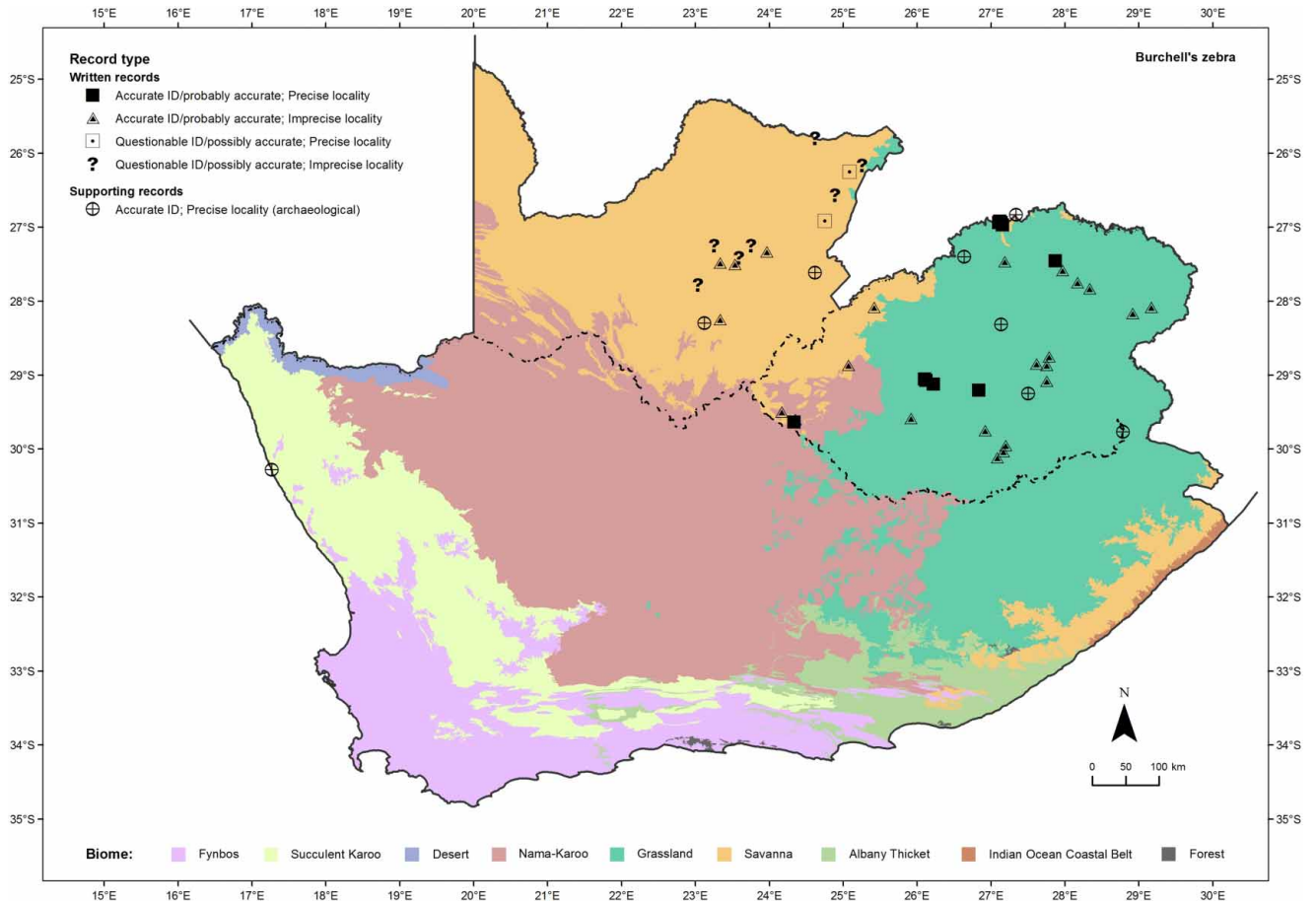


Figure 17. Early historical incidence of Burchell's (plains) zebra: mappable written and supporting distribution records (see the text), and biomes.

DISTRIBUTION PATTERNS

No written records of this equid could be located for the region to the south of the Orange River, and its historical distribution within the study area was seemingly confined to grassland and Kalahari bushveld (savanna type) in regions to the north of this river, where its water requirements were met.

BUSHPIG

Potamochoerus larvatus (F. Cuvier, 1822)

BOSVARK

DISTRIBUTION RECORDS

Written records in Rookmaaker (1989) and Skead (2007, 2011), together with selected supporting records in Klein & Cruz-Urbe (2000), Plug & Badenhorst (2001) and Skead (2007) indicate that in the study area the bushpig occurred in six biomes – Fynbos, Grassland, Savanna, Albany Thicket, Indian Ocean Coastal Belt, Forest. However, in most of these biomes the occurrence of this pig is not primarily linked to the various, broad, biophysical factors that define them, but rather to localised areas of suitable, densely vegetated, habitat that may exist within them. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 18.

Fynbos Biome

The presence of the bushpig in this biome is indicated by various written records and two (coastal) zoo-archaeological

records, from a number of bioregions; all these records lie to the east of 19° E.

Grassland Biome

Two written records (one with questionable identification) indicate its occurrence in the Sub-Escarpment Grassland Bioregion.

Savanna Biome

Its presence in this biome is revealed by a handful of records from or very close to the most westerly part of the Sub-Escarpment Savanna Bioregion.

Albany Thicket Biome

A few written records, supported by two zoo-archaeological records, indicate that the bushpig occurred in this biome.

Indian Ocean Coastal Belt

Two written records reveal its presence in this biome.

Forest Biome

A number of written records, notably in tracts of Southern Afrotemperate Forest on the incised coastal plateau south of the Outeniqua-Tsitsikamma mountains and between about 22° to 24°30' E, supported by a museum record, confirm the incidence of the bushpig in this biome.

DISTRIBUTION PATTERNS

Despite the bushpigs' preference for dense cover, and its mainly nocturnal activity regime, both of which would have

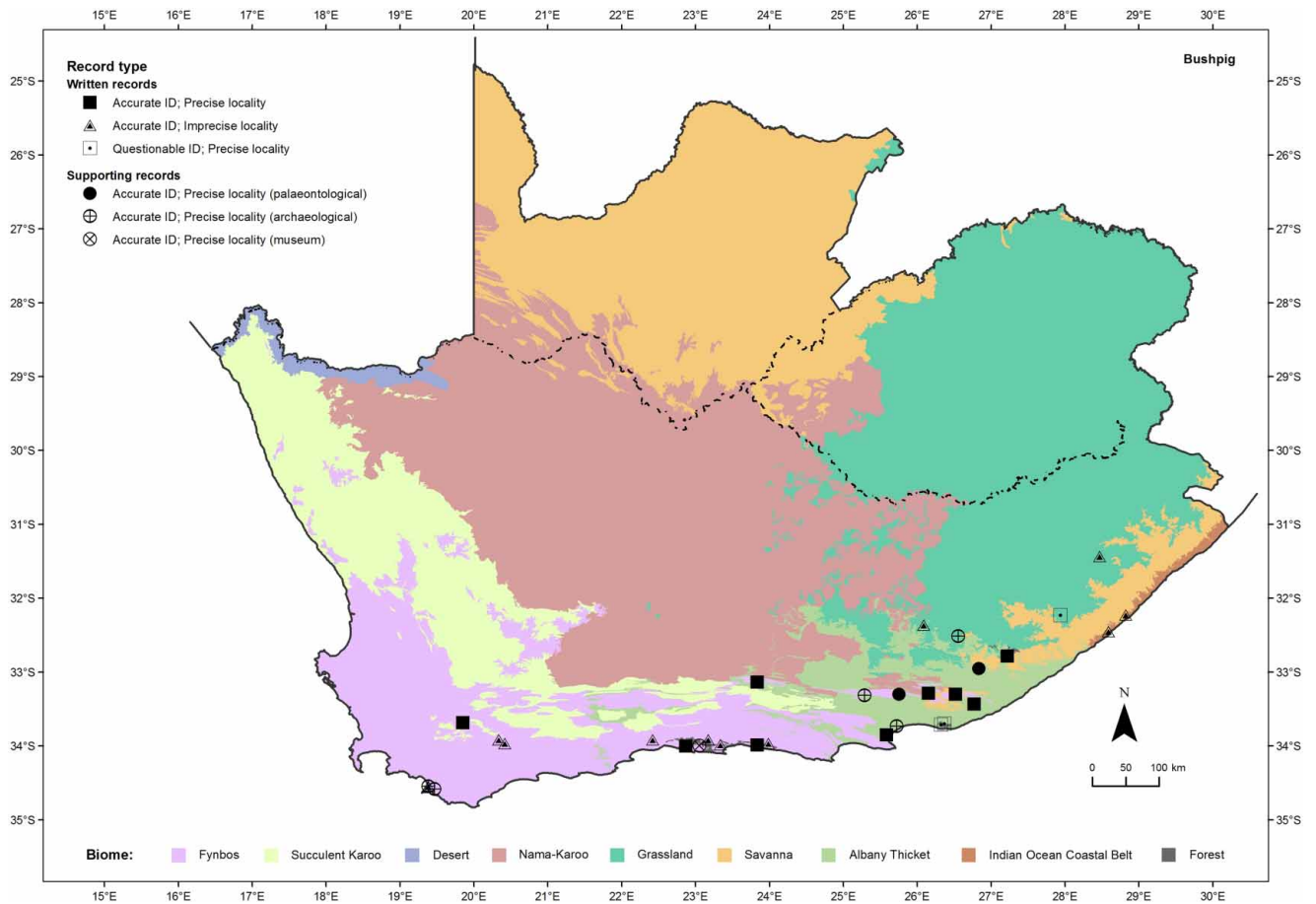


Figure 18. Early historical incidence of the bushpig: mappable written and supporting distribution records (see the text), and biomes.

mitigated against it being observed by day-travelling, early chroniclers, a number of distribution patterns can be discerned:

- (1) It was generally confined to the moister southern and south-eastern parts of the study area, i.e. where areas or patches of suitable habitat were most likely to have existed.
- (2) It occurred further westwards than is indicated by the studies of Du Plessis (1969) and Seydack (2013).
- (3) Despite the existence of patches or areas of potentially suitable habitat, no records are known from country to the east of 29° E, in the south-eastern part of the study area (i.e. the eastern parts of the Transkei). However, bushpig have apparently always been present in the Transkei (at least in the scarp and coastal forests), with the paucity of records owing to the fact that this nocturnal animal was rarely recorded by early literate travellers and settlers (De Villiers, 2002; D.J. de Villiers, *in litt.* January 2015). Thus, the bushpig was probably more widespread in the south-eastern part of the study than is indicated by the records shown in Figure 18.

CAPE WARTHOG

Phacochoerus aethiopicus (Pallas, 1766)

KAAPSE VLAKVARK

COMMON WARTHOG

Phacochoerus africanus (Gmelin, 1788)

VLAKVARK

Taxonomy

The so-called “desert” warthog *P. aethiopicus* comprises the extant Somali warthog *P. a. delamerei*, which is limited to the arid north-eastern region of Africa (known as the “Horn of Africa”), and the extinct Cape warthog *P. a. aethiopicus*, which apparently occurred in the arid and semi-arid southern, south-western and western parts of southern Africa (Grubb & d’Huart, 2010). There is general consensus that in southern Africa *Phacochoerus aethiopicus* represents the extinct Cape warthog while *P. africanus* represents the extant common warthog (Skinner & Chimimba, 2005; Cumming, 2013).

The date of the extinction of the Cape warthog is not known; the last specimen was collected (in today’s KwaZulu-Natal Province of South Africa, to the east of the study area) in 1871 (Grubb & d’Huart, 2010) and it is considered to have disappeared from its range in the study area sometime between 1820 and 1870 (Skead, 2007, 2011).

DISTRIBUTION RECORDS

Written records in Glyn (1863), Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Shortridge (1934), Plug & Badenhorst (2001), Skead (2007, 2011) and Boshoff & Kerley (2013), indicate that within the study area warthogs (*Phacochoerus* spp.) occurred in five biomes – Fynbos, Nama-Karoo, Grassland, Savanna, Albany Thicket. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 19.

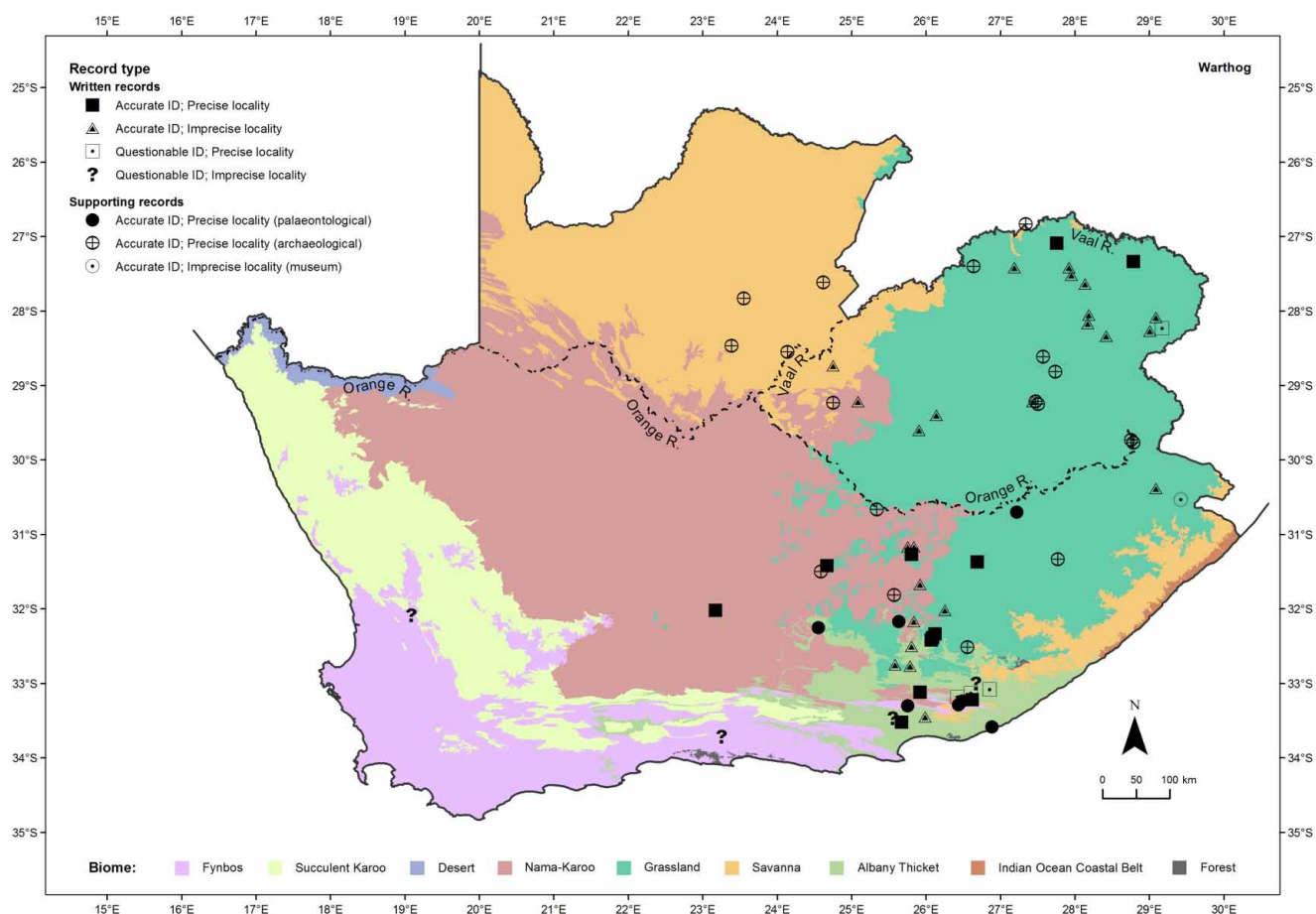


Figure 19. Early historical incidence of the warthog (*Phacochoerus* spp.), and biomes. Only mappable written and supporting records (see the text) are shown.

Fynbos Biome

The presence of warthog in this biome is confirmed by a single palaeontological record (just to the west of 26° E) from a far easterly outlier of the biome, comprising part of the Eastern Fynbos Renosterveld Bioregion. Two written records exist – one from the Eastern Fynbos Renosterveld Bioregion, and one from the Northwest Fynbos Bioregion; since in both cases the identification of the animal is questionable, they do not provide additional confirmatory material. Given that early chronicler coverage was reasonable to good in much of this biome (Figure 4), the paucity of confirmed records suggests that warthog were absent from the greater part of it, possibly being present only in the far eastern parts where the fynbos has a relatively well-developed grass component (Rebello *et al.*, 2006).

Nama-Karoo Biome

Several written records, supported by a palaeontological record, and a few zoo-archaeological records, reveal the presence of warthog in the Upper Karoo Bioregion. Apart from one written record, which falls in the southern part, all the records are from the eastern parts of this bioregion, which is relatively moist and grassy (Mucina *et al.*, 2006a).

Even though early chronicler coverage varies spatially within the biome (Figure 4), it seems reasonable to suggest that had warthog been widespread there, this would have

been revealed by the written record. The remainder of the biome is characterised by semi-arid to arid conditions, with grass cover and surface water being strongly linked to seasonal rainfall patterns.

Grassland Biome

The incidence of warthog in this biome is indicated as follows:

Dry Highveld Grassland Bioregion: a number of written records and a single supporting (zoo-archaeological) record.

Mesic Highveld Grassland Bioregion: a number of written records, supported by a single palaeontological record and a few zoo-archaeological records.

Drakensberg Grassland: the single written record bears a question mark over the identity of the animal; it may refer to a bushpig *Potamochoerus larvatus*, in a wooded ravine. The zoo-archaeological record from the southern outlier of this bioregion probably derives from warthog that could have occurred in wider valley bottoms. Overall, this mountainous bioregion does not offer suitable warthog habitat.

Sub-Escarpment Grassland Bioregion: two written records, one zoo-archaeological record, and one museum record.

Savanna Biome

The incidence of warthog in the Eastern Kalahari Bushveld Bioregion, to the north of the Orange River, is suggested by a single written record and a few supporting

(zoo-archaeological) records. The paucity of written warthog records from this bioregion is surprising, given that early chronicle coverage was good to reasonable in large parts of it (Figure 4), and that *Phacochoerus africanus* is sometimes called the savanna warthog.

No written records could be located for the Kalahari Duneveld Bioregion, to the west of the Eastern Kalahari Bushveld Bioregion (Figure 3), an arid region with highly ephemeral grass cover and surface water availability. However, early chronicle coverage was very poor in this region (Figure 4).

A single supporting (zoo-archaeological) record indicates warthog occurrence in the Central Bushveld Bioregion, in the far north-east of the study area.

Two palaeontological records reveal their presence in the most westerly outliers of the Sub-Escarpment Savanna Bioregion; no records could be located for the remainder of this bioregion, to the east.

Albany Thicket Biome

Two specimen records and a number of valid written records reveal or suggest the incidence of warthog in this biome. Since the warthog is not a true 'thicket' species, it is highly likely that these records refer to collections or observations from grassy areas within a greater matrix of thicket types.

DISTRIBUTION PATTERNS

Common vs Cape warthog

In southern Africa the common warthog, a mainly diurnal herbivore, occupies a wide range of habitats, notably open woodland, shrubland, shorter grassland and floodplains (Skinner & Chimimba, 2005). The preferred habitat of the Cape warthog is not known. The Cape warthog was mainly a grazer, while the common warthog, largely a grazer, has a higher proportion of browse in its diet than the Cape warthog (Skinner & Chimimba, 2005; Nyafu, 2009). Consequently, the Cape warthog could be expected to have occurred in grassland-dominated areas, and where patches or limited areas of these types occurred within a larger matrix of other types, whereas the common warthog (also called the "savannah" warthog) is largely an animal of savanna-dominated areas.

Which species occurred where?

Early to relatively recent works on southern African mammals (notably, Sclater, 1900; FitzSimons, 1920; Shortridge, 1934; Roberts, 1951; Du Plessis, 1969; Smithers, 1983; Skinner & Smithers, 1990) recognise but a single species of warthog in southern Africa, namely *P. aethiopicus*. It was only fairly recently (1993) that the existence of two species – the now extinct Cape ("desert") warthog *P. aethiopicus* and the extant common or savanna warthog *P. africanus* (Grubb & d'Huart, 2010, and the references therein) – was broadly recognised. Confusion between these two species also exists in the zoo-archaeological literature where, for example, a prominent work (Plug & Badenhorst, 2001) does not distinguish between the two species and uses *P. aethiopicus* throughout. In some publications (e.g. Brink, 2005), both subspecific names are used for the same skeletal element.

In addition to the above, written, historical records seldom provide sufficient clues to enable the identity of the animal under observation to be correctly allocated to either of the two taxa. Similarly, specimen records often do not comprise the tooth or skeletal material that would enable this distinction to be made.

The issues described above beg the question – which of the records (written and supporting) plotted on Figure 19, and mentioned in the literature but not plotted on Figure 19, represent the Cape warthog and which ones represent the common warthog? (see below).

Northern boundary between the Cape and the common warthog

The location of the northern boundary between the common warthog and the Cape warthog is not accurately known. There is currently no good evidence that the written and supporting records to the north of the Orange River refer specifically to one or both species. The only possibility is a warthog skull, which conforms to the characteristics of the Cape warthog, accessioned by at least 1873 in a museum in the village of Smithfield, in the southern Free State Province and some 40 km north of the Orange River; however, the provenance of this skull is unknown (Boshoff & Kerley, 2013) and therefore it cannot be used to confirm the incidence of the Cape warthog to the north of the Orange. Similarly, for most of the records (written and supporting) to the south of the Orange there is currently no good evidence that they refer either to the common warthog or to the Cape warthog, or to both taxa. Fortunately, there is some evidence (circumstantial and material) that certain of the mapped and non-mapped records from south of the river refer to the Cape warthog (Skead, 2007, 2011; Grubb & d'Huart, 2010, 2013).

D'Huart & Grubb (2001: Fig. 5) and Randi *et al.* (2002) have proposed the northern limit of the range of the Cape warthog as the Orange River area and, until further distribution information comes to hand, and which contradicts this suggestion, this must stand. Cumming (2013) contends that, historically, the common warthog did not occur in the arid Karoo (i.e. mostly south of the Orange River). On the basis of these comments, we have assumed that all the records to the south of the Orange River probably refer to the Cape warthog, and those to the north refer to the common warthog.

We speculate, however, that if the Cape warthog was predominantly a grazer then it could be expected to have occurred not only in the extensive, open, grasslands to the south of the Orange River but also in those to the north of it, i.e. to the Vaal River and beyond. If this was indeed the case, then some or all the written and supporting records to the north of the Orange River may refer to the Cape warthog, rather than to the common warthog, a predominantly savanna species. However, as mentioned above, there is currently no information that supports this possibility. Perhaps new information on this aspect can be obtained if the zoo-archaeological material is re-analysed.

An additional factor to be considered, in attempts to determine boundaries between the two warthog species, is that of possible sympatry. For example, the common warthog and the northern form of the "desert" warthog (*P. aethiopicus delamerei*) are sympatric in parts of northern Kenya (Grubb & d'Huart, 2013; de Jong & Butynski, 2014). Whether or not this situation occurred in the study area or adjacent country is not known.

Eastern boundary between the Cape and the common warthog

According to an interpretation of historical records (Du Plessis, 1969), warthog occurred historically in country to the immediate east of the study area; this being part of the political region formerly known as "Natal Colony" and "Natal Province", and currently "KwaZulu-Natal Province". The

occurrence of the Cape warthog in this region is indicated by a specimen that was obtained from “Port Natal” in 1843, and records of live Cape warthogs from “Port Natal” in 1850 and 1866 (Grubb & d’Huart, 2010). During the mid-1800s “Port Natal” (now Durban, South Africa) was a growing port for coastal and overseas trade and it is possible that the specimen and live animals referred to were brought there from elsewhere, prior to shipping overseas. Although their true provenance is unknown, it is unlikely that the live animals would have been captured very far from “Port Natal”, this owing to the logistical constraints of transporting and maintaining live warthog over a long distance. These “Natal” records therefore suggest that the range of the Cape warthog extended eastwards of the Mtamvuna River, which forms the south-eastern boundary of the study area. The broader region to the east of this river, i.e. the country between the Mtamvuna and Thukela (Tugela) rivers, is dominated by well-developed grassland (Sub-Escarpment Grassland Bioregion) and savanna (Sub-Escarpment Savanna Bioregion), of which the former, particularly, would have suited the Cape warthog. This information, together with the view (expressed by Rowe-Rowe, 1994) that the Thukela River marked the southerly limit of the natural distribution of the common warthog in KwaZulu-Natal Province, strongly suggests that the warthog records south of 30° S and between 27° and 30° E (Figure 19) refer to the Cape warthog.

Was the Cape warthog a true “desert” warthog?

The absence of confirmed, written, warthog records from the central, western, south-western and southern parts of the study area (i.e. south of about 28° 30' S and west of 23° E) is noteworthy. It is our contention that, notwithstanding some gaps, the early chronicler coverage (Figure 4) is deemed sufficient to have potentially provided at least a few confirmed written records of the existence of the warthog in these areas, had it occurred there during the early historical period.

The absence of written records is mirrored by a complete absence of warthog remains in archaeological samples from these areas, from as far back as 8000 years BP. In fact, there is no evidence of warthog in the zoo-archaeological record for the semi-arid to arid south-western, western, central western and north-western parts of the study area, from as early as 30 000 years BP (Plug & Badenhorst, 2001).

The lack of confirmed written records and the nature of the zoo-archaeological information raises the question – is it possible that the Cape warthog was not a true “desert” warthog after all and rather existed (at least in pre-recent and early historical times) further eastwards (and more specifically eastwards of about 23° E – see Figure 19), i.e. in a region where the rainfall, air temperature and soil productivity were higher, resulting in a more reliable (quantity, quality, year-round availability) supply of grass? This would make ecological sense, given that it was predominantly a grazer. If this was indeed the case, the Cape warthog was not confined to the arid to semi-arid Karoo region of South Africa, as is indicated by Grubb and d’Huart (2013). Insofar as its incidence in the Nama-Karoo is concerned, it appears that, at best, it only occurred in the far eastern part of this bioregion, where the grass component is relatively well-developed (Mucina *et al.*, 2006a).

Conclusion

Additional information about the early distribution of the two warthog species in the study area and beyond is required before definitive statements on their respective distribution

patterns in the study area, during the early historical period, can be made. A discussion around the possible reasons for the extinction of the Cape warthog during the 19th century is beyond the scope of the present study.

HIPPOPOTAMUS

Hippopotamus amphibius (Linnaeus, 1758)

SEEKOEI

DISTRIBUTION RECORDS

Written records in Cowan (1808), Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Klein & Cruz-Urbe (2000), Plug & Badenhorst (2001), Sadr (2007), Parsons (2008), Skead (2007, 2011), van der Merwe (1979) and Boshoff & Kerley (2013), indicate that within the study area hippo occurred in seven biomes – Fynbos, Desert, Nama-Karoo, Grassland, Savanna, Albany Thicket, Indian Ocean Coastal Belt. However, the historical incidence of this megaherbivore is not primarily linked to the various, broad, biophysical factors that broadly define the listed biomes, but rather to individual, localised areas of specialised wetland habitat that are available, year-round, within them. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 20.

DISTRIBUTION PATTERNS

- (1) Hippo appear to have potentially occurred wherever their specialised habitat was available, year-round.
- (2) The country to the west of about 23° E can be classified as semi-arid to arid and here most of the written and supporting records are confined to estuaries and wetlands at or near the coast, or to large perennial rivers, notably the Orange River in the north and the Berg River in the south-west. A few written records indicate the presence of hippo in the hinterland in the south-west. Thus, it appears that this megaherbivore had a restricted distribution pattern in this western zone.
- (3) In the medium to high rainfall areas to the east of about 23° E, written and supporting records are distributed not only in the coastal zone and along the large rivers of the interior (notably the Orange and Vaal rivers) but also widely away from the major drainage features in the interior. The latter pattern is presumably due to the higher rainfall maintaining year-round, suitable habitat at various localities on the landscape. Thus, it appears that in this eastern zone the hippo was relatively widespread.
- (4) Palaeontological records form the dominant record type in the hinterland south of the Orange River and east of about 22° E (Figure 20). The reasons for this are not known. We postulate that the preponderance of these records in this region reflects hippo incidence during a slightly wetter period during the later Holocene (for the latter see Deacon and Lancaster, 1988), which probably resulted in suitable habitat being available on a year-round basis. This is further hinted at by three written records (all made before 1840 (Skead, 2011)) from the courses of the Kuruman and Molopo rivers, to the north and west of the Orange and Vaal rivers. An early map (reproduced in Crampton, 2014) shows the presence of fountains, marshes and pools (in river courses) in the vicinity of the modern-day town of Kuruman. Today (2010s), these two rivers do not hold water except for very short periods after episodic rainfall events and are therefore no longer able to sustain hippo populations, even in formerly deep

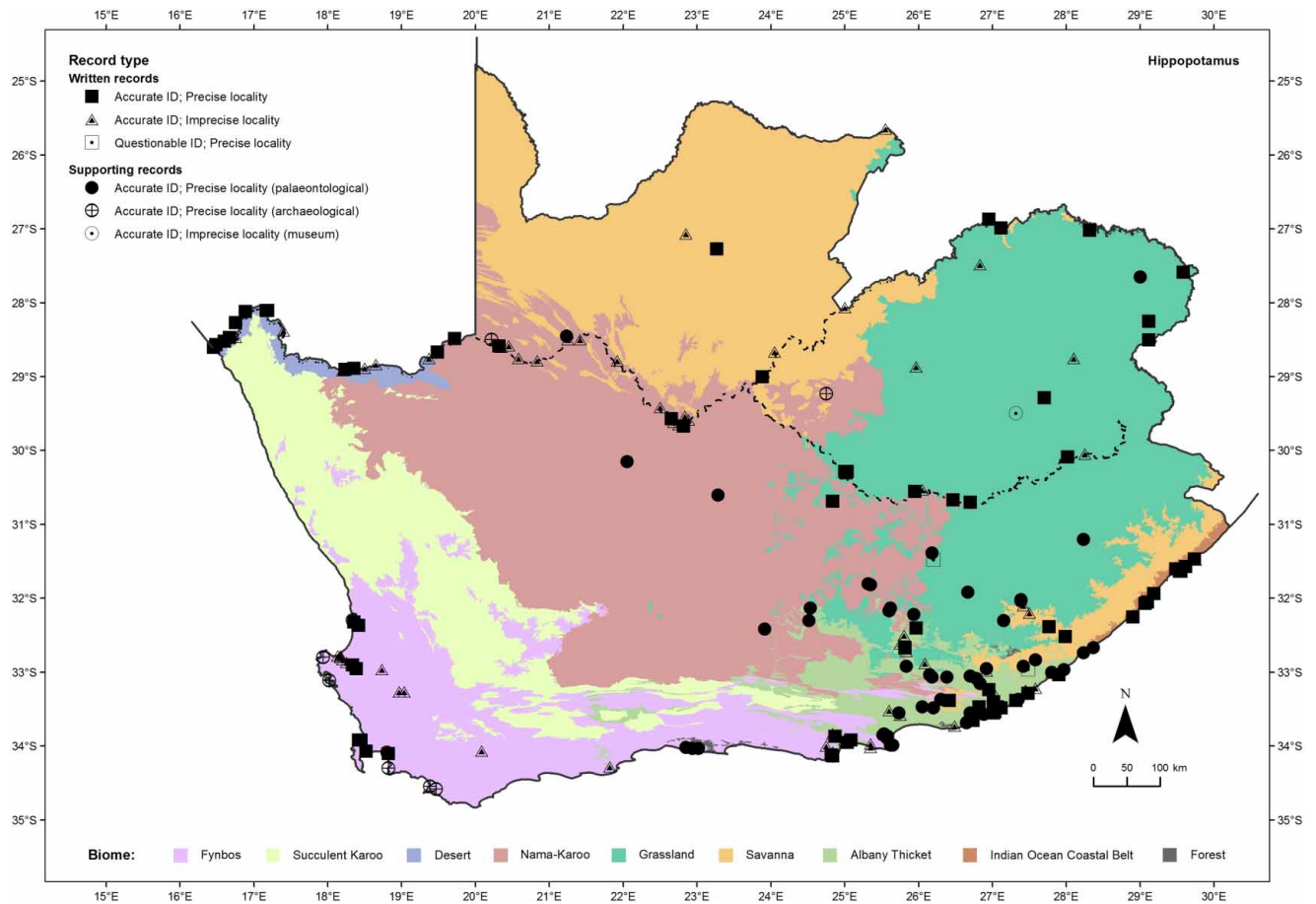


Figure 20. Early historical incidence of the hippopotamus: mappable written and supporting distribution records (see the text), and biomes.

pools. It is possible that 19th century stock-farming practices in this region contributed to the siltation and drying up of these rivers.

GIRAFFE

Giraffa camelopardalis (Linnaeus, 1758)

DISTRIBUTION RECORDS

Written records in Skead (2011) indicate that within the study area the giraffe occurred in four biomes – Desert, Succulent Karoo, Nama-Karoo, Savanna. Mappable written records, and the biomes within the study area, are shown in Figure 21.

Desert Biome

A handful of written records reveal its occurrence in the narrow strip of Gariiep Desert Bioregion in the north-western part of the study area; these records were made at or not far from the Orange River, which has a relatively well-developed riparian zone.

Succulent Karoo Biome

Its presence in this biome is indicated by a single written record (of two animals) near the mouth of the Spoeg River, some 225 km south of the mouth of the Orange River; this locality falls within the Namaqualand Sandveld Bioregion.

Nama-Karoo Biome

Several written records show its incidence in the northern part of the Bushmanland Bioregion; all these records were

made at localities along or close to the Orange River, which has a relatively well-developed riparian zone.

Savanna Biome

A number of written records indicate the presence of giraffe in the Eastern Kalahari Bushveld Bioregion, to the north of the Orange River. This bioregion offers highly suitable giraffe habitat and, had the early chronicler coverage (Figure 4) been better, this animal may have been shown to be more widespread in this region. A written record from 1850 (not shown on Figure 21 as its locality is too vague to be mapped) alludes to the occurrence of giraffe in this bioregion, where it occurs to the south-east of the Vaal River.

Only a single written record could be found for the Kalahari Duneveld Bioregion, to the north-west of the Orange River; this record was made in an area that contains a western outlier of the Eastern Kalahari Bushveld Bioregion. Poor early chronicler coverage (Figure 4) makes it difficult to estimate the incidence of the giraffe in this bioregion. However, given that the species in question, i.e. the southern or Cape giraffe *G. c. giraffa*, is not averse to living in arid country (Skinner & Chimimba, 2005; Ciofolo & Le Pendu, 2013), it was probably more widespread in the Kalahari Duneveld Bioregion than the written record indicates.

DISTRIBUTION PATTERNS

- (1) The written record shows that in the study area the giraffe was present in the Savanna Biome to the north of the

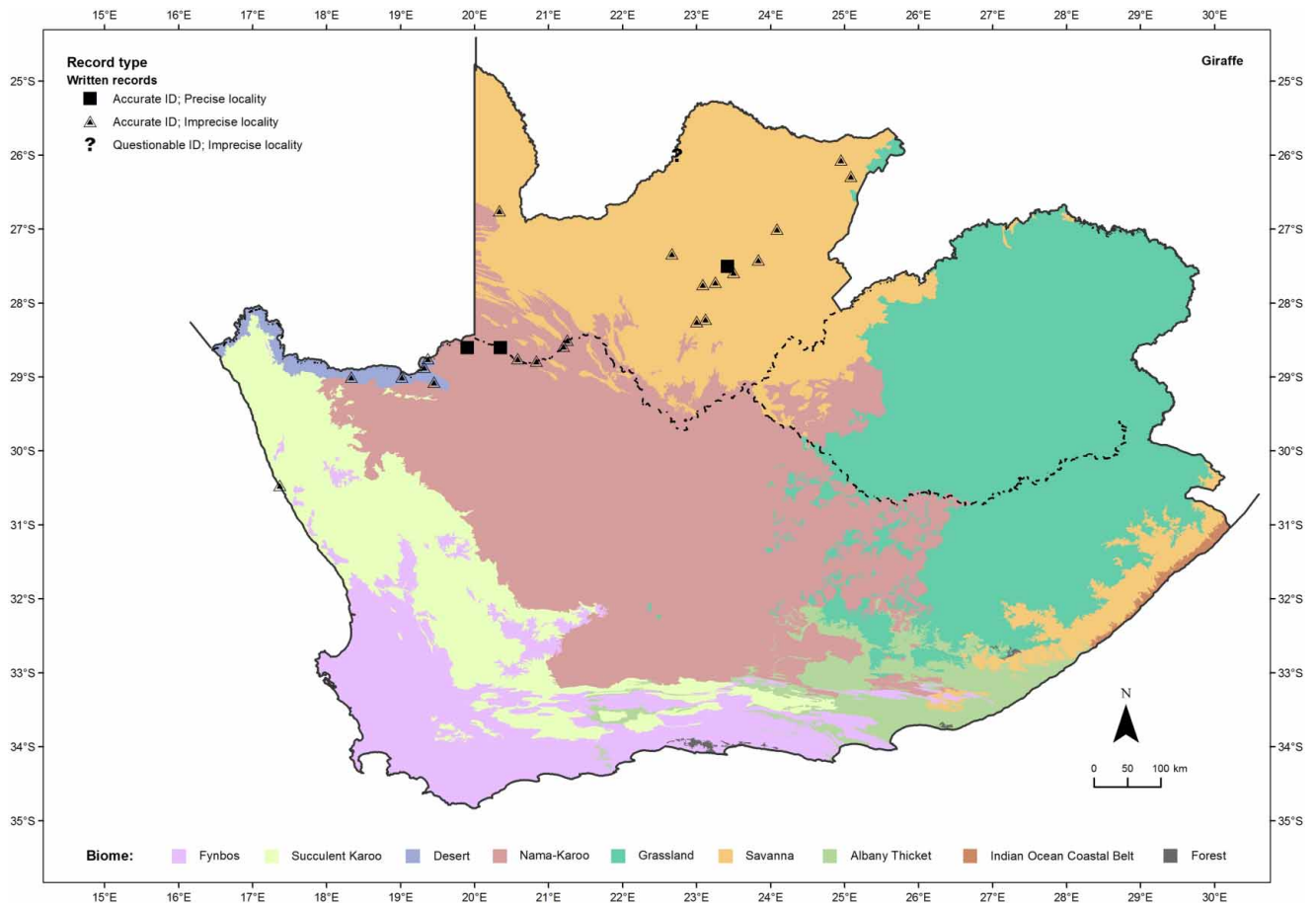


Figure 21. Early historical incidence of the giraffe: mappable written distribution records (see the text), and biomes.

Orange River. This population extended westwards, from about 21°30' E, in a narrow corridor formed by the Orange River, which has a relatively well-developed riparian zone. While it may have occurred along this river to the east of about 21°30' E, no records to confirm this have been located. The giraffe is known to have been present in southern Namibia, to the north-west (Shortridge, 1934; Skead, 2011), and it is therefore likely that the population there was contiguous with that in that part of the Savanna Biome under consideration here. This animal was probably more widespread in the western part of the Savanna Biome than is suggested by the information in Figure 21.

- (2) The single, written record, from a coastal locality far to the south of the Orange River, and the lack of any other records from this region, suggest that giraffe (most likely from the Orange River area, to the north) undertook nomadic or seasonal movements in the coastal areas of Namaqualand. Elsewhere in Africa giraffe are known to undertake long-distance, seasonal, dispersal movements, aggregating near rivers in the dry season (Ciafola & Le Pendu, 2013). However, the possibility exists that this southerly record refers to vagrants.
- (3) Skead (2007) discusses the possibility that some early (c. 1600s) aboriginal paintings in rock shelters in grasslands and savannas in the south-eastern part of the study area depict giraffe, thereby indicating its incidence in the region in pre-colonial times. This possibility is repeated by Ciafola & Le Pendu (2013). However, in a more recent

appraisal (Skead, 2007) it is contended that the long-necked animals in the paintings in question are not giraffe but rather antelopes. In one case what had been called a “giraffe” was clearly a mountain reedbuck *Redunca fulvorufula*. All five shelters with paintings purporting to show “giraffes” were revisited and no unequivocal depictions of giraffes could be found (Skead, 2007). In support of the re-appraisal, it is known that the early rock artists painted wild animals in a symbolic context and a common tendency was to elongate various body elements (of both humans and animals), e.g. necks, legs (Vinnicombe, 2009). Hence, it could be quite easy to misidentify a long-necked antelope in a rock painting as a giraffe. In the light of this new information, the issue of rock paintings depicting giraffe in this region needs re-assessment, especially in view of the absence of written records and supporting zoo-archaeological material (Skead, 2007).

AFRICAN BUFFALO

Syncerus caffer (Sparrman, 1779)

BUFFEL

DISTRIBUTION RECORDS

Written records in Cowan (1808), Skead (2007, 2011), Boshoff & Kerley (2013) and Crampton *et al.* (2013), together with selected supporting records in Klein & Cruz-Urbe (2000), Plug & Badenhorst (2001), Skead (2007) and Boshoff & Kerley (2013), indicate that within the study area the African buffalo occurred in eight biomes – Fynbos, Desert, Nama-

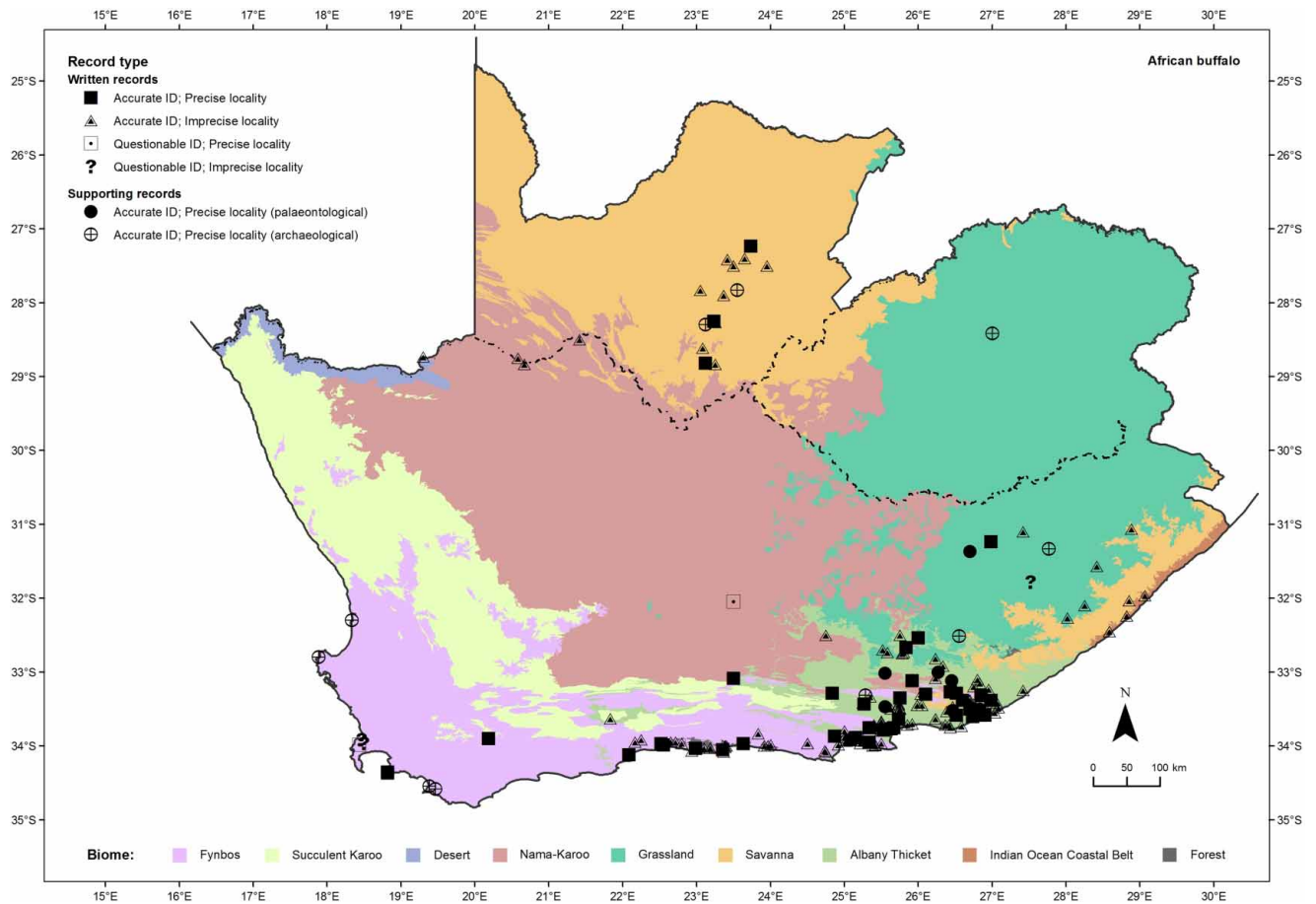


Figure 22. Early historical incidence of the African buffalo: mappable written and supporting distribution records (see the text), and biomes.

Karoo, Grassland, Savanna, Albany Thicket, Indian Ocean Coastal Belt, Forest. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 22.

Fynbos Biome

The presence of African buffalo in the lowlands of the south-western part of this biome is revealed by a few written records, and potential records, from the Southwest Fynbos and East Coast Renosterveld bioregions, respectively, supported by zoo-archaeological records from coastal sites in the West Strandveld and South Coast Fynbos bioregions. Although the reasons for the lack of records from the immediate hinterland of the Cape Peninsula, despite good early chronicler coverage (Figure 4), are not known, it seems likely that the generally poor quality of the habitat – cold wet winters, hot dry summers, leached soils, nutrient-poor vegetation, poorly developed grass component, preponderance of sour grasses (Rebello *et al.*, 2006) – would have mitigated against a strong presence of this bulk grazer in this region.

In contrast to the above, in the eastern part of the Fynbos Biome there are numerous written records from the incised coastal plain south of the Cape Fold Belt, between about 22° and 26° E, within the Eastern Fynbos-Renosterveld Bioregion. In this area this vegetation unit, which has a relatively high grass component, that increases progressively from west to east (Rebello *et al.*, 2006; Radloff, 2008), forms ecotones with Southern Afrotropical Forest (notably in the zone south of

the Outeniqua-Tsitsikamma mountains) in places and these would have offered suitable African buffalo habitat.

Desert Biome

The single written record from the Gariep Desert Bioregion is from, or from a locality close to, the course of the Orange River, where the relatively well-developed riparian zone would have provided suitable African buffalo habitat.

Nama-Karoo Biome

There are a handful of written records from the Bushmanland Bioregion but these are at or close to the Orange River, where the riparian zone of this river and the lower sections of its tributaries would have provided suitable African buffalo habitat.

The lack of records from most of the Bushmanland and Upper Karoo bioregions, and from the central and western parts of the Lower Karoo Bioregion, is not unexpected, given the arid to semi-arid nature of these areas, the lack of suitable, year-round forage, and limited shade opportunities. It is therefore considered unlikely that increased chronicler coverage in the central and southern Bushmanland Bioregion would have affected this pattern. The few written records associated with the southern and eastern parts of the Lower Karoo Bioregion (where early chronicler coverage is reasonable – see Figure 4) may indicate suitable habitat (perhaps on a highly ephemeral basis) owing to a relatively high level of grassiness, associated with a relatively high rainfall, there (Mucina *et al.*, 2006a).

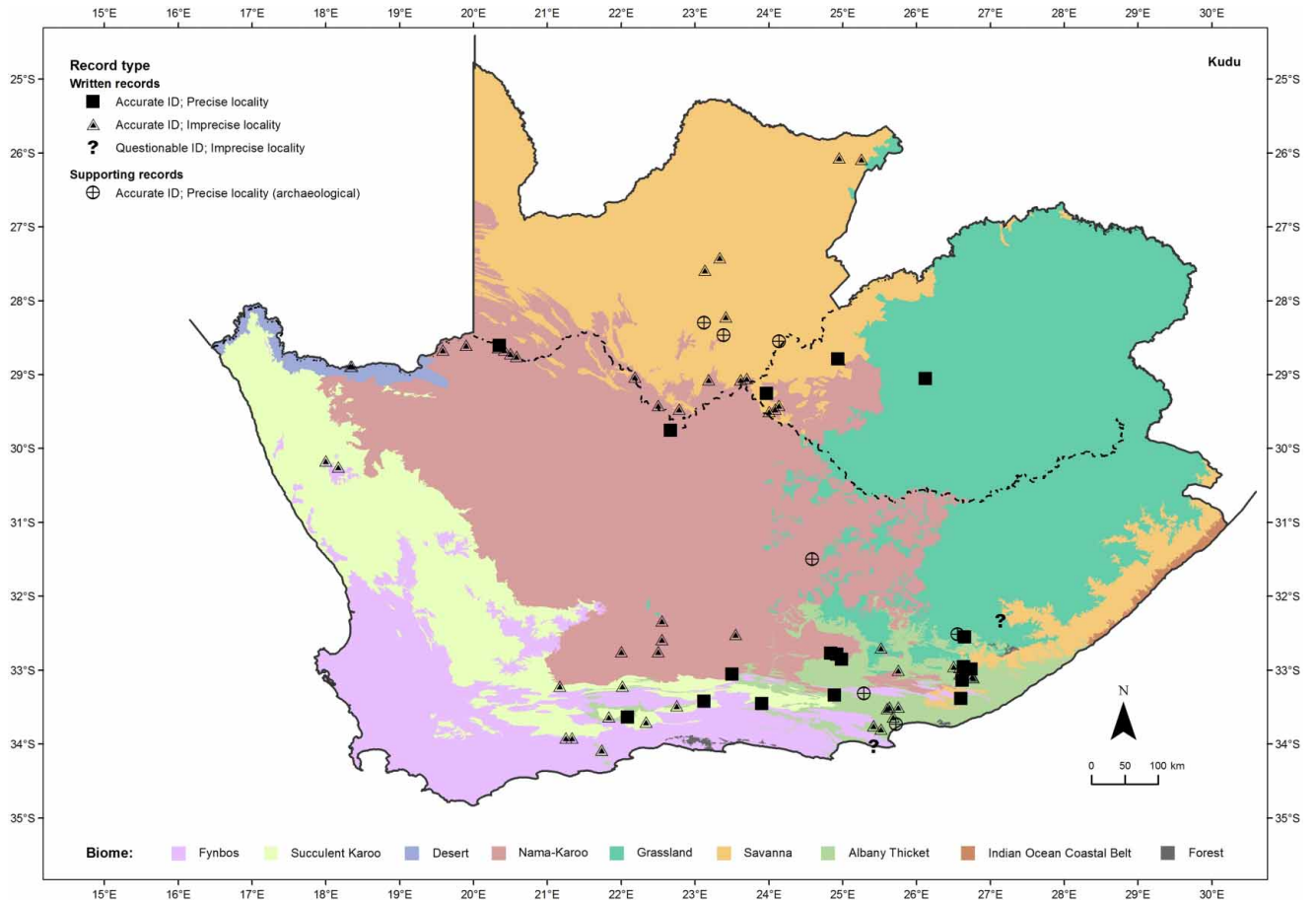


Figure 23. Early historical incidence of the greater kudu: mappable written and supporting distribution records (see the text), and biomes.

Grassland Biome

Despite an abundance of forage, and a relatively high rainfall, and despite generally good early chronicle coverage (Figure 4), there are no written records from the Dry Highveld Grassland and Mesic Highveld Grassland bioregions. It is postulated that the general lack of shade and the cold, dry winters rendered these parts unsuitable for the African buffalo. The single zoo-archaeological supporting record, which is based on a low number of skeletal elements, from the Dry Highveld Grassland cannot be easily explained; perhaps it represents a summer visitor, penetrating the open grassland along a river course flanked by riparian vegetation.

The two written records and single palaeontological record from the southern parts of the Drakensberg Grassland Bioregion, which is characterised by rugged, mountainous terrain, are considered to endorse the contention that in such terrain “buffaloes would have gone up the rivers and fed over adjacent country” (Skead, 2007).

A number of written records, and a single zoo-archaeological record, indicate the presence of African buffalo in the Sub-Escarpment Grassland Bioregion, in the south-eastern part of the study area.

Savanna Biome

A number of written records, supported by two zoo-archaeological records, indicate the presence of African buffalo in the

central part of the relatively well-watered Eastern Kalahari Bushveld Bioregion, to the north-east of the Orange River. Early chronicle coverage in the eastern part of this bioregion was, however, relatively poor (Figure 4) and therefore this bulk grazer was possibly more widespread in this bioregion than is indicated by the records in Figure 22.

A single written record suggests its occurrence in the Sub-Escarpment Savanna Bioregion, in the south-eastern part of the study area.

Albany Thicket Biome

Numerous written records from this biome (where chronicle coverage is good in all but the western parts – see Figure 4) are supported by a zoo-archaeological record and by various palaeontological records, as well as the relict population in the Addo district. Since the African buffalo is not a true “thicket” species, it is almost certain that these records refer to animals observed in predominantly grassy areas within a matrix of thicket vegetation. In this regard, this biome is not homogeneous and incorporates areas of other biomes.

There is a written record from the Little Karoo, a broad east-west running valley bordered by the Swartberg mountains in the north and the Outeniqua mountains in the south. Patches or areas of thicket vegetation, and associated riparian areas, that occur in and near this valley, and which form western outliers of the biome under consideration, could have supported African buffalo in the past.

Indian Ocean Coastal Belt Biome

A few written records suggest its occurrence in this biome, in the south-eastern part of the study area.

Forest Biome

While the African buffalo is not a true “forest” species, a number of written records reveal its presence on the incised coastal plateau between the coast and the Outeniqua-Tsitsikamma mountains, i.e. between about 22° and 24° E in the far south of the study area. Here ecotones comprising moderately grassy fynbos and Southern Afrotropical Forest would have provided suitable habitat. The presence of African buffalo in the Southern Afrotropical Forest (Skead, 2011), at least, may indicate its use as a refuge, in response to direct persecution by humans (Kerley *et al.*, 2012).

DISTRIBUTION PATTERNS

- (1) The Fynbos Biome was seemingly not a stronghold for the species.
- (2) It was apparently absent from, or a very rare visitor in, the extensive, open, grasslands of the Highveld plateau, where this physical feature occurs to the north of the Orange River.
- (3) It occurred within two nodes: a northerly one associated with at least part of the course of the Orange River and the relatively well-watered Kalahari bushveld (a savanna type) to the north of this river, and a southerly one which incorporates the thicket-, grassland- and savanna-dominated southern and south-eastern parts (i.e. eastwards of about 22° E and to the south of the Great Escarpment), including the coastal and sub-coastal areas.

GREATER KUDU

Tragelaphus strepsiceros (Pallas, 1766)

KOEDOE

DISTRIBUTION RECORDS

Written records in Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Plug and Badenhorst (2001), indicate that within the study area the greater kudu was recorded in seven biomes – Fynbos, Succulent Karoo, Desert, Nama-Karoo, Grassland, Savanna, Albany Thicket. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 23.

Fynbos Biome

Two written records associated with the Namaqualand Cape Shrublands, a Fynbos Biome outlier in the Kamiesberg area in Namaqualand in the north-west of the study area, indicate its (highly localised) occurrence in this region. Even today (2010s), suitable greater kudu habitat can be found there (AB pers. rec.) Aside from these records, no confirmed written or supporting records for the greater kudu in the Fynbos Biome could be located, this despite a large part of it exhibiting good to reasonable early chronicle coverage (Figure 4). Two written records (just to the north of 34° S and just to the east of 21° E) have “imprecise locality” status and, therefore, they may be associated with the adjacent Rainshadow Valley Karoo Bioregion (of the Succulent Karoo Biome) to the immediate north, where greater kudu could have occurred in riparian zones (see “Succulent Karoo Biome”). Thus, the greater kudu was apparently not a fynbos species.

Succulent Karoo Biome

Several written records in or possibly associated (via “imprecise locality” status) with the eastern part of the Rainshadow Valley Karoo Bioregion suggest the presence of the greater kudu there; these records all lie to the east of 21° E. Given the habitat preferences of this antelope, it is likely that these records represent observations made in riparian woodland or wooded ravines; this is confirmed by information in Skead (2011).

Desert Biome

The single written record from the Gariep Desert Bioregion refers to greater kudu observed along the course of the Orange River, which has a relatively well developed riparian zone, and not in the adjacent true desert.

Nama-Karoo Biome

Several written records indicate the presence of greater kudu in the Lower Karoo Bioregion, where it would have occurred in riparian corridors, and the Bushmanland Bioregion, where the records are from, or close to, the course of the Orange River, with its well-developed riparian zone. The non-existent or poor early chronicle coverage in most of the Bushmanland Bioregion (figures 3 and 4) may have resulted in under-reporting of this ungulate there. However, it is speculated that those areas of this arid bioregion that are away from the Orange River would have offered little suitable habitat.

Even though early chronicle coverage was reasonable in the Upper Karoo Bioregion (Figure 4), only a handful of confirmed written records and a single supporting (zoo-archaeological) record suggest its historical presence there. The possibility that the bulk of this bioregion, together with the central and southern parts of the Bushmanland Bioregion, formed a natural, zoo-geographical, “gap” that separated two “nodes” of occurrence is discussed below.

Grassland Biome

Apart from a single written record from the Dry Highveld Grassland Bioregion, and a supporting (zoo-archaeological) record from the Drakensberg Grassland Bioregion, this biome is devoid of records, of any type. Both of the records mentioned here are likely to be of animals utilising riparian zones within an extensive matrix of open grassland, in flat or rugged terrain.

Savanna Biome

A few written records and a handful of supporting (zoo-archaeological) records indicate its presence in the relatively well-watered Eastern Kalahari Bushveld Bioregion, to the north-east of the Orange River. This savanna type offers large areas of excellent greater kudu habitat. The localities of these records broadly reflect the distribution pattern of the early chronicles in this bioregion (Figure 4). More spatially dispersed such records would probably show the greater kudu to have been widespread there.

No records, of any type, could be located for the arid Kalahari Duneveld Bioregion, to the north-west of the Orange River. Even though early chronicle coverage was poor in this bioregion (Figure 4), it is speculated that the greater kudu was probably absent there, as a resident species, owing principally to the lack of an all-year round supply of surface water, to supplement that obtained from the sparse tree and shrub layers of the vegetation.

The absence of records from the Sub-Escarpment Savanna Bioregion, in the south-eastern part of the study area, is intriguing.

Albany Thicket Biome

A number of written records, supported by two zoo-archaeological records, indicate the occurrence of the greater kudu in this biome, which provides prime habitat for this animal. These include a far westerly record, associated with an outlier of thicket vegetation in the Gouritz River Valley (south of 34° S and just west of 22° E), as well as a few records associated with outliers of thicket vegetation in the Little Karoo and its environs.

Given the excellent early chronicler coverage in a large part of this biome (Figure 4), the number of written records is surprisingly low. The reasons for this are not known, but may include its habit of staying within cover during much of the day, i.e. when travellers on horseback and in wagons were likely to be on the move, and perhaps neglect on the part of the chroniclers to record it owing to its relative commonness.

DISTRIBUTION PATTERNS

(1) The written and supporting records indicate the existence of two distinct distribution nodes within the study area, these being separated by a physical gap of about 250 km. The northern node, located to the north of about 30° S, comprised a population that inhabited, at least, well-watered bushveld (a savanna type) to the north-east of the Orange River and also country in the vicinity of this river where it traverses arid regions. In the case of the latter, this animal's existence was undoubtedly linked to the existence of riparian vegetation associated with the main river and with the lower sections of its tributaries. The isolated population in the Kamiesberg region (about 30°15' S 18° E) of Namaqualand was possibly an extension of that in the vicinity of the Orange River to the north and north-east.

The southern node, located to the south of 32° S and between 21° and 27° E, comprised a population supported by areas or patches of riparian woodland and succulent thicket, including those in the southern Karoo and the Little Karoo and environs, and which extended eastwards to extensive areas of thicket, which provide highly suitable greater kudu habitat. An outlying population, to the south of the Cape Fold Belt and associated with an isolated patch of Albany Thicket vegetation in the Gouritz River Valley, surrounded by the Fynbos Biome, is included in this node.

(2) The absence of confirmed records, of any type, from the region south of 30° S and east of 27° E, where early chronicler coverage is reasonable (Figure 4), and which would seem to offer suitable greater kudu habitat, is intriguing. This may represent a natural zoo-geographical "gap" between the southern node and the population some 600 km to the east, in the vicinity of the Thukela (Tugela) River in today's KwaZulu-Natal Province. The possible reasons for this "gap", which is mirrored by the black rhino (also a browser), require further investigation. This "gap" phenomenon is discussed in some detail by Skead (2007).

ELAND

Tragelaphus oryx (Pallas, 1766)

DISTRIBUTION RECORDS

Written records in Cowan (1808), Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Plug & Badenhorst (2001), Sealy *et al.* (2004), Skead (2007) and Boshoff & Kerley (2013), indicate that within the study area the eland occurred in eight biomes – Fynbos, Succulent Karoo, Desert, Nama-Karoo, Grassland, Savanna, Albany Thicket, Indian Ocean Coastal Belt. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 24.

Fynbos Biome

The presence of the eland in this biome is indicated by several written records that fall within, or possibly within, the West Coast Renosterveld, East Coast Renosterveld, North West Fynbos, South West Fynbos, Karoo Renosterveld and Eastern Fynbos-Renosterveld bioregions. These records are supported by a number of zoo-archaeological records, all from coastal archaeological sites in the South West Fynbos and West Strandveld bioregions.

Succulent Karoo Biome

A number of written records from four (Namaqualand Sandveld, Namaqualand Hardeveld, Knersvlakte, Trans-Escarpment Succulent Karoo) of the six bioregions that constitute this biome indicate the potentially widespread distribution of the eland therein. There is also a zoo-archaeological record from a coastal archaeological site in the Namaqualand Sandveld Bioregion.

Desert Biome

A few records suggest its occurrence in the Southern Namib Desert and Gariiep Desert bioregions, which make up this biome. However, although the localities of these records are "imprecise", it is known that they are associated with the course of the Orange River (Skead, 2011) and therefore, until more information becomes available, the status of the eland as a true desert species remains unconfirmed.

Nama-Karoo Biome

A handful of written records show that the eland occurred along the course of the Orange River and the far eastern parts, in the arid Bushmanland Bioregion. Poor early chronicler coverage in a large part of this bioregion (Figure 4) may have contributed to the relative lack of written records. Numerous written records from the Upper Karoo Bioregion, supported by a zoo-archaeological record, reveal potentially widespread occurrence therein. There are two written records from the Lower Karoo Bioregion.

Grassland Biome

A number of written records, supported by several zoo-archaeological records, from all four of the constituent bioregions (Drakensberg Grassland, Dry Highveld Grassland, Mesic Highveld Grassland, Sub-Escarpment Grassland) suggest its potentially widespread occurrence in this biome.

Savanna Biome

Several written records, supported by a couple of zoo-archaeological records, reveal the presence of the eland in the Eastern Kalahari Bushveld Bioregion, to the north of the Orange River. The single written record from the Kalahari Duneveld Bioregion, to the west of the Eastern Kalahari

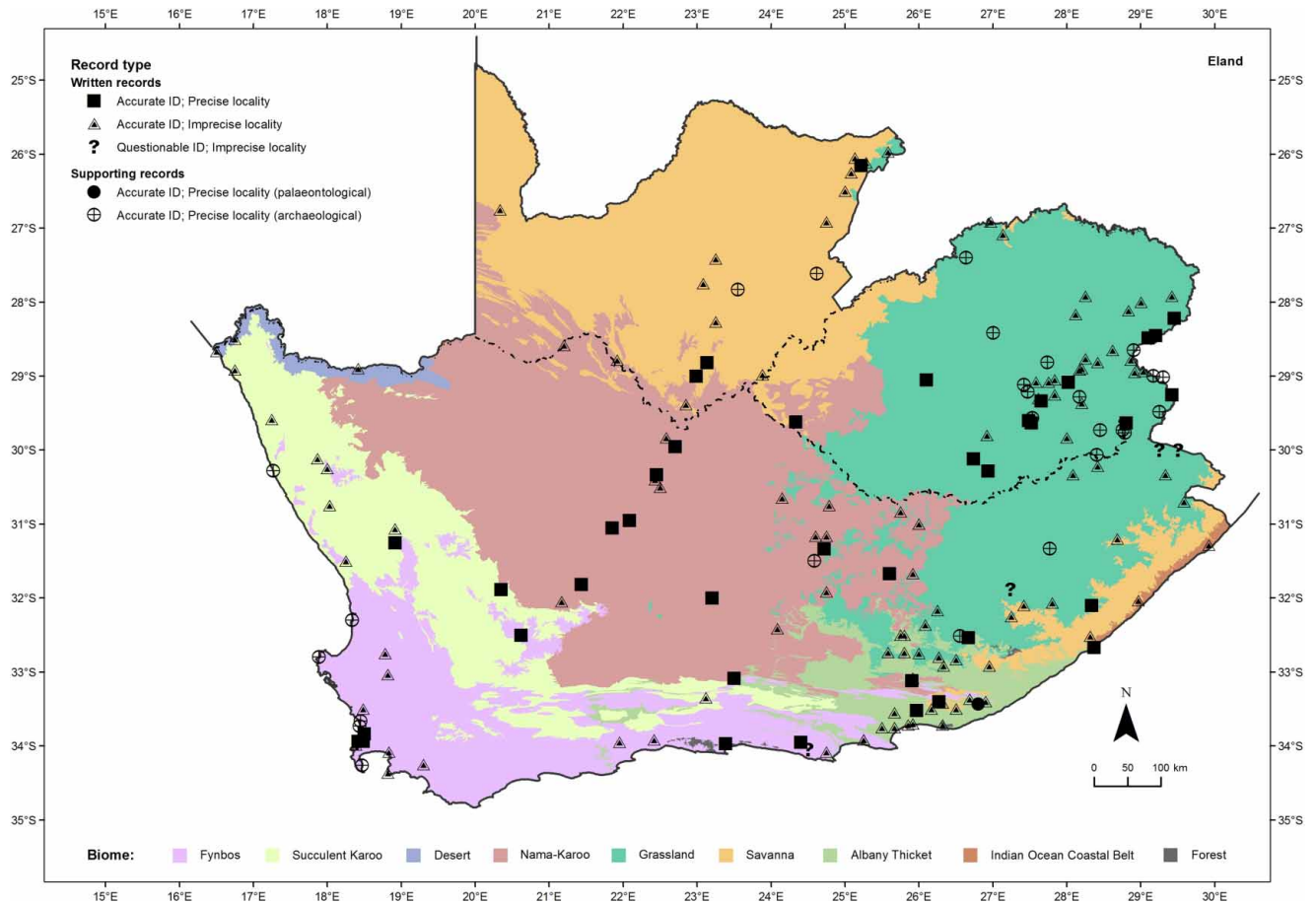


Figure 24. Early historical incidence of the eland: mappable written and supporting distribution records (see the text), and biomes.

Bushveld Bioregion, appears to be associated with an outlier of the latter. The paucity of records from the Kalahari Duneveld Bioregion is thought to result from a combination of poor chronicler cover in this area (Figure 4) and the fact that the eland is nomadic or migratory there (Knight, 1991; Verlinden, 1998). Two written records suggest its presence in the Sub-Escarpment Savanna Bioregion in the south-eastern part of the study area.

Albany Thicket Biome

Numerous written records, supported by a palaeontological record, reveal the occurrence of the eland in the southern and south-eastern parts of this biome. The absence of records from the northern and north-western parts may largely reflect poor early chronicler coverage there (Figure 4), and it is expected to have been present there.

Indian Ocean Coastal Belt Biome

A handful of written records suggest the presence of the eland in this coastal biome.

DISTRIBUTION PATTERNS

(1) Although written and supporting records are few in large parts of the study area, we contend that they suggest that the eland was widespread there (see below). If this contention is correct, then the relative paucity of written records (for a large, ponderous and easily identifiable animal)

from many parts is intriguing, especially given that the coverage of potential chroniclers in most of the study area is good to reasonable (Figure 4). We postulate that the relative lack of records is, perhaps to a large extent, linked to the early overhunting of this easily hunted animal by European colonists and visitors using horses and firearms, and subsequently by native peoples who adopted the use of these same tools, to provide a supply of meat and skins. Because the eland was large and easy to hunt, it was targeted first by modern (post-colonial) hunters.

This postulation is based on information on this topic in the historical literature (collated and discussed in Skead, 2007, 2011 and Boshoff & Kerley, 2013). For example, the very few records from the south-western and western parts of the Fynbos Biome (where early chronicler coverage was generally good) may indicate the very early extermination of this animal as European colonists progressively settled the immediate hinterland of the Cape, starting in the late 1600s.

(2) There is a broad cluster of written records in the hilly and mountainous eastern parts of the Mesic Highveld Grassland Bioregion and the mountainous, adjacent Drakensberg Grassland Bioregion (to the east). It is postulated that this cluster reflects the fact that it was difficult to hunt eland, and to move their large carcasses, in rugged country and that this allowed them to survive here until as late as the early 20th century; this in turn increased their potential to be recorded by chroniclers who

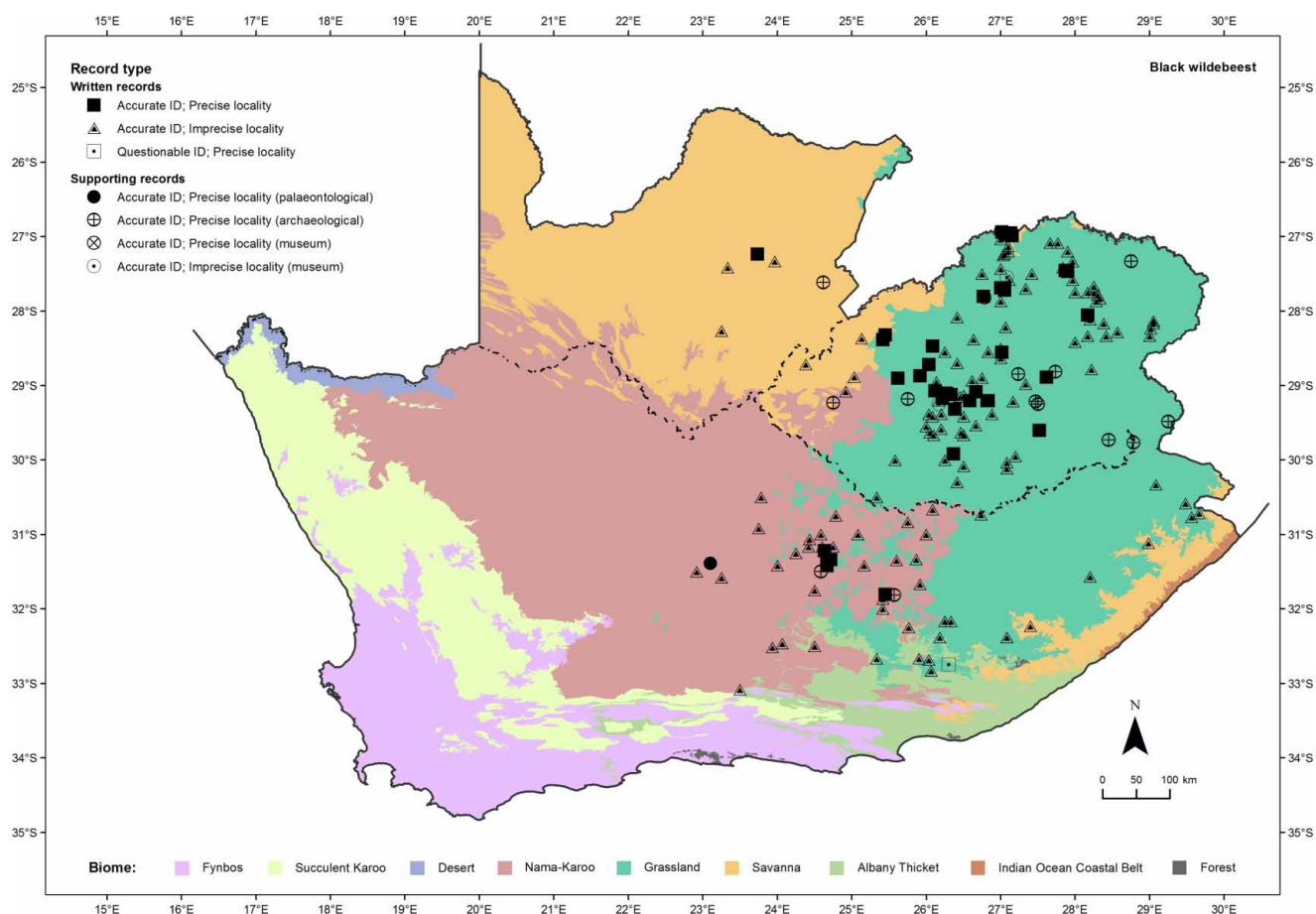


Figure 25. Early historical incidence of the black wildebeest: mappable written and supporting distribution records (see the text), and biomes.

increasingly visited these inhospitable parts during the latter part of the 19th century and the early part of the 20th century (Boshoff & Kerley, 2013).

- (3) Support for the contention that the eland was indeed more common and widespread than is suggested by the information in Figure 24, and by its supporting literature, is provided by a closer examination of the very obvious “trail” of written records that runs from south-west to north-east from the northern part of the Fynbos Biome through the Nama-Karoo Biome and into the Savanna Biome to the north of the Orange River. This trail follows the route of the Truter-Somerville expedition from the Cape to the interior in 1801/2, and of other early literate travellers in the region. The leaders of the Truter-Somerville expedition clearly were diligent chroniclers of some of the larger wildlife that they encountered on route and the number of eland observations made by them (Bradlow & Bradlow, 1979; Skead, 2011), at a time before the wide-scale introduction of firearms to the interior, strongly suggests that this ungulate was widespread in the regions they traversed. This gives the impression that a similar picture may have emerged for other inland parts of the study area, had they been visited by diligent chroniclers around and before 1800.
- (4) The general pattern exhibited in Figure 24 is considered to generally belie the true extent of the distribution of the eland in the study area, i.e. it is considered to have been more widespread than is suggested by the distribution

information at hand. For example, the paucity of records from the Bushmanland Bioregion (Nama-Karoo Biome) and the Kalahari Duneveld Bioregion (Savanna Biome) are believed to largely reflect poor early chronicler cover in these regions (see figures 3 and 4).

BLACK WILDEBEEST

Connochaetes gnou (Zimmermann, 1780)

SWARTWILDEBEEES

DISTRIBUTION RECORDS

Written records in Glyn (1863), Skead (2007, 2011), Boshoff & Kerley (2013) and Crampton *et al.* (2013), together with selected supporting records in Plug & Badenhorst (2001), Skead (2011) and Boshoff & Kerley (2013), indicate that, within the study area, the black wildebeest occurred in three biomes – Nama-Karoo, Grassland, Savanna. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 25.

Nama Karoo Biome

Several written records indicate that the black wildebeest came as far south as the southern and eastern parts of the Lower Karoo Bioregion, and numerous written records, supported by two zoo-archaeological records, show its incidence in the eastern part of the Upper Karoo Bioregion, particularly where it forms a matrix with areas of Grassland Biome. In both of these bioregions, the moister eastern parts possess a

relatively higher grass component, than do the western parts (Mucina *et al.*, 2006a).

Grassland Biome

A large number of written records, along with several supporting records (zoo-archaeological and museum), indicate that the Dry Highveld Grassland and Mesic Highveld Grassland bioregions to the north-east of the Orange River, a region with good early chronicler coverage (Figure 4), served as the stronghold for the black wildebeest. One of the zoo-archaeological records is associated with an offshoot of the Mesic Highveld Grassland Bioregion that penetrates deep into the mountainous terrain via the Senqu (Orange) River Valley.

No written records could be located for the Drakensberg Grassland Bioregion; this is not unexpected since this bioregion, being dominated by rugged, mountainous terrain, does not offer suitable habitat for this plains-living ungulate. The three zoo-archaeological records in this bioregion cannot easily be explained; it is postulated that black wildebeest skeletal elements may have been transported to the archaeological sites in question by humans.

A few written records indicate the presence of this wildebeest in the Sub-Escarpment Grassland Bioregion, in the south-eastern part of the study area.

Savanna Biome

A number of written records, supported by a single zoo-archaeological record, reveal its presence in the Eastern Kalahari Bushveld Bioregion, lying to the north of the Orange River. These records are located within the central part of this bioregion, being the area where early chronicler coverage is relatively good (Figure 4). Had chronicler coverage been better in the eastern part of this bioregion, i.e. towards the ecotone with the Grassland Biome, it may have been shown to be more widespread there. It is postulated that this animal utilised localised areas of short grass within the Eastern Kalahari Bushveld Bioregion, where medium- to tall-grass prevails.

Only a single, written record indicates its presence in (a part of) the Sub-Escarpment Savanna Bioregion.

DISTRIBUTION PATTERNS

- (1) The distribution records confirm the statement by Vrahimis (2013), to the effect that the black wildebeest is a short-grass grazer, primarily of open grassland on the plains of the Highveld plateau, to the north-east of the Orange River. However, they also show that it occurred relatively widely within a matrix comprising components of the Nama-Karoo and Grassland biomes to the south of this river, and in Kalahari bushveld to the north-east of the Vaal River.
- (2) There is some anecdotal and circumstantial evidence to suggest that at least a part of the black wildebeest population on the Highveld undertook aggregated, landscape-level, seasonal movements (migrations), i.e. moving off the cold and dry interior plateau during winter, when the nutritional quality of the grass there was poor (Boshoff & Kerley, 2013). In view of this, the possibility that the distribution records from north-west of the Vaal River and south of the Orange River may, at least to some extent, represent overwintering animals, requires further investigation.
- (3) Records from grassland in the south-eastern part of the study area show that the population occurring to the

west of 26°30' E was linked to that occurring to the east of about 29°30' E, i.e. in today's KwaZulu-Natal Province

BLUE WILDEBEEST

Connochaetes taurinus (Burchell, 1823)

BLOUWILDEBEEES

DISTRIBUTION RECORDS

Written records in Skead (2011) and Boshoff & Kerley (2013), together with selected supporting records in Plug & Badenhorst (2001), Parsons (2008) and Boshoff & Kerley (2013), indicate that within the study area the blue wildebeest occurred in three biomes – Nama-Karoo, Grassland, Savanna. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 26.

Nama-Karoo Biome

A single zoo-archaeological record, and a single written record and two zoo-archaeological records, suggest the occurrence of this ungulate in the Bushmanland and Upper Karoo bioregions, respectively. No further records of this animal from south of the Orange River were found.

Since the blue wildebeest is not a typical Karoo species, it is likely that it was but a visitor to the northerly parts of this biome, perhaps as a nomad or migrant escaping the harsh Highveld winter.

Grassland Biome

There are written records for the blue wildebeest from two bioregions – the Dry Highveld Grassland Bioregion and the Mesic Highveld Grassland Bioregion. Two supporting records (museum specimens) confirm its incidence in the northern part of the Dry Highveld Grassland Bioregion.

It is striking that, despite good early chronicler coverage in the Dry Highveld Grassland and Mesic Highveld Grassland bioregions where these occur to the north-east of the Orange River (see Figures 3 and 4), all the mappable written and supporting records fall within their northerly parts, i.e. country north of 29° S. There are, however, a few (unmappable) written records which make mention of blue wildebeest as far south as the vicinity of the Orange River (Boshoff & Kerley, 2013), in the Dry Highveld Grassland Bioregion. A possible explanation for this pattern may be that this ungulate often occurred in very large aggregations in the northern parts of these two bioregions, which probably increased the likelihood of it being noted by early chroniclers, whereas in the southern parts (i.e. south of about 29° S) it may have occurred as a straggler or in dispersed, small groups (winter migrants from the Highveld?), which in turn probably counted against it being frequently recorded, which it often was where it occurred in spectacularly large aggregations.

No written or supporting records could be found for this plains-living wildebeest in the Drakensberg Grassland Bioregion. This is not unexpected, given that its mountainous terrain provides highly unsuitable habitat. No written or supporting records could be found for the Sub-Escarpment Grassland Bioregion, in the south-eastern part of the study area.

Savanna Biome

All the written records for this biome are from the region to the north of the Orange River. Almost all these records lie in the north-eastern part of this region, i.e. within the relatively well-watered Eastern Kalahari Bushveld Bioregion, which provides typical blue wildebeest habitat. Support for its

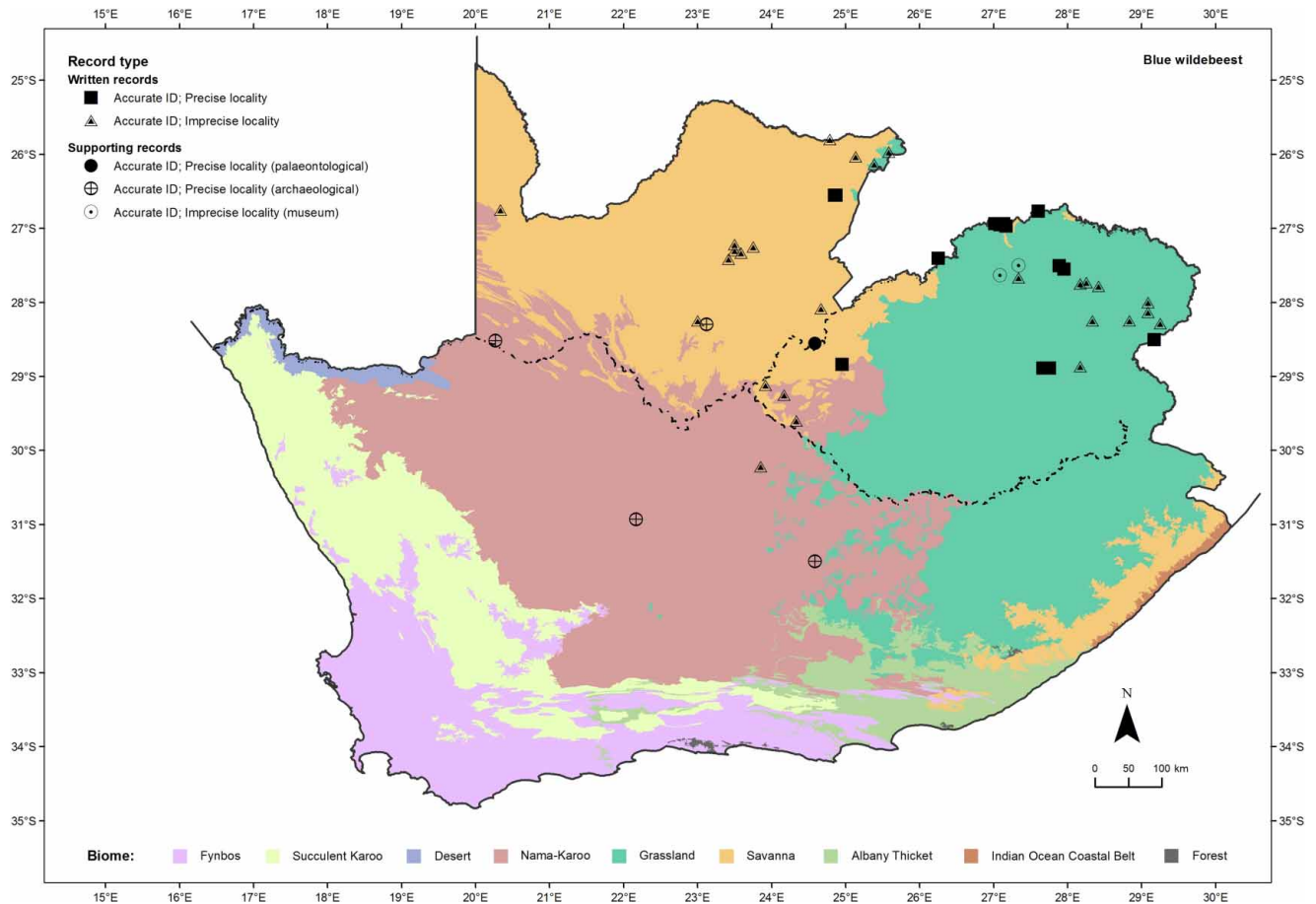


Figure 26. Early historical incidence of the blue wildebeest: mappable written and supporting distribution records (see the text), and biomes.

occurrence in this bioregion is provided by a zoo-archaeological record. The pattern of the records suggests that this wildebeest potentially occurred throughout the Eastern Kalahari Bushveld Bioregion, which was relatively well visited by early chroniclers (Figure 4).

There is only a single written record from the north-western part of this biome in the study area; it falls within an area where outliers of the Eastern Kalahari Bushveld Bioregion occur within a matrix formed by the Kalahari Duneveld Bioregion. The lack of records from the Kalahari Duneveld is believed to reflect a combination of the dearth of 19th century chroniclers (Figure 4) and the general lack of permanent surface water, the latter resulting in its presence here being of a highly ephemeral nature. Research conducted on the black wildebeest in the south-western Kalahari “Desert” has shown that this animal is highly nomadic or migratory in this region (Knight, 1991; Verlinden, 1998), where the rainfall has a strongly seasonal pattern.

DISTRIBUTION PATTERNS

(1) Within the study area the blue wildebeest appears to have been confined largely to flat or undulating grassland and savanna country to the north of the Orange River. Its indicated presence in the northerly parts of the Nama-Karoo Biome is intriguing; these records may reflect nomadic or migratory movements in this arid region. This ungulate reportedly undertook migratory

movements in the grassland-dominated Highveld region (Boshoff & Kerley, 2013).

(2) While the overall distribution pattern reaffirms this ungulate’s traditional status as a typically savanna-living species, this, together with unmapped distribution information in Boshoff & Kerley (2013), clearly shows that it also occurred, often in large aggregations, in open grassland, well away from extensive, savanna-dominated, areas.

RED HARTEBEEST

Alcelaphus buselaphus (Pallas, 1766)

ROOIHARTEBEEES

DISTRIBUTION RECORDS

Written records in Cowan (1808), Glyn (1863), Blaine (1868), Skead (2007, 2011), Boshoff & Kerley (2013) and Crampton *et al.* (2013), together with selected supporting records in Plug & Badenhorst (2001), Sealy *et al.* (2004), Skead (2007, 2011), Parsons (2008) and Boshoff & Kerley (2013), indicate that within the study area the red hartebeest occurred in seven biomes – Fynbos, Succulent Karoo, Desert, Nama-Karoo, Grassland, Savanna, Albany Thicket. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 27.

Fynbos Biome

Written and supporting records provide strong evidence for the occurrence of the red hartebeest in the Fynbos Biome. Notably, these records show that this ungulate occurred in

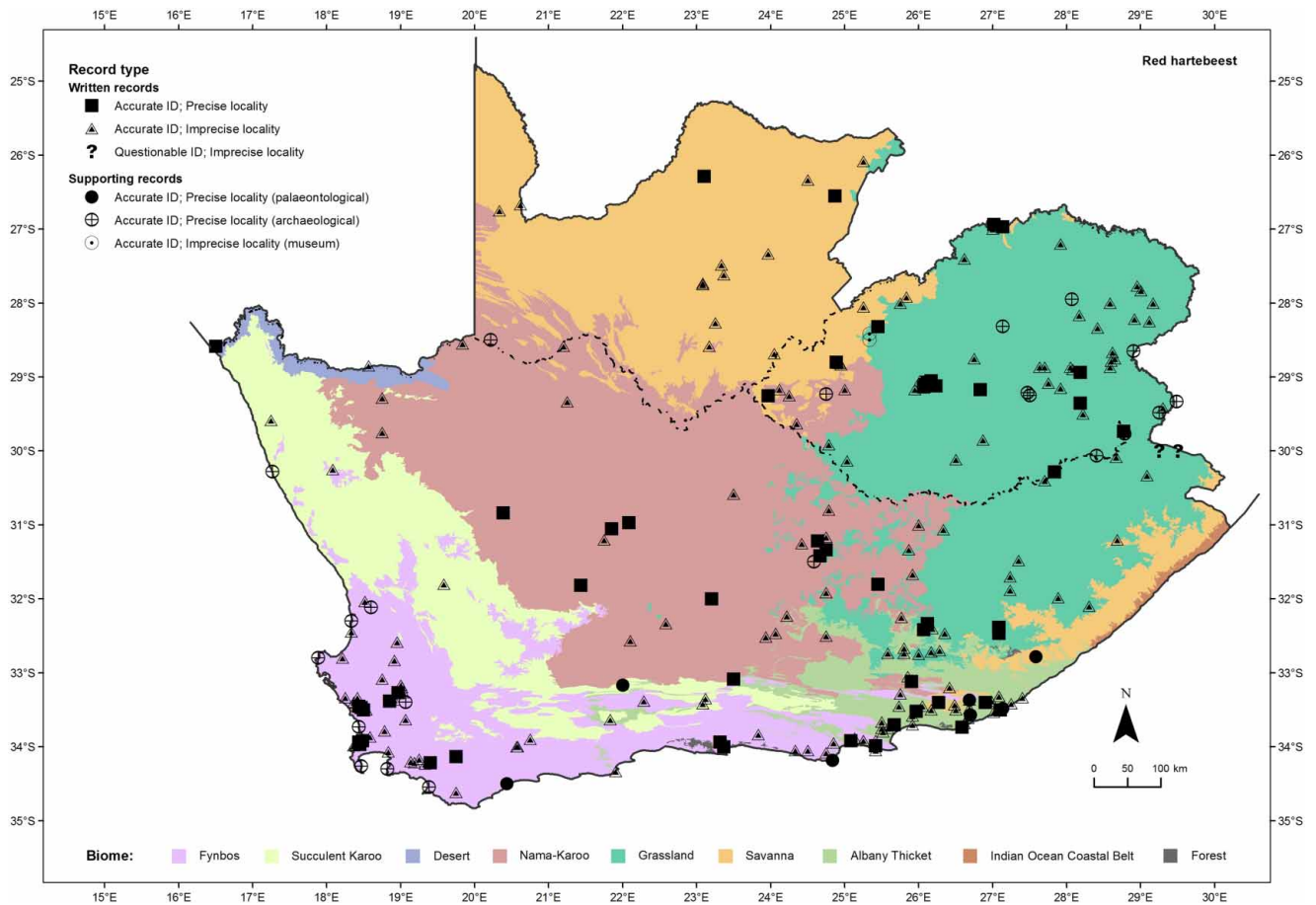


Figure 27. Early historical incidence of the red hartebeest: mappable written and supporting distribution records (see the text), and biomes.

all three major vegetation units that constitute the Fynbos Biome, namely fynbos, renosterveld and strandveld (Rebello *et al.*, 2006). These units incorporate a complex pattern of distinct bioregions (Figure 3). Thus, the red hartebeest appears to have occurred widely in this biome. However, the generally poorly developed grass component of this biome, particularly in the western and south-western parts, is likely to have mitigated against the biome supporting large herds of this ungulate.

Succulent Karoo Biome

Single written and supporting (zoo-archaeological) records from the Namaqualand Sandveld Bioregion, and a handful of written records and a supporting (palaeontological) record from the Rainshadow Valley Karoo Bioregion, indicate the incidence of the red hartebeest in this biome. The very poorly developed, and highly seasonal, grass component of this biome is likely to have resulted in the existence of mainly marginal habitat for this animal.

Desert Biome

There are two written records associated with this biome – one each from the Southern Namib Desert and Gariiep Desert bioregions. However, both records are associated with the course of the Orange River, with its relatively well-developed riparian zone, and therefore they cannot be used to confirm the former presence of this ungulate in these true desert regions.

Nama-Karoo Biome

There are written records from all three constituent bioregions within this biome, *viz.* the Bushmanland, Upper Karoo and Lower Karoo bioregions. In addition, red hartebeest remains were discovered at two archaeological sites, one in the northern part of the Bushmanland Bioregion and one in the Upper Karoo Bioregion. These records suggest that it was potentially widespread in this arid biome.

Grassland Biome

Not unexpectedly, there is strong support from the early record for the occurrence of this predominantly grazing species in the Grassland Biome. There are written records from all four constituent bioregions, *viz.* Dry Highveld Grassland, Mesic Highveld Grassland, Drakensberg Grassland and Sub-Escarpment Grassland bioregions, as well as several zoo-archaeological records from the first three. It would thus appear that the hartebeest was potentially widespread within this biome.

Savanna Biome

A reasonable number of written records, and a zoo-archaeological record, indicate the presence of the red hartebeest in that part of the Savanna Biome that lies to the north of the Orange River. Almost all these records fall within the north-eastern part of this region, *i.e.* within the relatively well-watered Eastern Kalahari Bushveld Bioregion. The pattern of the records suggests that this animal potentially occurred throughout this bioregion.

Two written records suggest its presence in the Kalahari Duneveld Bioregion, lying to the north-west of the Orange River and to the west of the Eastern Kalahari Bushveld Bioregion. However, one of these records may be associated with a western outlier of the Eastern Kalahari Bushveld Bioregion. The lack of records from the Kalahari Duneveld Bioregion is believed to reflect a combination of the dearth of 19th century chroniclers (Figure 4) and the general lack of permanent surface water, the latter resulting in its presence here being of a highly ephemeral nature. Research conducted in the south-western Kalahari "Desert" has shown that this animal is highly nomadic or migratory in this region (Knight, 1991; Verlinden, 1998), where the rainfall has a strongly seasonal pattern.

Only a single palaeontological record (in the far western part) provides support for the former presence of the hartebeest in the Sub-Escarpment Savanna Bioregion in the south-eastern part of the study area. The reasons for the general absence of written records from this bioregion, where early chronicler coverage was reasonable (Figure 4), are not known.

Albany Thicket Biome

There are a number of written records from this biome; these are mainly from the southern parts. In addition, palaeontological records provide support for the former presence of this ungulate in this bioregion. Since the red hartebeest is not considered a typical "thicket" species, it is almost certain that these records refer to predominantly grassy areas within a matrix of thicket vegetation types. In this regard, the Albany Thicket Biome is not homogeneous and incorporates areas of other biomes. The absence of written records in the north-western part of the biome may be, in part, due to poor early chronicler coverage in this region (Figure 4).

DISTRIBUTION PATTERNS

- (1) The red hartebeest was seemingly widespread in the study area. It occurred from the coast to the high mountains, and from arid to high rainfall areas. Not unexpectedly, there is no known record of its former incidence in the Forest Biome, and its occurrence in the Desert Biome is linked to the existence there of the riparian zone of the Orange River.
- (2) The lack of records from the Sub-Escarpment Savanna Bioregion (of the Savanna Biome) in the south-eastern part of the study area, despite the apparent availability of suitable habitat, requires further investigation.
- (3) The absence of records from the Indian Ocean Coastal Belt Biome may reflect the former predominance of forest and dense woodland and thicket in most of the southern part of this biome, i.e. prior to their anthropogenic transformation (by clearing and burning) to secondary grassland (Mucina *et al.*, 2006b).

BONTEBOK and BLESBOK

Taxonomy

Two forms of *Damaliscus pygargus* occur in southern Africa, namely *D. p. pygargus* (bontebok) and *D. p. philippi* (blesbok).

BONTEBOK

Damaliscus pygargus pygargus (Pallas, 1767)

DISTRIBUTION RECORDS

Written records in Skead (2011), together with a selected supporting record in Skead (2011), indicate that within the study area the bontebok occurred within a single biome – Fynbos. Mappable written records and the qualifying supporting record, and the biomes within the study area, are shown in Figure 28.

Fynbos Biome

All the written records, as well as a supporting record (museum specimen, from 1897), indicate that the bontebok was confined to only two bioregions within this winter-rainfall biome – the South Coast Fynbos Bioregion, and inland of it the East Coast Renosterveld Bioregion – with the majority of the records falling within the latter, which possesses the better developed grass component of the two.

DISTRIBUTION PATTERNS

- (1) The most striking pattern for the bontebok is its confinement to a single biome (Fynbos), and to only two of the 12 bioregions that constitute it. Given the reasonable to good early observer coverage in most of the area of the Fynbos Biome (Figure 4), this pattern is considered to realistically represent the distribution of this animal in early historical times.
- (2) The historical ranges of the bontebok and blesbok are separated by a zoo-geographical "gap" of over 350 km.

BLESBOK

Damaliscus pygargus philippi (Harper, 1939)

DISTRIBUTION RECORDS

Written records in Glyn (1863), Blaine (1868), Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Plug & Badenhorst (2001), Skead (2011) and Boshoff & Kerley (2013), indicate that within the study area the blesbok occurred in three biomes – Nama-Karoo, Grassland, Savanna. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 28.

Nama-Karoo Biome

A number of written records, supported by two zoo-archaeological records, indicate the occurrence of the blesbok in the eastern part of the Upper Karoo Bioregion.

A single outlying record (south of 33° S and east of 26° E) is from country where areas of Lower Karoo Bioregion occur within a matrix formed by other biomes and bioregions, in the far southern part of its distribution range in the study area. Since there are no other written records in its general vicinity, an area with good early chronicler coverage (Figure 4), this record may represent a vagrant.

The eastern parts of the Upper and Lower Karoo bioregions, being relatively moist and warm, possess a more developed grass component than do the more arid and colder central and western parts of these bioregions (Mucina *et al.*, 2006a). In addition, the eastern part of the Upper Karoo Bioregion incorporates numerous fragments of the Dry Highveld Grassland Bioregion (Grassland Biome), being one that provides highly suitable blesbok habitat (see below), and some or many of the written records in this part of the Upper Karoo Bioregion (all of which have "imprecise" locality status) may be in or closely associated with these fragments.

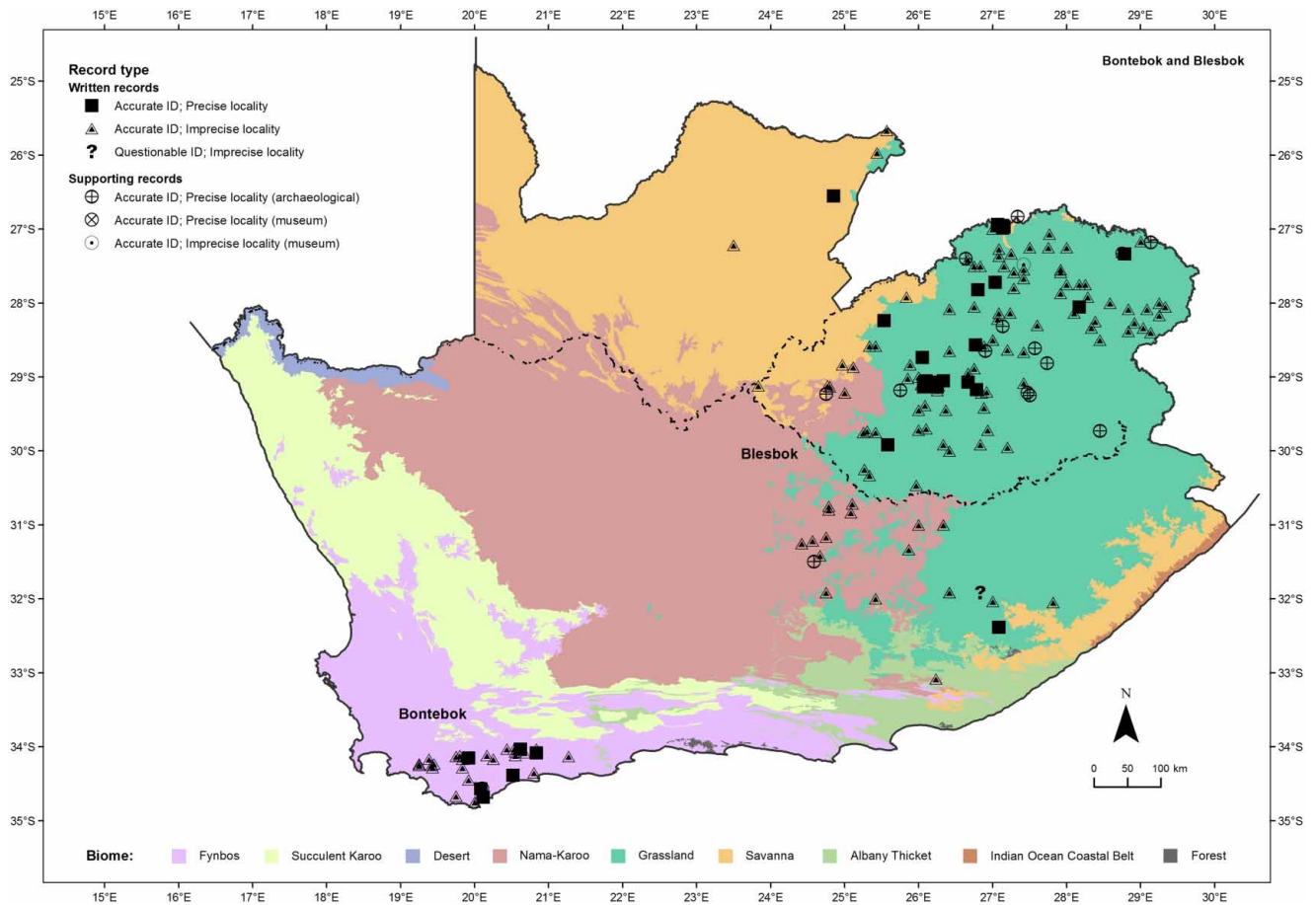


Figure 28. Early historical incidence of the bontebok and the blesbok: mappable written and supporting distribution records (see the text), and biomes.

Grassland Biome

Numerous written records, supported by a number of zoo-archaeological records, indicate that the blesbok was widespread in the Dry Highveld Grassland Bioregion and the Mesic Highveld Grassland Bioregion in the Highveld region to the north-east of the Orange River.

A single zoo-archaeological record attests to its incidence in the Drakensberg Grassland Bioregion. However, this bioregion generally offers unsuitable habitat (mountainous terrain) for this plains species. The archaeological site which contained blesbok remains is very close to the Senqu (Orange) River Valley and its tributaries, where Mesic Highveld Grassland occurs; it is surmised that these remains were taken from there to this site by hunter-gatherers.

Four (possibly five) written records indicate its presence in the western part of the Sub-Escarpment Grassland Bioregion, in the south-eastern part of the study area.

Savanna Biome

A handful of written records reveals the presence of the blesbok in the Eastern Kalahari Bushveld Bioregion, to the north-east of the Orange River. The paucity of records from this bioregion, despite parts of it having relatively good early chronicle coverage (Figure 4), are postulated to reflect a paucity habitat for this short-grass grazer in a bioregion dominated by medium- to tall-grass. Thus, it may have occurred

there on an ephemeral basis, exploiting patches of temporarily suitable grassland (perhaps utilised mainly as a winter refuge from the Highveld, to the east?)

DISTRIBUTION PATTERNS

- (1) The stronghold of the blesbok in the study area was on the grassland-dominated plains to the north of the Orange River, which form the central and southern section of that part of the Highveld region (1200–2100 m.a.m.s.l.) lying south of the Vaal River and north-west of the Caledon River.
- (2) The blesbok is one of the ungulate species that migrate in large aggregations (Harris *et al.*, 2009) and there is reference to it being migratory in the Highveld region and adjacent areas (Boshoff & Kerley, 2013). Hence, it is speculated that the possibly small population in the Kalahari bushveld to the north-west of the Vaal River, and the much larger population to the south of the Orange River, may represent, to an unknown extent, animals undertaking seasonal migrations in order to escape the cold and dry Highveld winters, when the nutritional quality of the grass there was poor. The black wildebeest, also a short-grass grazer principally of the Highveld, may exhibit similar movement patterns. This aspect requires further research.
- (3) The possible reasons for the lack of records from east of 28° E in the Sub-Escarpment Grassland Bioregion, in the

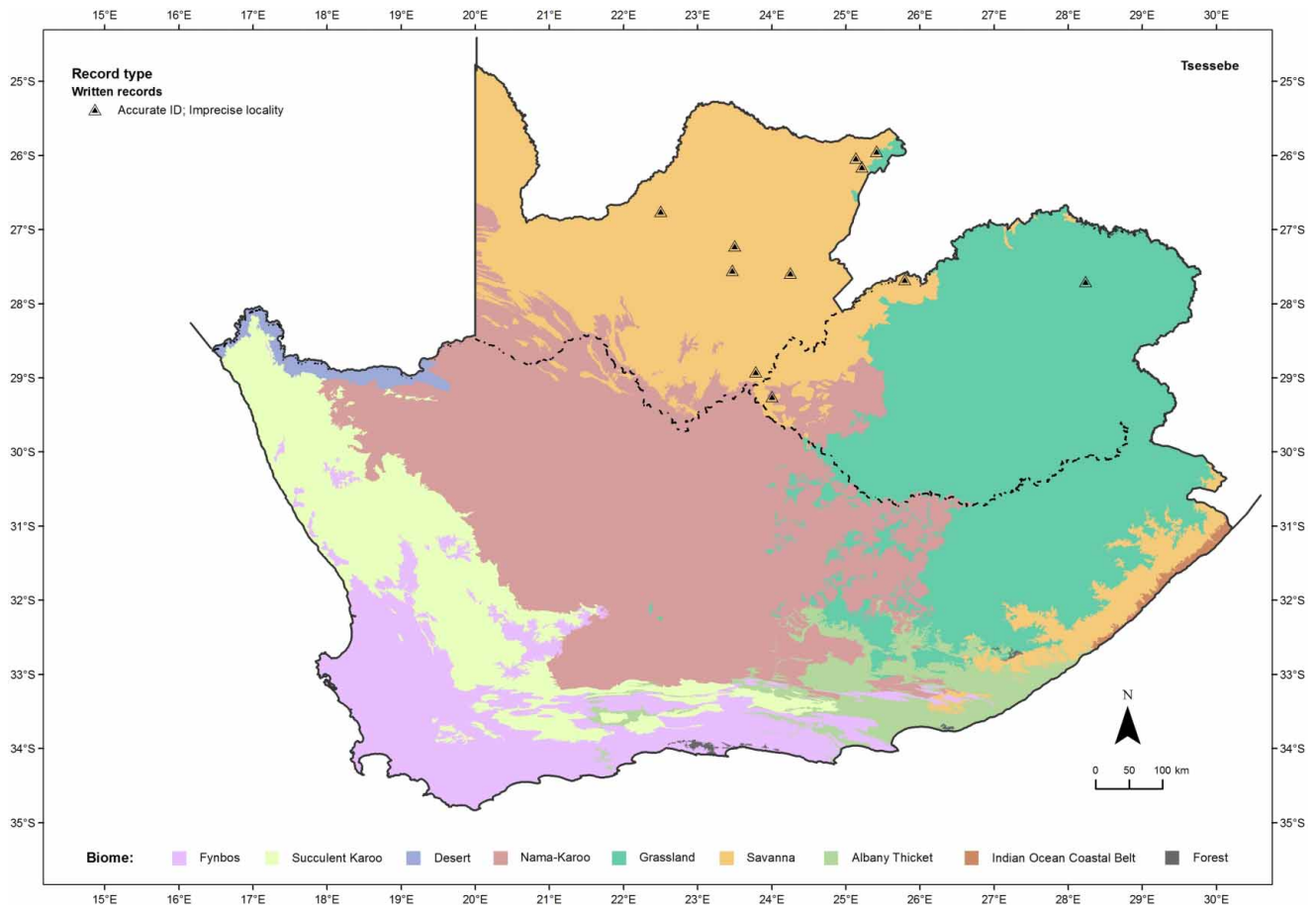


Figure 29. Early historical incidence of the tsessebe: mappable written and supporting distribution records (see the text), and biomes.

south-eastern part of the study area, are not known. Being a short-grass grazer, the medium to tall grassland that is prevalent in this region would not have suited the blesbok. (4) The ranges of the bontebok and blesbok were separated by a “gap” of over 350 km.

TSESSEBE

Damaliscus lunatus (Burchell, 1823)

DISTRIBUTION RECORDS

Written records in Skead (2011) and Boshoff & Kerley (2013) indicate that within the study area the tsessebe occurred in two biomes – Grassland, Savanna. Mappable written records, and the biomes within the study area, are shown in Figure 29.

Grassland Biome

The single written record from the Mesic Highveld Grassland Bioregion is intriguing. It was made by the Swedish naturalist and hunter Johan August Wahlberg (Craig & Hummel, 1994) in October 1841. Since Wahlberg is considered to have been a reliable observer and chronicler, it is considered unlikely that the record represents a misidentification. If the identification is indeed correct, the observed animal may have been a vagrant.

Despite relatively good early chronicler coverage in the northern part of the Grassland Biome, within the study area (Figure 4), no further tsessebe records could be located. This suggests that it was uncommon or perhaps a temporary visitor to these parts.

Savanna Biome

A number of written records suggest that it was widespread in the Eastern Kalahari Bushveld Bioregion, north of the Orange River, this being a region that offers excellent tsessebe habitat. The early chronicler coverage in the eastern and western parts of this bioregion is relatively poor (Figure 4) and, had this not been the case, it is possible that it might have been shown to be more widespread there.

DISTRIBUTION PATTERNS

The distribution pattern indicated for the tsessebe in the study area is unequivocal – its stronghold was the Eastern Kalahari Bushveld Bioregion (a savanna type), to the north of the Orange River. The single record in grassland, and some way to the east of this bioregion, may refer to a nomad or vagrant; the validity of this record is discussed by Boshoff & Kerley (2013).

ROAN

Hippotragus equinus (E. Geoffrey Saint-Hilaire, 1803)

BASTERGEMSBOK

DISTRIBUTION RECORDS

Written records in Skead (2011) and Boshoff & Kerley (2013), together with selected supporting records in Plug & Badenhorst (2001), indicate that within the study area the roan occurred in three biomes – Nama-Karoo, Grassland, Savanna. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 30.

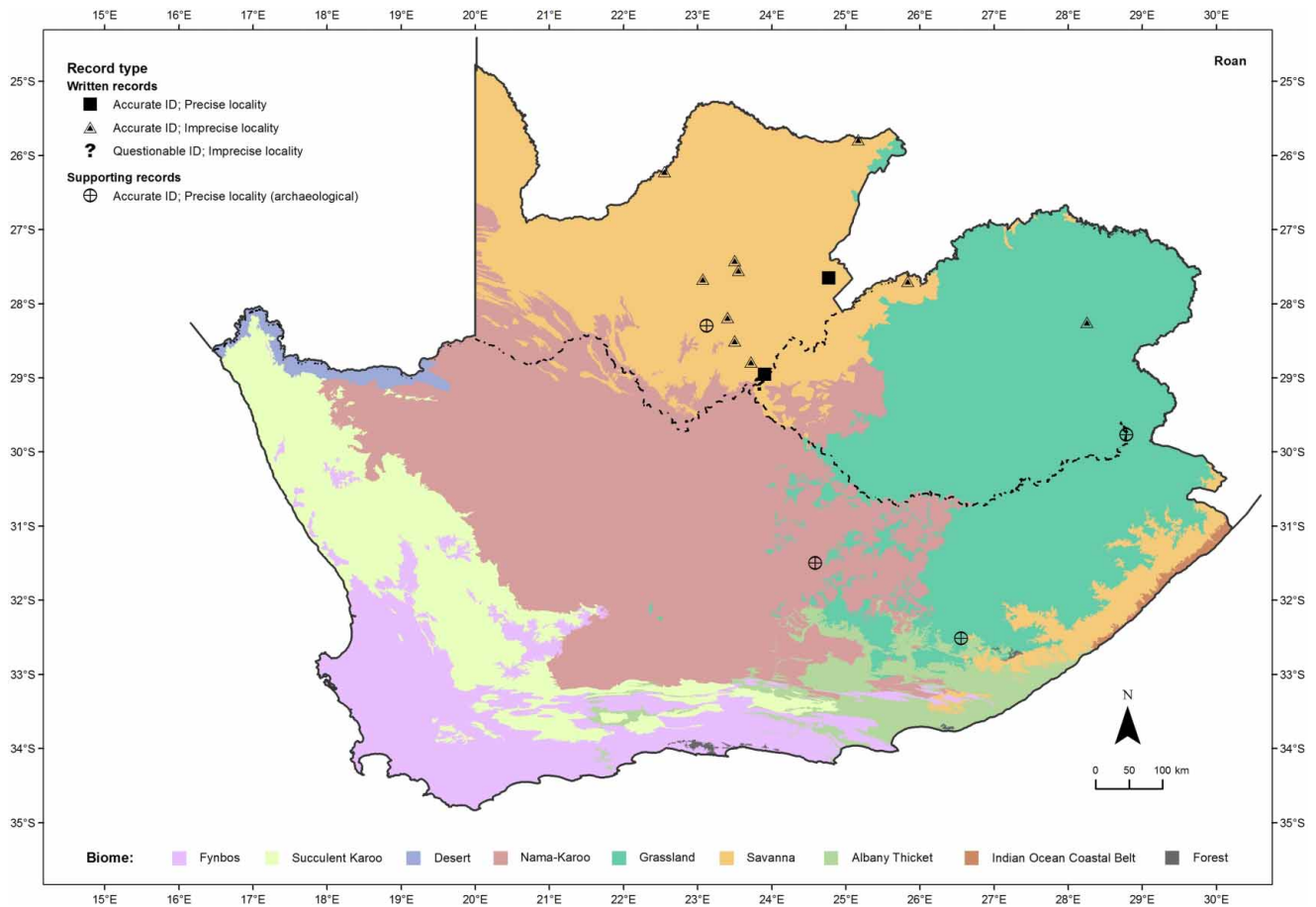


Figure 30. Early historical incidence of the roan: mappable written and supporting distribution records (see the text), and biomes.

Nama-Karoo Biome

A single zoo-archaeological record (comprising a very low number of skeletal elements) suggests the incidence of this ungulate in the Upper Karoo Bioregion (see “Distribution patterns”).

Grassland Biome

A single written record, and a single zoo-archaeological record (from a site near the head of the Orange (Senqu) River Valley), reveal its presence in the Mesic Highveld Grassland Bioregion. It has been suggested (Colahan, 1990) that the written record could have referred to the blue antelope *Hippotragus leucophaeus* but this is considered unlikely (Boshoff & Kerley, 2013; blue antelope account in this paper), and there is no further support in the scientific literature.

A single zoo-archaeological record (comprising a very low number of skeletal elements) from a valley in the far southern part of the Drakensberg Grassland Bioregion suggests its occurrence in this biophysical unit (see “Distribution patterns”).

Savanna Biome

A number of written records, supported by a single zoo-archaeological record, show that this ungulate occurred in the Eastern Kalahari Bushveld Bioregion, north of the Orange River; this bioregion provides suitable roan habitat. Early chronicler coverage in large parts of the eastern and

western Eastern Kalahari Bushveld Bioregion is relatively poor (Figure 4) and, had this not been the case, this animal would possibly have been shown to be more widespread in this bioregion.

DISTRIBUTION PATTERNS

- (1) The zoo-geographical pattern indicated for the study area is unequivocal – the stronghold for the roan during the period under study was the Eastern Kalahari Bushveld Bioregion (of the Savanna Biome), to the north of the Orange River.
- (2) Four widely dispersed records (one written and three zoo-archaeological) that fall outside the Eastern Kalahari Bushveld Bioregion are intriguing, especially since the habitats in the areas where they were made would not normally be associated with this animal. These records need to be viewed within the context of the possibility that the range of the roan in southern Africa may have been wider than is traditionally thought. In particular, it is believed that this animal may have occurred further southwards than was previously thought (Skead, 2011; Chardonnet & Crosmary, 2013). If the four records under discussion are valid they would provide support for this view.
- (3) An argument has been made for accepting that a specimen of a hippotragine-type ungulate, acquired by the soldier/explorer/naturalist Robert Jacob Gordon near Plettenberg

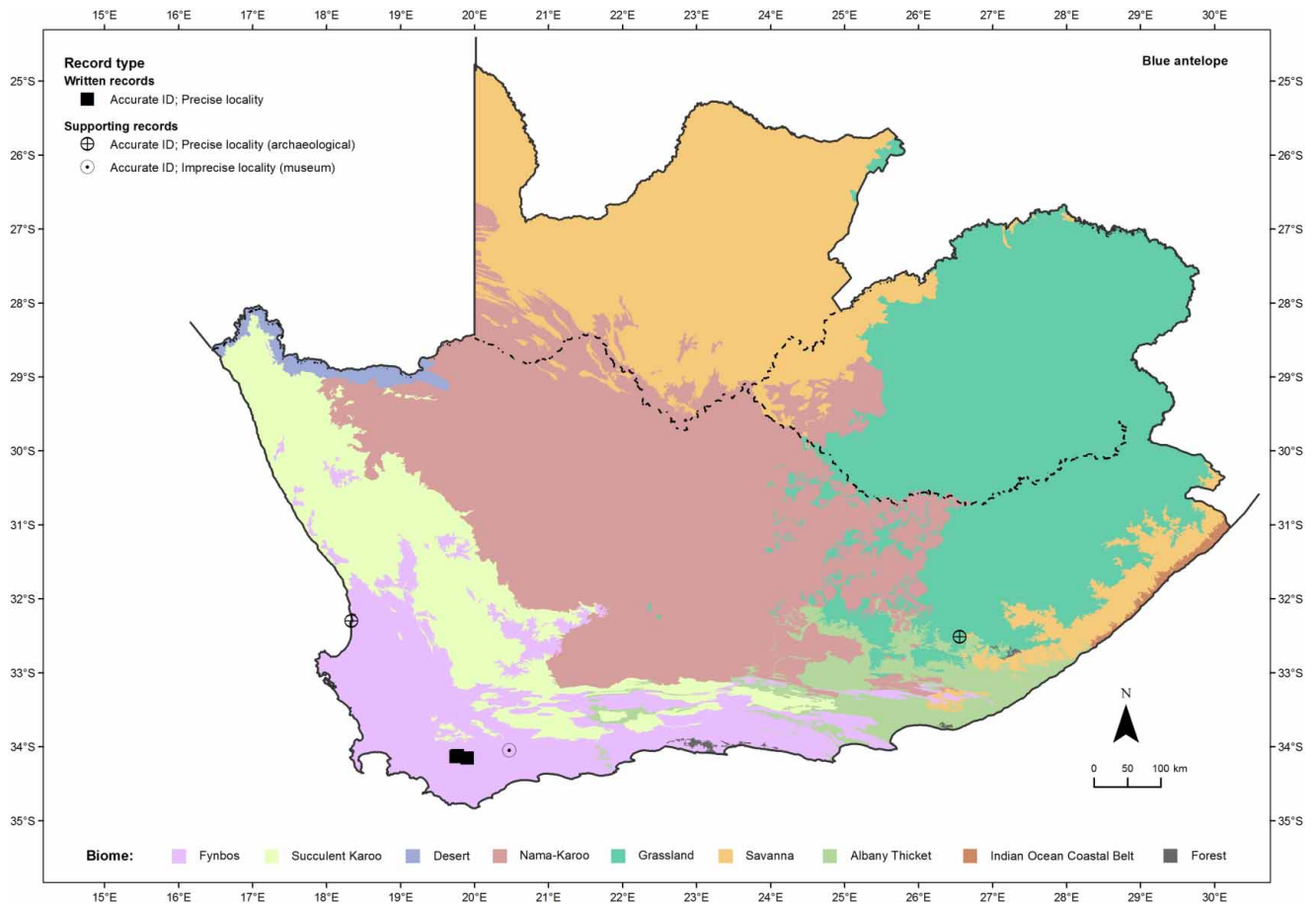


Figure 31. Early historical incidence of the blue antelope: mappable written and supporting distribution records (see the text), and biomes. This ungulate went extinct around 1800.

Bay (34°03' S 23°22' E) on the Southern Cape coast in 1778 (Rookmaaker, 1989) is that of a roan (Faith, 2012). This possibility is also discussed by Mohr (1967) and Klein (1974). The habitat in the vicinity comprises a patchwork of grassy fynbos and forest; the former is more likely to have supported this grazer. Owing to the fact that a reasonable element of doubt about the true identity of this specimen, and its provenance, still exists, it has not been mapped in Figure 30. Should it be shown to be valid then it, together with the two zoo-archaeological records from south of the Orange River could provide support for the view that this antelope occurred as far south as the Southern Cape coast, perhaps until as recently as the late 1700s. However, despite reasonable to good early chronicler coverage in much of the region to the south of the Orange River (Figure 4), no written records for the roan have come to light and therefore the written record does not support the presence of a population there, at least during the early historical period. Alternatively, if a population did indeed exist near Plettenberg Bay as late as the 1770s, it must have been extremely small (a mere handful of individuals?) and possibly in an extinction vortex situation, i.e. similar to its extinct congener *H. leucophaeus*, the global range of which contracted to a small area in the southern part of the Fynbos Biome, prior to going extinct around 1800 (Kerley *et al.*, 2009).

BLUE ANTELOPE

Hippotragus leucophaeus (Pallas, 1766)

BLOUBOK

DISTRIBUTION RECORDS

Mappable and unmappable written records collated in Skead (2011), as well as selected supporting records in Plug & Badenhorst (2001), indicate that, within the study area, the blue antelope occurred in two biomes – Fynbos, Grassland – during the period under consideration (Figure 31). Supporting records provided by palaeontological material from the Holocene period (listed in Klein, 1974) have not been mapped, owing to uncertainty about whether they date to the later Holocene (up to 4000 years BP).

Fynbos Biome

Two written records from the East Coast Renosterveld Bioregion, a single specimen record from the Southern Fynbos Bioregion, and a zoo-archaeological record from the coast in the West Strandveld Bioregion, provide evidence for the incidence of this antelope in this biome.

Nama-Karoo Biome

Roberts (1951) mentions a “Karoo blue antelope” (*Ozanna aethiopica*), which was described by HR Schinz, based on a painting made (prior to 1805) by artist Samuel Daniell (Daniell, 1805). This animal is said to have been recorded in arid Karoo plains habitat. However, the possibility that the

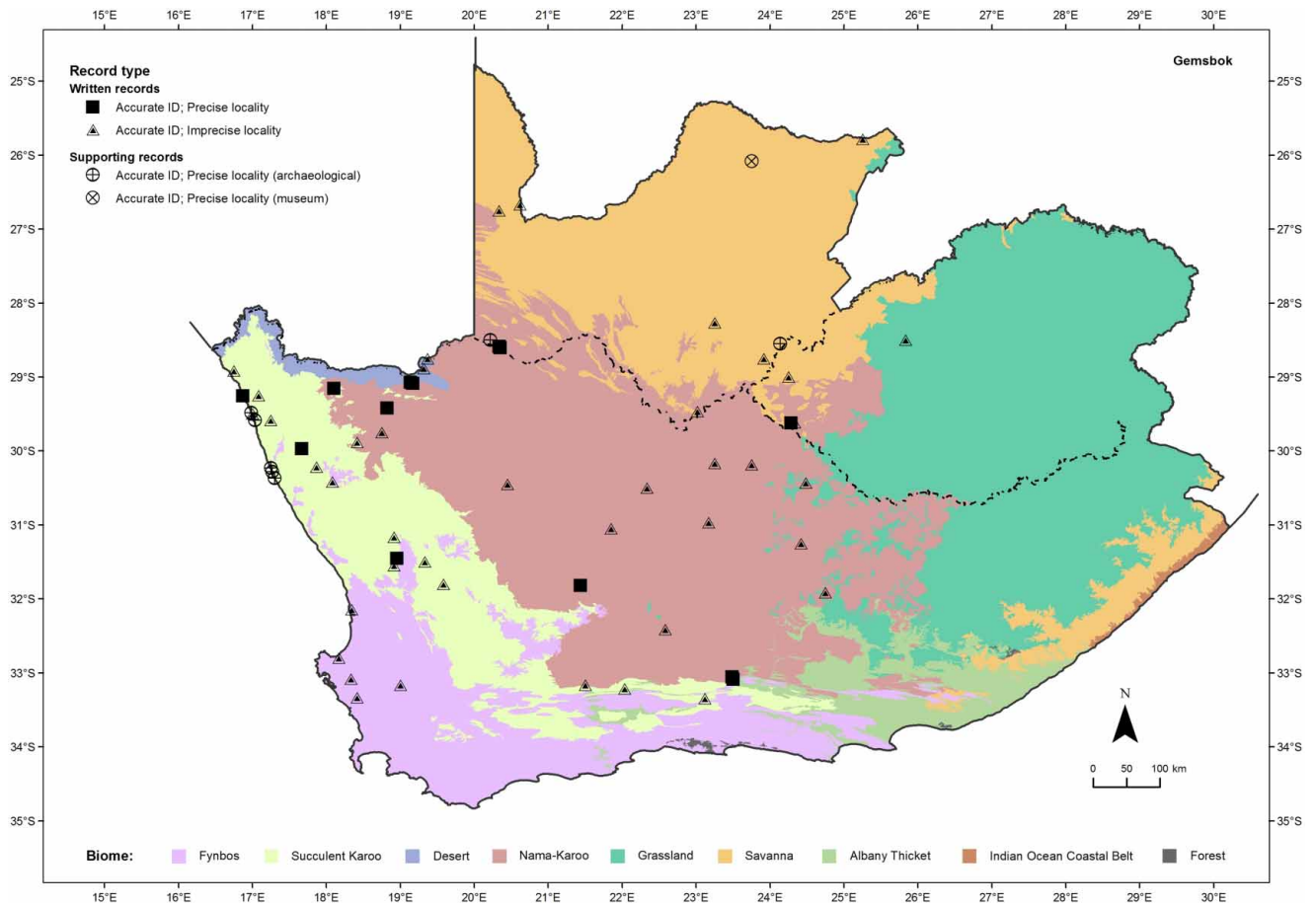


Figure 32. Early historical incidence of the gemsbok: mappable written and supporting distribution records (see the text), and biomes.

animal depicted by Daniell was a blue antelope is discounted by Skead (2011).

Grassland Biome

There is a zoo-archaeological record from the Drakensberg Grassland Bioregion, in the south-eastern part of the study area.

It has been suggested (Colahan, 1990) that a written record of "... a troop of about ten or twelve bastard gemsbok ..." exhibiting "... a bluish-grey colour" (Schoeman, 1988) from the Mesic Highveld Grassland Bioregion and far to the north of the Orange River may in fact refer to a group of blue antelope. This possibility is discussed by Boshoff & Kerley (2013) who consider, for a number of reasons, it unlikely. In addition, information given in the roan account reveals that this ungulate (roan) occurred in non-savanna areas.

DISTRIBUTION PATTERNS

(1) Although palaeontological and zoo-archaeological records suggest that in the pre-historical period the blue antelope had a fairly wide distribution in the Fynbos Biome, and also that its range extended to parts of the Grassland Biome in the high interior (Kerley *et al.*, 2009), the written record shows that during the early historical period, and prior to it going extinct around 1800 (Figure 31; Kerley *et al.*, 2009, and the references therein), this ungulate had an extremely limited distribution, being confined within a small area centred on today's neighbouring towns of

Riviersonderend and Swellendam, in the south-western part of the Fynbos Biome.

(2) Although it has been indicated (Lichtenstein, 1812) that prior to 1800 the blue antelope occurred in the environs of the Ladismith Karoo, over the Langeberg and north-east of Swellendam, no sightings or material records that provide confirmation of this have yet been discovered.

GEMSBOK

Oryx gazella (Linnaeus, 1758)

DISTRIBUTION RECORDS

Written records in Cowan (1808), Simon (1959), Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Plug & Badenhorst (2001), Dewar (2008) and Orton *et al.* (2011), indicate that within the study area the gemsbok occurred within six biomes – Fynbos, Succulent Karoo, Desert, Nama-Karoo, Savanna, Grassland. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 32.

Fynbos Biome

A handful of written records are associated with the West Strandveld, Southwest Fynbos and West Coast Renosterveld bioregions. Although dominated by mountainous terrain, the Southwest Fynbos Bioregion incorporates large areas of open, sandy country (sandveld) which would have provided suitable gemsbok habitat. Some of the records are associated

with the West Strandveld Bioregion, which also could have provided suitable habitat. Thus, according to the locations of the records at hand, it appears that the gemsbok was limited to the arid north-western part of this biome, where it occurred as far south as about 33°30' S.

Succulent Karoo

A few written records indicate its presence in the Rainshadow Valley Karoo, Knersvlakte, Trans-Escarpment Succulent Karoo and Namaqualand Hardeveld bioregions. Written records, supported by zoo-archaeological records, reveal its incidence in the Namaqualand Sandveld Bioregion.

Notwithstanding the fact that relatively few records could be located, it would appear that the gemsbok was widespread in this arid biome.

Desert Biome

Three written records in the far eastern part of the Gariep Desert Bioregion, all of which are close to the interface between this bioregion and adjacent Bushmanland Bioregion (Nama-Karoo Biome) to the south, indicate the presence of this ungulate in this highly arid area.

Nama-Karoo Biome

A number of written records reveal its occurrence in all three bioregions that constitute the arid Nama-Karoo Biome, namely Bushmanland, Upper Karoo and Lower Karoo. The absence of written records for the greater part of the Bushmanland Bioregion probably reflects, to a large extent, poor early chronicle coverage in this region (Figure 4).

Grassland Biome

The record for the Grassland Biome is extremely weak, with only a single written record from the Dry Highveld Grassland Bioregion, where it occurs to the north of the Orange River. There is a written record to the south of the Orange River and where patches of Dry Highveld Grassland Bioregion exist in a matrix of Upper Karoo Bioregion (Nama-Karoo Biome); owing to the "imprecise" status of this record it is not known into which of these two bioregions it falls. The paucity of records in the relatively well travelled (by early chroniclers – see Figure 4) Grassland Biome suggests that it may have been a nomad or vagrant there.

Savanna Biome

A handful of written records, together with two supporting records, indicate the occurrence of this ungulate in the Eastern Kalahari Bushveld Bioregion, to the north of the Orange River. One of the written records may be associated with a far western outlier of the Eastern Kalahari Bushveld Bioregion within the Kalahari Duneveld Bioregion, to the west of the Eastern Kalahari Bushveld Bioregion, for which a single written record could be located.

The paucity of written records from the Kalahari Duneveld Bioregion is considered largely a reflection of the poor early chronicle coverage in this region (Figure 4). The gemsbok does not undertake major seasonal movements in the Kalahari "Desert" (Knight, 1991; Verlinden, 1998) and it is postulated that it was more widespread in the Kalahari Duneveld Bioregion than is indicated on the distribution map.

DISTRIBUTION PATTERNS

The pattern of records confirms that the gemsbok is principally an animal of the semi-arid to arid regions in the

central, northern and western parts of the study area (compare Figures 2 and 32). As such, it was absent from the moister eastern, north-eastern and south-eastern parts of this area (i.e. east of about 25° E), and from relatively well-watered country to the south of the west-east axis of the Cape Fold Belt (i.e. south of about 33°30' S). It is considered to have been more widespread in the north-western Nama-Karoo Biome (comprising the Bushmanland Bioregion) and the western part of the Savanna Biome to the north of the Orange River (formed by the Kalahari Duneveld Bioregion) than is indicated by the records on Figure 32; early chronicle coverage was poor in these two bioregions (Figure 4).

SOUTHERN REEDBUCK

Redunca arundinum (Boddaert, 1785)

RIETBOK

DISTRIBUTION RECORDS

Written records in Skead (2007, 2011), Boshoff & Kerley (2013) and Crampton *et al.* (2013), together with selected supporting records in Plug & Badenhorst (2001), Skead (2007) and Boshoff & Kerley (2013), indicate that within the study area the southern reedbuck occurred in five biomes – Nama-Karoo, Grassland, Savanna, Albany Thicket, Indian Ocean Coastal Belt. Its occurrence in a sixth biome – Fynbos – is questionable. However, the occurrence of this medium-sized herbivore is not primarily linked to the various, broad, biophysical factors that define the broad biomes, and their constituent bioregions, but rather to individual, localised, areas of suitable specialised (moist, grassy) habitat, available year-round, within these units.

Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 33. Despite good to fairly good early chronicle coverage in many parts of the study area (Figure 4), relatively few written records could be located for this ungulate. This is considered to reflect a combination of factors, notably its medium-size, its coat colour, its similarity to other similar-looking antelope, and, especially, its specialised habitat preference, all of which must have made its detection and identification by early chroniclers rather difficult.

DISTRIBUTION PATTERNS

- (1) The historical occurrence of the southern reedbuck in the south-western part of the study area is hinted at by two written records. However, since in neither of these cases could the identity of the animals observed be confirmed, its incidence in this region remains unproven.
- (2) Its distribution appears to be confined to country to the east of 25° E, which falls broadly within the medium- to high-rainfall area of the study area (Figure 2). Here it occurred, or potentially occurred, in localised patches or areas of suitable habitat, wherever these occurred within the five biomes listed above. It would have been absent from true forests, dense woodland and thicket, and the high mountains.

MOUNTAIN REEDBUCK

Redunca fulvorufula (Afzelius, 1815)

ROOIRIBBOK

DISTRIBUTION RECORDS

Written records in Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Plug &

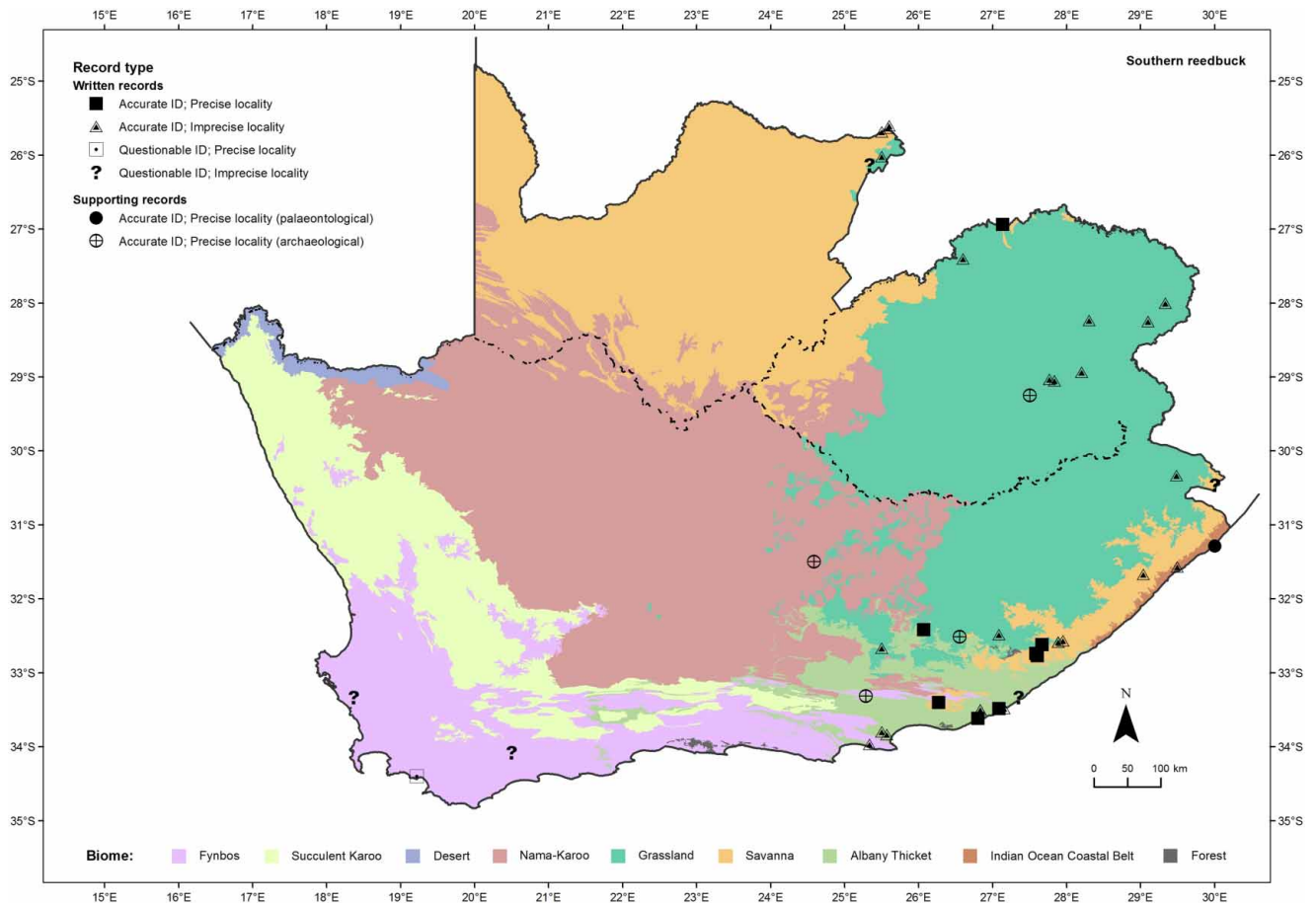


Figure 33. Early historical incidence of the southern reedbuck: mappable written and supporting distribution records (see the text), and biomes.

Badenhorst (2001), Parsons (2008) and Boshoff & Kerley (2013), indicate that within the study area the mountain reedbuck occurred in five biomes – Fynbos, Nama-Karoo, Albany Thicket, Savanna, Grassland. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 34.

That relatively few written records could be located for this ungulate is believed to reflect a combination of factors, notably its medium-size, its unremarkable coat colour, its similarity to other similar-looking antelope, and its habitat preferences, all of which must have made its detection and identification by early chroniclers problematic.

The fact that zoo-archaeological records outnumber written records possibly reflects high levels of utilisation of this animal by pre-colonial inhabitants. This view is supported by an analysis that shows that mountain reedbuck remains were found in archaeological samples from all five time periods between 4000 years BP and the Recent period (Plug & Badenhorst, 2001).

Fynbos Biome

The single zoo-archaeological record, involving a very low number of skeletal elements, from this biome must be treated with caution, given that it is not supported by any other records, of any type, in a part of the study area that had reasonable to good early chronicler coverage (Figure 4).

Nama-Karoo Biome

Two written records, supported by two zoo-archaeological records, indicate the occurrence of this ungulate in the far eastern parts of the Upper Karoo Bioregion, while a single written record suggests its incidence in the eastern part of the Lower Karoo Bioregion. Its occurrence in the eastern parts of these two bioregions is considered feasible, given that they possess a relatively well developed grass component, compared to that of the central and western parts (Mucina *et al.*, 2006a).

The single zoo-archaeological record from the south-eastern part of the arid Bushmanland Bioregion should be treated with circumspection. It is not supported by any other records, of any type, from this bioregion, although it must be said that early chronicler coverage in most of this bioregion was very poor (Figure 4). The region's aridity would mitigate against its occurrence there.

Grassland Biome

A number of written records, together with several zoo-archaeological records, indicate the presence of this animal in the Dry Highveld Grassland, Mesic Highveld Grassland and Drakensberg Grassland bioregions. Owing to its fairly specialised habitat requirements, its incidence in the first two bioregions would have been of a highly patchy nature, whereas in the latter bioregion it was potentially widespread.

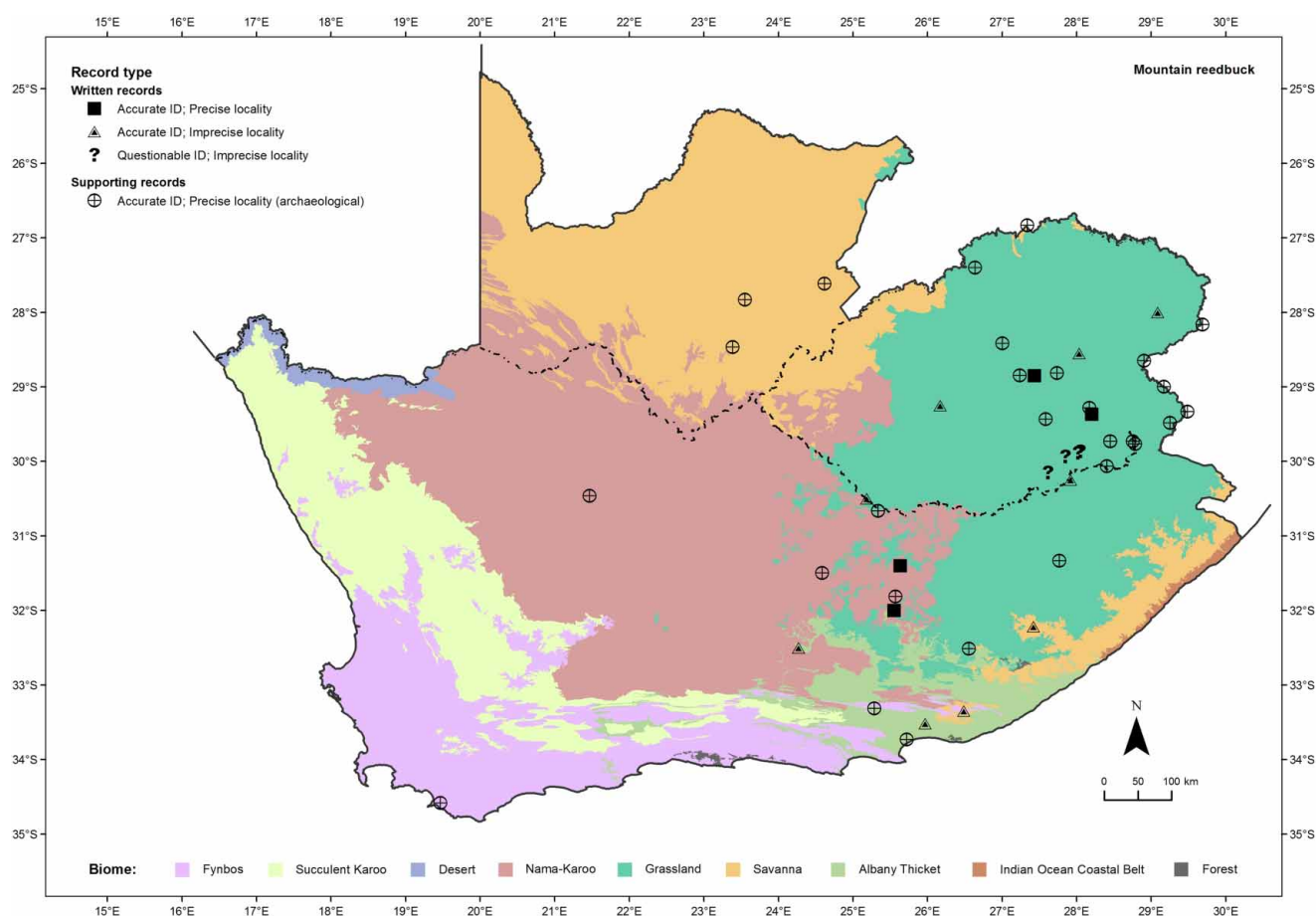


Figure 34. Early historical incidence of the mountain reedbuck: mappable written and supporting distribution records (see the text), and biomes.

Savanna Biome

Three zoo-archaeological records indicate its occurrence in the Eastern Kalahari Bushveld Bioregion, to the north of the Orange River. Here it would have been confined to areas incorporating broken topography, and therefore cannot be expected to have been widely distributed in this bioregion. A single written record hints at its incidence in the western part of the Sub-Escarpment Savanna Bioregion, in the south-eastern part of the study area.

Albany Thicket Biome

Despite good early observer coverage in a large part of this biome (Figure 4), only a couple of written records for it could be located. These are supported by two zoo-archaeological records.

The mountain reedbuck is not a true “thicket” species and therefore it would probably have occurred only in rather limited patches of suitable habitat (rocky, grass-dominated slopes) where they occur in a thicket matrix within this biome.

DISTRIBUTION PATTERNS

(1) While the written records indicate that this ungulate occurred in the eastern and south-eastern parts of the study area (i.e. east of about 24° E), the supporting records (zoo-archaeological) suggest that it had a somewhat wider distribution during the late pre-historical period.

- (2) The region encompassed by the written records is characterised by medium- to high-rainfall (Figure 2), a relatively well-developed grass component (Mucina & Rutherford, 2006), and abundant rocky hillslopes. The distribution of this antelope would have been patchy or discontinuous in extensive, flat areas.
- (3) The results of a fairly recent (1969–1974) study by Lloyd & Millar (1983) provide some support for the suggested overall distribution presented in (1) above. Given that this antelope is not known to have been widely translocated, the results of that study are considered to reflect natural populations.
- (4) The lack of written records from the Eastern Kalahari Bushveld Bioregion (a savanna type) to the north of the Orange River, despite the presence there of suitable habitat in places and reasonable to good early chronicler coverage (Figure 4), is intriguing and deserves further investigation.

GREY RHEBOK

Pelea capreolus (Forster, 1790)

VAALRIBBOK

DISTRIBUTION RECORDS

Written records in Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records, including those in Klein & Cruz-Urbe (2000), Plug & Badenhorst (2001), Jerardino (2003), Sealy *et al.* (2004), Boshoff & Kerley (2013) and Steele & Klein (2013), indicate that within the

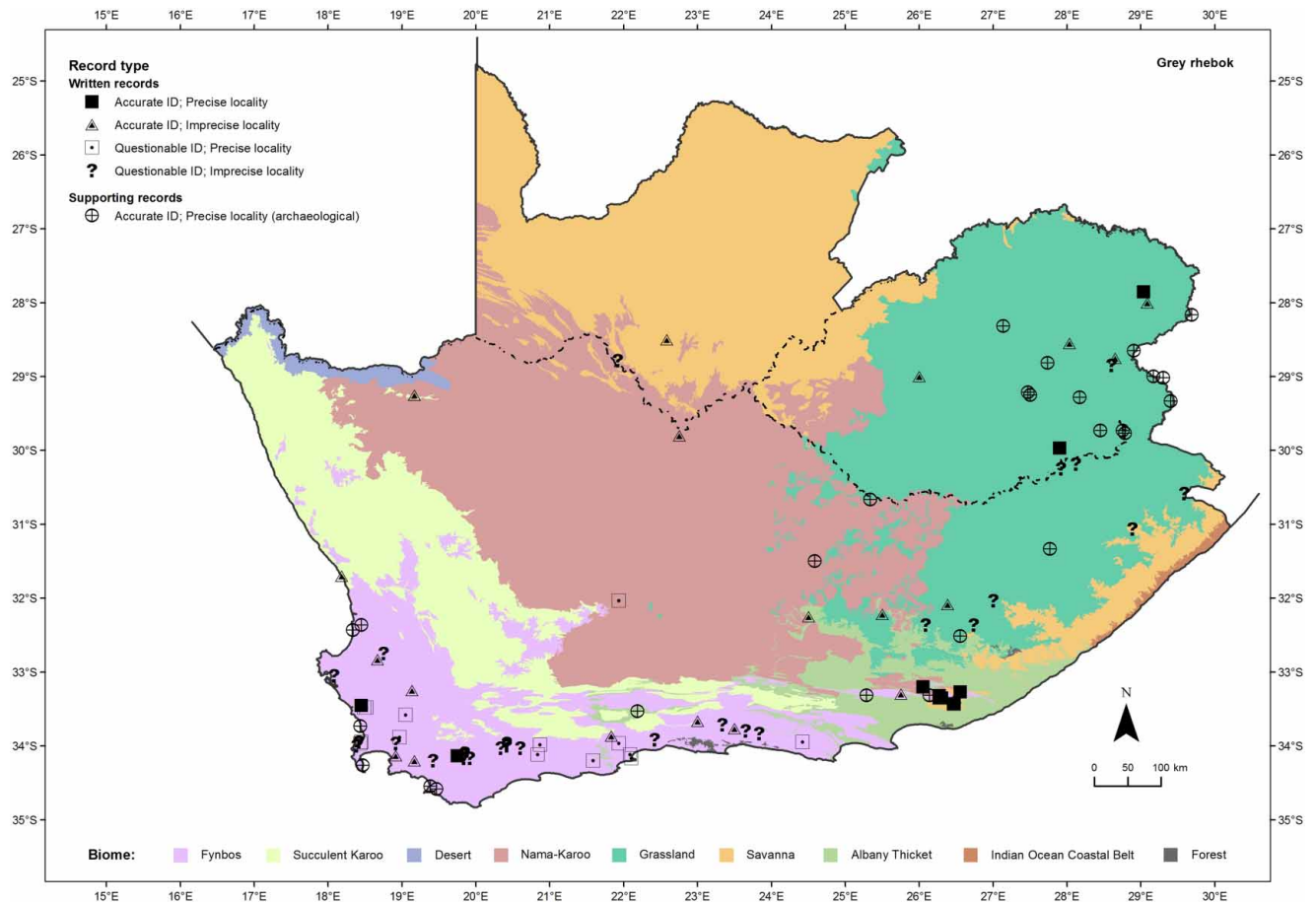


Figure 35. Early historical incidence of the grey rhebok: mappable written and supporting distribution records (see the text), and biomes.

study area the grey rhebok occurred in five biomes – Fynbos, Succulent Karoo, Nama-Karoo, Grassland, Savanna. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 35.

Despite good to fairly good early chronicler coverage in many parts of the study area (Figure 4), relatively few high-quality written records could be located for this ungulate. This is considered to reflect a combination of factors, notably its medium-size, its unremarkable coat colour, its similarity to other similar-sized antelope, its habitat preference and the patchiness of the habitat in some areas; together, these factors are believed to have rendered its detection and identification by early chroniclers problematic, leading to the relatively large number of “Questionable ID” records on Figure 35.

The high proportion of zoo-archaeological records probably reflects high levels of utilisation of this animal by pre-colonial inhabitants. This view is supported by an analysis that shows that grey rhebok remains were found in archaeological samples from all five time periods between 4000 years BP and the Recent period (Plug & Badenhorst 2001).

Fynbos Biome

The incidence of the grey rhebok in this biome is indicated, or suggested, by several written records from a number of constituent bioregions. In the case of those written records for which the identification of the observed animal is “questionable”, the general areas in which these observations were made, and the probable absence there of the mountain

reedbuck (which occurs to the east of 24° E, and with which the grey rhebok can easily be confused), increases the probability that these records, all lying to the west of 24° E, are of grey rhebok, although it is possible that some may refer to the Cape grysbok *Raphicerus melanotis*. Finally, the occurrence of the grey rhebok in this biome is supported by a number of widely scattered zoo-archaeological records, of which the majority come from coastal or near-coastal sites. The relatively large number of records, written and supporting, indicate that the grey rhebok was widespread in the Fynbos Biome, a region with good to reasonable early chronicler cover (Figure 4).

Succulent Karoo Biome

Only two written records (one from the coast in the Namaqualand Sandveld Bioregion, and one associated with an eastern outlier of the Richtersveld Bioregion in the far north-western part of the study area) indicate the incidence of this ungulate in this biome.

Nama-Karoo Biome

Four written records, supported by a single zoo-archaeological record, indicate that the rhebok occurred in the Bushmanland and Upper Karoo bioregions. Even though early chronicler coverage is poor in a large part of the former (Figure 4), it is postulated that the general lack of records, despite reasonable to good coverage elsewhere in this arid biome, suggests that this ungulate occurred patchily and at a low density.

Grassland Biome

A number of written records, supported by several zoo-archaeological records, indicate or suggest its presence in all four bioregions within this biome – Dry Highveld Grassland, Mesic Highveld Grassland, Drakensberg Grassland, Sub-Escarpment Grassland – where suitable habitat is known to exist. In the two first-mentioned bioregions, which incorporate extensive areas of flat, featureless terrain, its distribution could be expected to have been patchy, whereas in the latter two bioregions, which incorporate extensive hilly and mountainous terrain, it was probably widespread.

Savanna Biome

The historical record for this biome is extremely poor, with only a single written record from the Eastern Kalahari Bushveld Bioregion, to the north of the Orange River. Notwithstanding the paucity of records, there is suitable habitat in this bioregion, albeit of a highly patchy distribution, and therefore it is postulated that this antelope was more widespread (but patchy) there than is suggested by the single record.

DISTRIBUTION PATTERNS

- (1) Although there are some notable gaps in the distribution pattern for this poorly recorded antelope (Figure 32), the records at hand suggest that, within the study area, it occurred widely but patchily. The results of a fairly recent (1969–1974) study by Lloyd & Millar (1983), and

recent records in Skead (2007, 2011), reveal that it was widespread in a large part of the study area, thus providing support for this view; given that this antelope is not known to have been widely translocated, these records are considered to represent natural populations. Its estimated distribution range includes the hilly and mountainous parts of the study area.

- (2) The relatively large number of “Questionable ID” written records reflects confusion, on the part of the chroniclers, with other similar-sized, similar-shaped and similar-coloured antelope, notably mountain reedbuck and klip-springer, and perhaps oribi.

SPRINGBOK

Antidorcas marsupialis (Zimmermann, 1780)

DISTRIBUTION RECORDS

Written records in Cowan (1808), Glyn (1863), Blaine (1868), Simon (1959), Skead (2007, 2011), Boshoff & Kerley (2013) and Crampton *et al.* (2013), together with selected supporting records in Plug & Badenhorst (2001), Dewar (2008), Parsons (2008) and Boshoff & Kerley (2013), indicate that within the study area the springbok occurred in seven biomes – Fynbos, Succulent Karoo, Desert, Nama-Karoo, Grassland, Savanna, Albany Thicket. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 36.

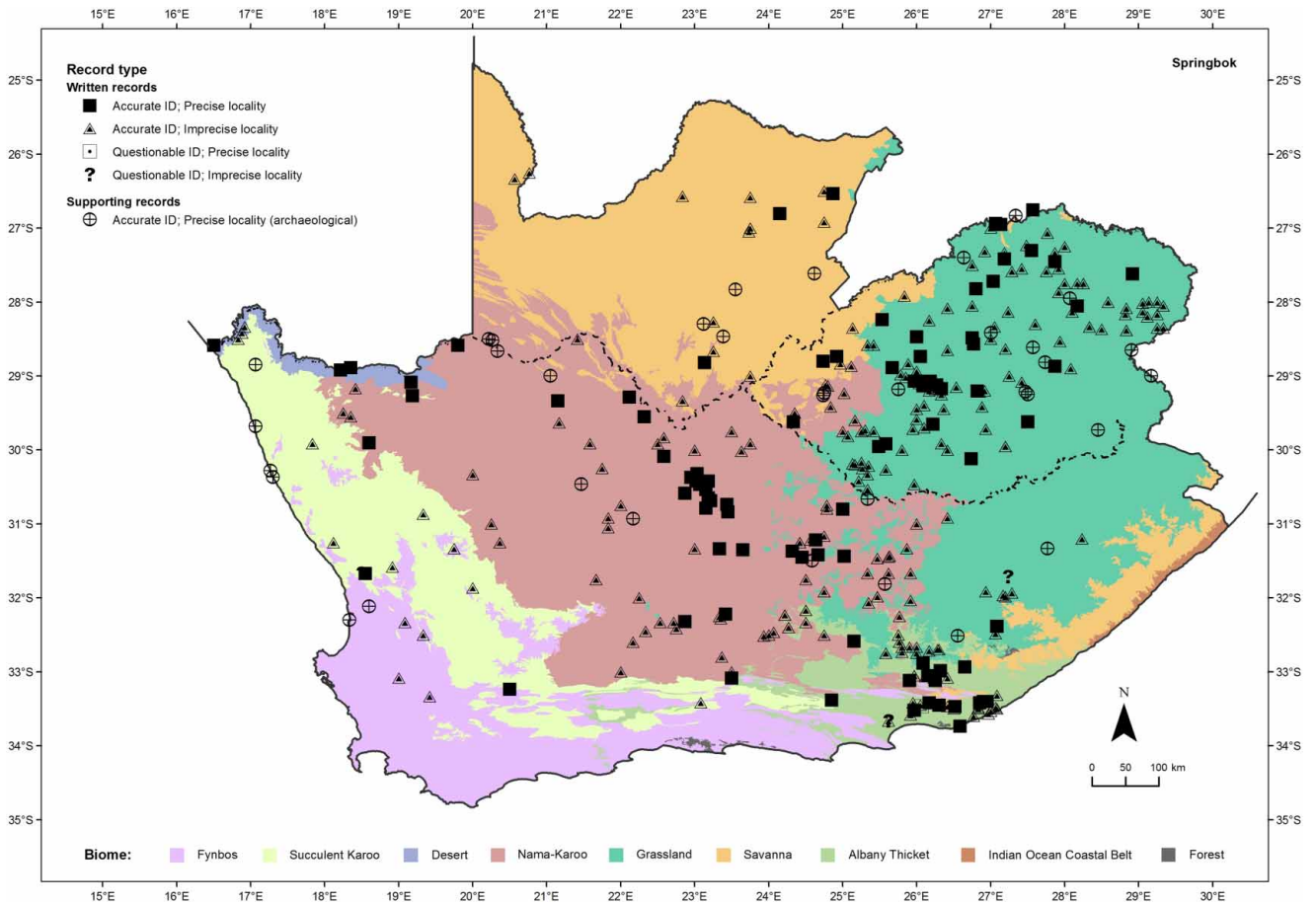


Figure 36. Early historical incidence of the springbok: mappable written and supporting distribution records (see the text), and biomes.

Fynbos Biome

The early historical record for the springbok in this biome is weak. The few written records that could be located are in or associated with the Northwest Fynbos Bioregion, in the western part of this biome. This bioregion is characterised by both mountains and flat or rolling sandy areas ("sandveld") (Rebelo *et al.*, 2006); the springbok records are presumably from the latter areas. Its presence in this bioregion is supported by a zoo-archaeological record from the northern part. There is also a written record from the Karoo Renosterfeld Bioregion, in the hinterland. A zoo-archaeological record from the West Strandveld Bioregion, a vegetation unit that is likely to have provided suitable habitat, albeit probably on a seasonal basis, shows its incidence in this part of the West Coast.

No written or supporting records could be found for the country to the south-west and south of the Cape Fold Belt, this being a region well-travelled by early chroniclers (Figure 4).

Succulent Karoo Biome

The picture for this biome is not particularly strong, in terms of the number of individual written records. This may, however, to a certain extent, reflect the relative paucity of chroniclers in parts of the region occupied by this arid biome (Figure 4). A number of written records indicates or suggest this ungulates' association with all six bioregions within this biome. Its presence in the Richtersveld Bioregion, and in the coastal section of the Namaqualand Sandveld Bioregion, is supported by a number of zoo-archaeological records. Written records from the far northern part of the Richtersveld Bioregion are close to the interface with the adjacent Namib Desert Bioregion (Desert Biome).

Desert Biome

A written record from near the mouth of the Orange River, and from the general area where the Southern Namib Desert Bioregion intergrades with the Richtersveld Bioregion (Succulent Karoo Biome), indicates its presence in this arid region. A couple of written records, in the vicinity of the Orange River, suggest its presence in the Gariiep Desert Bioregion.

Nama-Karoo Biome

The record for the springbok in the Nama-Karoo Biome is strong, with numerous written records located for all three bioregions, namely Bushmanland, Upper Karoo and Lower Karoo. Some of the gaps broadly coincide with areas with poor chronicler cover (Figure 4). A number of zoo-archaeological records provide support for its early presence in the Upper Karoo and Lower Karoo bioregions.

Grassland Biome

There is strong evidence for the occurrence of the springbok in a substantial part of this biome during the early historical period. This is reflected by the large number of written records for the Dry Highveld Grassland Bioregion, to the north of the Orange River, and also in the area where areas of this bioregion occur in a matrix of Upper Karoo Bioregion (Nama-Karoo Biome) to the south of it. Its presence in the Dry Highveld Grassland Bioregion is supported by the existence of several zoo-archaeological records from there. It is also reflected in the large number of written records from the Mesic Highveld Grassland Biome, supported by a number of zoo-archaeological records.

Unsurprisingly, no written records could be found for the mountainous Drakensberg Grassland Bioregion; which does not provide suitable habitat for the springbok, a plains-living animal. The three zoo-archaeological records in this bioregion are intriguing. It is postulated that they may refer to material obtained, through transhumance, from adjacent grassland bioregions, to the east and west of the Great Escarpment.

A handful of written records and a single zoo-archaeological record confirm the former incidence of the springbok in the Sub-Escarpment Grassland Bioregion. However, no records of any kind could be found for country south of 30° S and east of 28°30' E, in this bioregion.

Savanna Biome

Despite some gaps in early chronicler coverage (Figure 4), written records, supported by a number of zoo-archaeological records, indicate the occurrence of the springbok in the relatively well-watered Eastern Kalahari Bushveld Bioregion, located to the north of the Orange River. The pattern of these records suggests that this ungulate occurred throughout this bioregion.

There are only two written records from the north-western part of this region which is formed by the Kalahari Duneveld Bioregion. The paucity of records from this bioregion probably reflects a combination of the dearth of 19th century chroniclers (Figure 4) and the strongly seasonal nature of the rainfall (and hence availability of grazing), the latter resulting in its presence here being of a highly ephemeral nature. Research conducted on the springbok in the dune country of the south-western Kalahari "Desert" (Knight, 1991; Verlinden, 1998) has revealed that this animal was nomadic or migratory in this arid region.

Albany Thicket Biome

Within the area of this biome, one which was well covered by early chroniclers (Figure 4), there is a cluster of written records between about 25° 30' E and about 27° 30' E. This cluster coincides broadly with the region known locally as the Zuurveld (sourveld), which is characterised by extensive areas of open grassland, or grassland with shrubs and trees, and which forms a wide corridor that links the population in the interior (especially in the Nama-Karoo Biome) to part of the south-eastern coast.

The springbok is not a typical "thicket" species and its presence in this biome is considered to have been related to the occurrence, in places, of areas of open or relatively open grassland and karoo vegetation.

DISTRIBUTION PATTERNS

- (1) While this antelope may appear to have been widely distributed in the study area, there are some notable gaps in this overall distribution pattern – these are discussed in more detail below.
- (2) Its distribution within the Fynbos Biome appears to have been limited to areas of sandveld and strandveld in its far western part. The absence of records from country to the south-west and south of the Cape Fold Belt is noteworthy; whether these mountains form a barrier to dispersal or whether the habitat there is unsuitable is currently unknown.
- (3) Unmapped records indicate that it was more widespread than is shown in Figure 36 in the Kalahari Duneveld

- Bioregion (a savanna type, to the north of the Orange River) where it occurred as a nomad or migrant.
- (4) The absence of records, of any type, from the eastern part of the Sub-Escarpment Grassland Bioregion, and from the Sub-Escarpment Savanna Bioregion, in the south-eastern part of the study area, both of which might be expected to have provided suitable springbok habitat, is worthy of further investigation.
 - (5) Despite the springbok being traditionally regarded as a species of semi-arid to arid country, the distribution information provided here clearly shows that its natural range extended eastwards into the high altitude and high rainfall plains parts of the study area (i.e. the Highveld), which are dominated by open, medium- to tall-grasslands (in the Grassland Biome north of the Orange River). There is some evidence that it was migratory, or partially migratory, in the Highveld region (Boshoff & Kerley, 2013).
 - (6) The lack of records from the grasslands of the Maloti-Drakensberg massif confirm its status as an animal of flat to undulating or lightly broken terrain.

ORIBI

Ourebia ourebi (Zimmermann, 1783)

Written records in Glyn (1863), Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Plug and Badenhorst (2001), Skead (2007) and Boshoff & Kerley (2013), indicate that within the study area the oribi occurred in five biomes – Fynbos, Grassland,

OORBIETJIE

Savanna, Albany Thicket, Indian Ocean Coastal Belt. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 37.

Despite reasonable to good early chronicler coverage in many parts of the study area (Figure 4), relatively few written records could be located for this ungulate. This is considered to reflect a combination of factors, notably its medium-size, unremarkable coat colour, similarity to other similar-sized antelope, and occupation of areas with medium- to tall-grass, all of which must have made its detection and identification by early chroniclers problematic.

Fynbos Biome

A number of written records reveal the presence of this ungulate to the east of 23°30' E in the Eastern Fynbos-Renoster-veld Bioregion. The eastern parts of this bioregion contain areas with a generally well-developed grass component (Rebello *et al.*, 2006); these provide suitable oribi habitat.

Grassland Biome

There is a single written record, from an area where fragments of the Dry Highveld Grassland Bioregion occur, to the south of the Orange River, in a matrix formed by the eastern part of the Upper Karoo Bioregion (Nama-Karoo Biome).

Its incidence in the Mesic Highveld Grassland Bioregion is confirmed by four written records, supported by two zoo-archaeological records. This high altitude, moist grassland

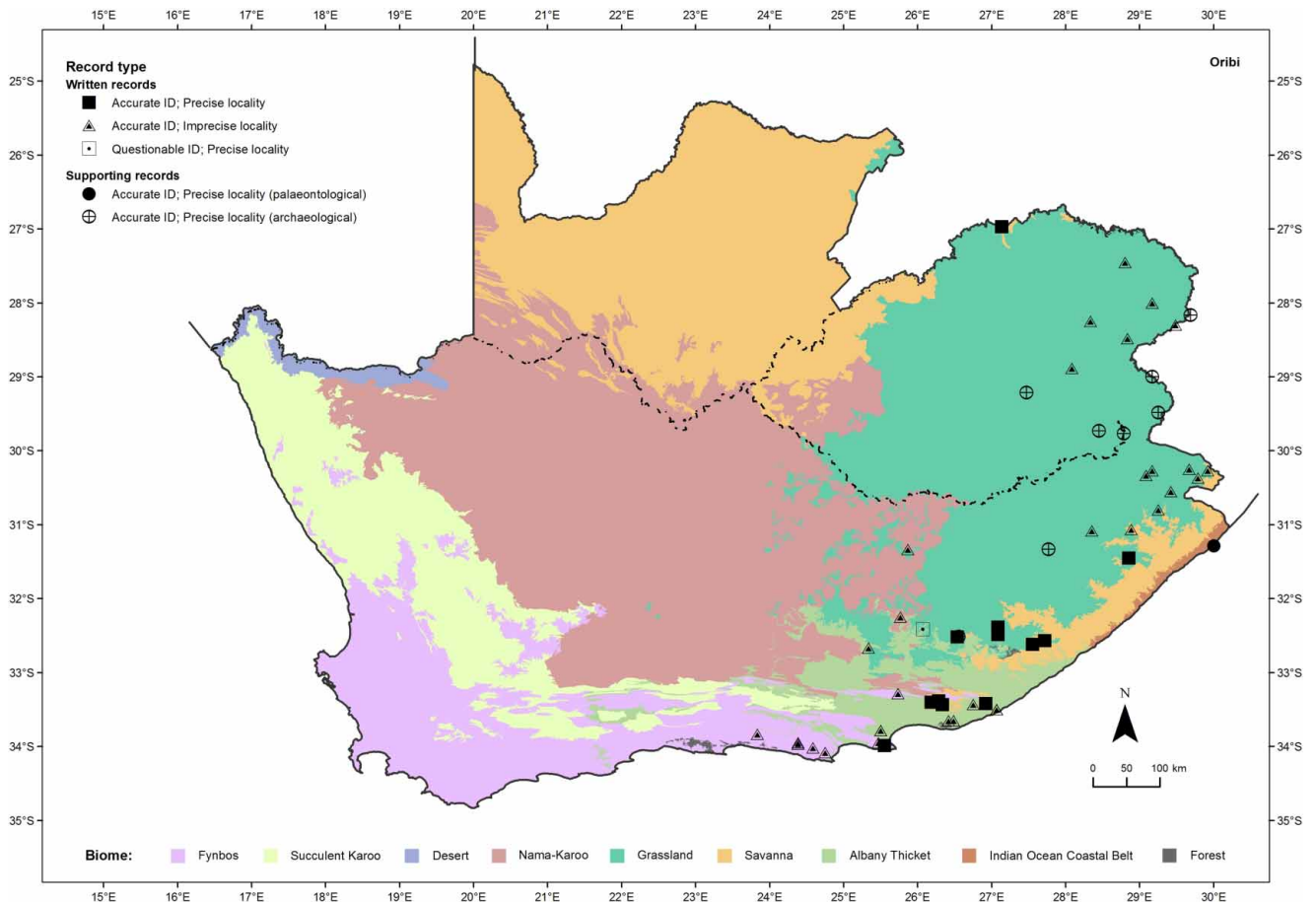


Figure 37. Early historical incidence of the oribi: mappable written and supporting distribution records (see the text), and biomes.

region, including where it occurs south of the Orange River, would have provided ideal habitat for this species.

The presence of this ungulate in the northern section of the Drakensberg Grassland Bioregion is suggested by three supporting (zoo-archaeological) records. This extremely rugged part of the bioregion was little travelled by potential chroniclers during the 19th century (Figure 4) and, in a large part, this small antelope was apparently heavily persecuted by local people during the latter part of that century. Notably, in mountainous Lesotho, which is dominated by Drakensberg Grassland, it was considered to be extinct by 1905 (Ambrose & Talukdar, 2000). Recent (1975–1980) field records confirm that oribis can exist on the top of the Drakensberg Escarpment (Boshoff & Kerley, 2013). Thus, it is likely that it was more widespread there, during the early historical period, than is suggested by the lack of written records. Its incidence in the southern section of this bioregion is indicated by a handful of written records and a single zoo-archaeological record.

The occurrence of the oribi in the Sub-Escarpment Grassland Bioregion, to the south and east of the Drakensberg Grassland, is indicated by a number of written records and a single supporting (zoo-archaeological) record. This moist grassland would have provided prime habitat for this animal.

Savanna Biome

With only a single written record (of “Questionable ID” status), and no supporting records, the incidence of the oribi in the Sub-Escarpment Savanna Bioregion is unclear.

Albany Thicket Biome

There are a number of written records from this biome. Since the oribi is not known to be a true “thicket species”, it is almost certain that these records refer to animals observed in predominantly grassy areas, within a matrix of thicket vegetation types. In this regard, this biome is not homogeneous and incorporates areas of other biomes.

Indian Ocean Coastal Belt Biome

While no written records could be found, a single palaeontological record suggests its occurrence in this biome. The locality of the latter record is within the Pondoland-Ugu Sandstone Coastal Sourveld, a vegetation unit that has a well-developed grassy component (Mucina *et al.*, 2006b), thereby potentially providing suitable oribi habitat.

DISTRIBUTION PATTERNS

The written and supporting records indicate that the oribi was restricted to the eastern and south-eastern parts of the study area, where it occurred from the coast to the hinterland, including the high Drakensberg Escarpment region and beyond, i.e. in areas where the rainfall is high or relatively so (Figure 2), and, critically, where suitable grass cover is present throughout the year. The most westerly record is from just west of 24° E. It was not recorded from the arid and semi-arid areas in the central, south-western, western and northern parts, which lack year-round, suitable, grass cover.

IMPALA

Aepyceros melampus (Lichtenstein, 1812)

DISTRIBUTION RECORDS

Written records in Cowan (1808) and Skead (2011), together with selected supporting records in Plug & Badenhorst (2001)

and Boshoff & Kerley (2013), indicate that within the study area the impala occurred in a single biome – Savanna – with its presence in another biome – Grassland – being open to question. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 38.

Grassland Biome

There are single zoo-archaeological records from the Mesic Highveld Grassland and the Drakensberg Grassland bioregions, respectively. Since the impala (a mixed feeder) is not known to be a species of areas dominated by extensive, open, grassland, these records must be treated with circumspection. They both involve a very low number of skeletal elements (Plug & Badenhorst, 2001) and therefore might represent mis-identifications. On the other hand, it is possible that impala elements were transported from savanna areas further north to the two archaeological sites by humans.

Savanna Biome

A number of written records, supported by a single zoo-archaeological record, indicate its occurrence in the Eastern Kalahari Bushveld Bioregion, to the north of the Orange River, an area that offers excellent impala habitat.

DISTRIBUTION PATTERNS

The distribution pattern indicated for the impala is unequivocal – its stronghold in the study area is the Eastern Kalahari Bushveld Bioregion (Savanna Biome), to the north of the Orange River.

KLIPSPRINGER

Oreotragus oreotragus (Zimmermann, 1783)

DISTRIBUTION RECORDS

Written records in Glyn (1863), Simon (1959), Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Kleyn & Cruz-Urbe (2000), Plug & Badenhorst (2001), Jerardino (2003), Parsons (2008), Boshoff & Kerley (2013) and Steele & Klein (2013), indicate that within the study area the klipspringer occurred in seven biomes – Fynbos, Succulent Karoo, Desert, Nama-Karoo, Grassland, Savanna, Albany Thicket. Mappable written records and qualifying supporting records, and the biomes within the study area, are shown in Figure 39.

Despite reasonable to good early chronicler coverage in many parts of the study area (Figure 4), few written records could be located for this ungulate. This paucity of written records is considered to reflect, to a large extent, a combination of its small size and inconspicuousness (its coat blends with the background), its occurrence as pairs or small groups, its similarity to other similar-sized antelope, and the generally inhospitable (for humans) nature of the terrain that it inhabits (hills, mountains), these being areas usually avoided by early travellers on horseback and in wagons. It was also not an antelope that was highly sought after by early European travellers for the pot or for sport hunting.

In fact, in much of the study area its occurrence receives more support from the zoo-archaeological record than it does from the written record. The finding of klipspringer remains in archaeological samples, from sites in southern

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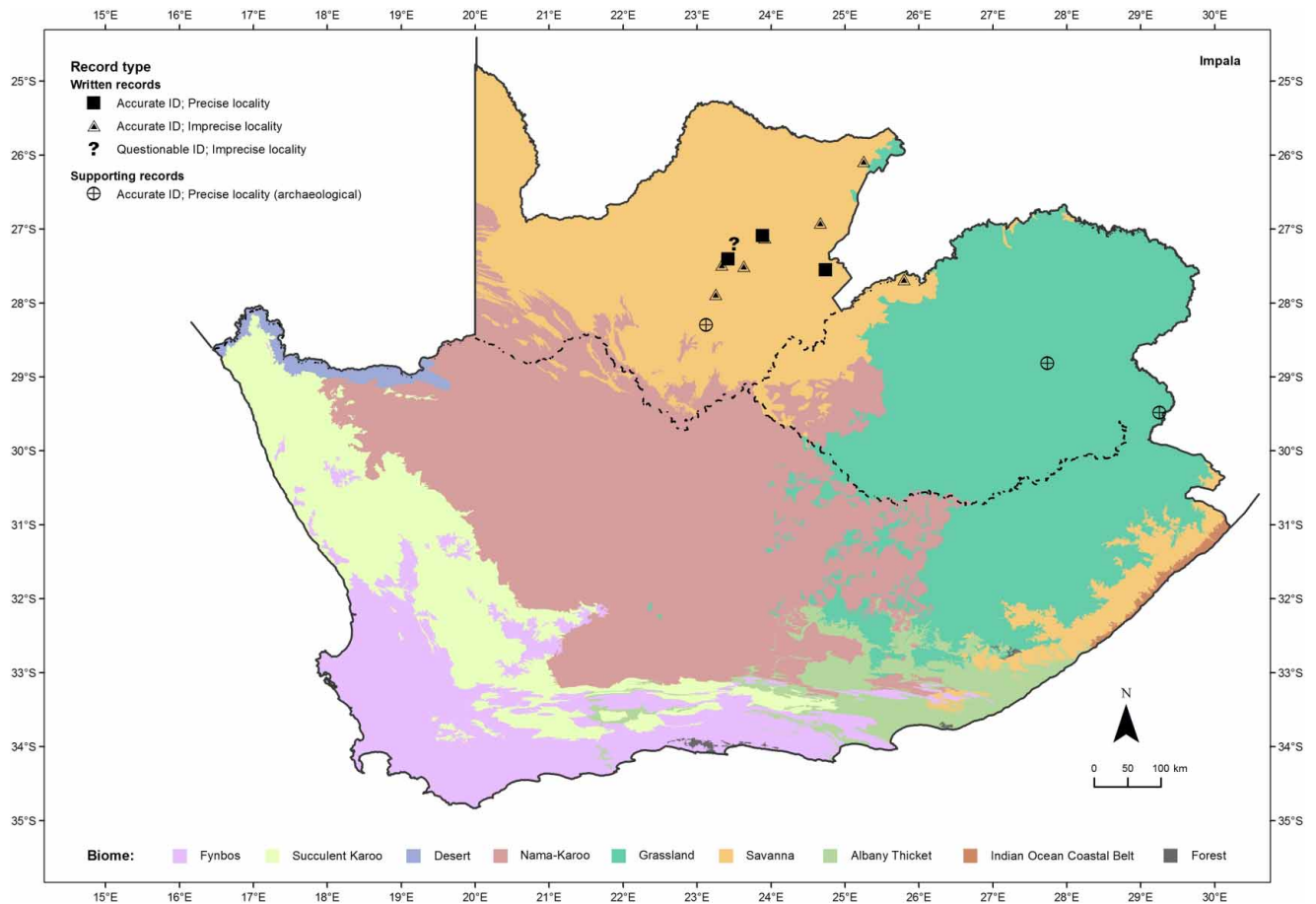


Figure 38. Early historical incidence of the impala: mappable written and supporting distribution records (see the text), and biomes.

Africa within four of the five time periods defined for the “4000 years BP-Recent” era (i.e. that is relevant to this study) (Plug & Badenhorst, 2001), indicates widespread use of this animal by humans.

Fynbos Biome

A number of written records and/or zoo-archaeological records indicate the presence of this small antelope in the Northwest Fynbos, Southwest Fynbos, Southern Fynbos, Eastern Fynbos-Renosterveld, West Coast Renosterveld and East Coast Renosterveld bioregions, thereby suggesting that it was widespread within this biome.

Succulent Karoo Biome

Its presence in this arid biome is indicated by a written record from the Richtersveld Bioregion and a supporting (zoo-archaeological) record from the coastal area in the Namaqualand Sandveld Bioregion.

Desert Biome

Single written records from the Southern Namib Desert and Gariep Desert bioregions, respectively, reveal its incidence in this arid region.

Nama-Karoo Biome

A single zoo-archaeological record from the Bushmanland Bioregion and one written and two zoo-archaeological records from the Upper Karoo Bioregion, as well as a single

written record from the interface between the latter bioregion and the Lower Karoo Bioregion, provide some evidence for its occurrence in this biome.

Grassland Biome

A few written records and a number of supporting (zoo-archaeological) records indicate the occurrence of this ungulate in all four bioregions (Dry Highveld Grassland, Mesic Highveld Grassland, Drakensberg Grassland, Sub-Escarpment Grassland) that constitute this biome.

Savanna Biome

That the klipspringer was present in this biome is indicated by one written and two zoo-archaeological records from the Eastern Kalahari Bushveld Biome, to the north of the Orange River, and two written records from the Sub-Escarpment Savanna Biome, in the south-eastern part of the study area.

Albany Thicket Biome

A single written record and three supporting (zoo-archaeological) records provide evidence for the incidence of the klipspringer in this biome; two records in the latter category refer to sites in a thicket outlier in Little Karoo region, to the west of the main area of this biome. Since the oribi is not known to be a true “thicket” species, it is almost certain that these records refer to animals observed in or from predominantly open, rocky areas, within a matrix of thicket and other vegetation types (most often fynbos).

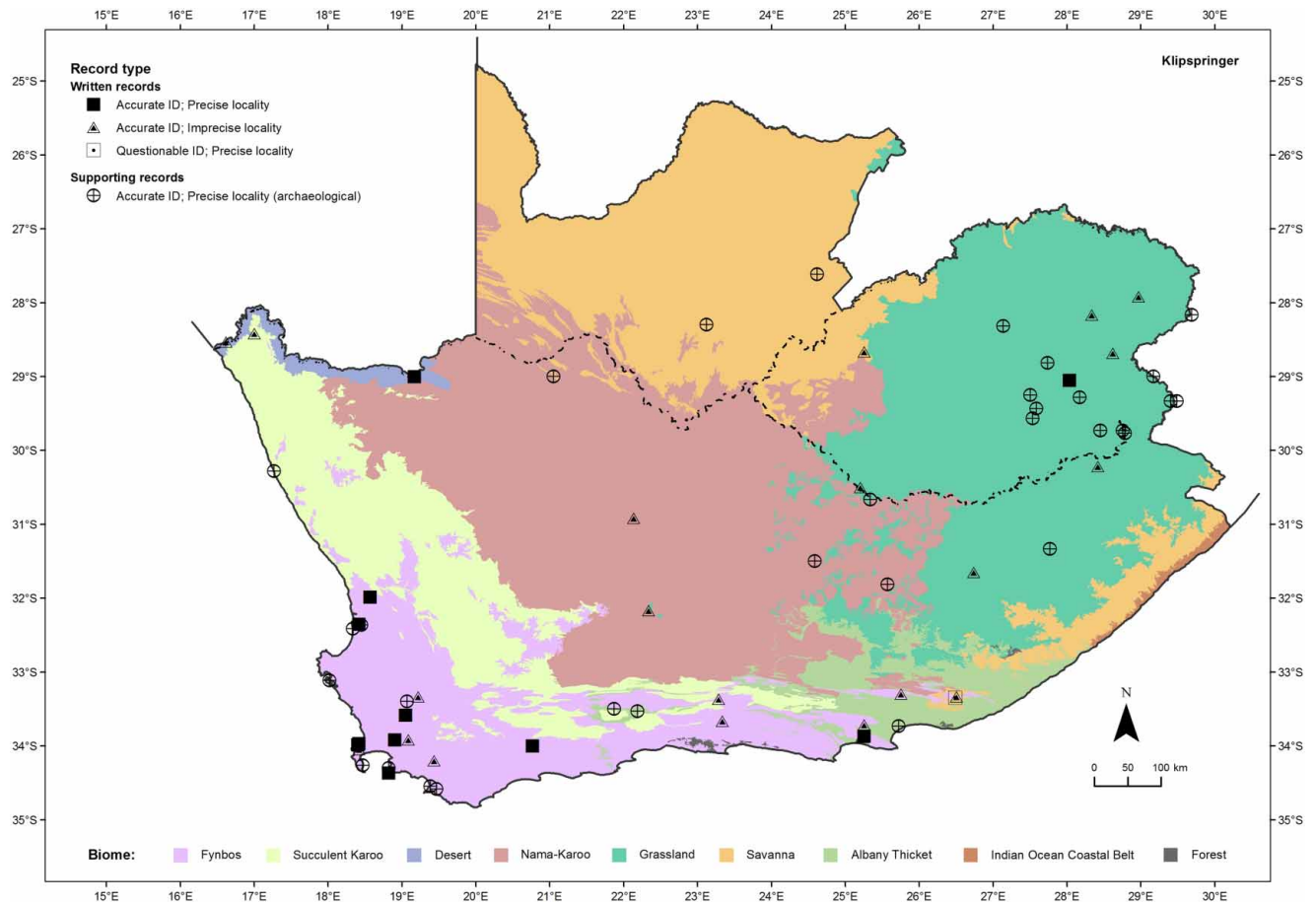


Figure 39. Early historical incidence of the klipspringer: mappable written and supporting distribution records (see the text), and biomes.

DISTRIBUTION PATTERNS

- (1) The paucity of written records makes it difficult to estimate the distribution of the klipspringer in the study during the early historical period. Notwithstanding this constraint, the spatial information in [Figure 39](#) is adequate to show that this ungulate was relatively widespread in the study area during this period. A number of general statements in the early literature provide support for this view. Further support comes from the results of a fairly recent (1969–1974) study by [Lloyd & Millar \(1983\)](#), which show that the klipspringer was widespread in a large part of the study area. Given that this antelope is not known to have been widely translocated, the results of the [Lloyd & Millar](#) study are considered to reflect natural populations.
- (2) Owing to the nature of its preferred habitat (rocky hills and mountain slopes), it would have had a patchy and discontinuous distribution in areas where this was absent, such as featureless plains.

DISCUSSION

We submit that, notwithstanding the various challenges associated with the use of written and supporting records, realistic patterns of early historical distribution were obtained for the majority of the 37 taxa covered by this study, and that these outputs, which benefit from combining and standardising the classification of records from a range of sources, significantly

enhance our knowledge in this regard. As such, they improve the basis for conducting zoo-geographical and taxonomic research on, and for informing conservation strategies and plans for, these species in the area in question. Comments on other aspects of the results follow below.

Map quality

Inevitably, and for a number of reasons (discussed in some detail by [Skead, 2007, 2011](#) and [Boshoff & Kerley, 2010, 2013](#)), the quantity and quality of the written records varies, especially in terms of the spatial coverage achieved and of the quantity and quality of the information that comprises each individual record. This must be considered in any interpretations of, and comparisons between, the indicated distribution patterns. The overriding reason for this variation is considered to be the non-systematic manner in which the written records were made, with this being manifest in four important aspects. First, not all areas were visited by chroniclers and potential chroniclers of wildlife, and while some areas received relatively many such people, others received few or none. Second, records of species observed were made by individual chroniclers on a highly selective and irregular basis. Third, the amount of information (notably physical description, behaviour, habitat and locality) that was recorded by the same or different observers differs greatly. Fourth, very few chroniclers recorded the absence of species. Because of the complications introduced by these factors we have avoided the use of the terms “extent of occurrence” and “area of

occupancy" (IUCN, 2015), which are commonly used to describe species distributions. We believe that these problems have been ameliorated, at least to some extent, by interpreting the distribution patterns within the context of the broad ecological requirements of a species (Boshoff & Kerley, 2010, and the references therein). This approach has been applied in the present study, assisted by overlaying written (and supporting) records onto broad habitat surrogates. Hopefully, as new written records come to light they can be used to fill some of the presence/absence gaps that still exist on the maps, thereby enhancing the existing distribution patterns.

The decision to use selected palaeontological, zoo-archaeological and museum records as supporting material for the written records is considered to have been justified, given that the results of our study reveal that the majority of these records closely corroborates the ranges derived solely from the written records. Nevertheless, the locations of some of the zoo-archaeological records are difficult to explain, especially given the possibility that skeletal elements may have been transported far away from kill sites by humans.

Comparison of record patterns between species groups

It is clear that the extent and frequency of historical records varies considerably among the different species included in this compilation. We argue that this largely reflects the features of the species, as these features influence the level of interest in the species for early chroniclers; we explore this proposition here.

In general, the ungulates (herbivores) that lived in open, plains country and that periodically formed medium to large or very large aggregations were frequently recorded by the early chroniclers, resulting in well-defined and reliable distribution patterns. Eight medium- to large-sized species fall within this category: true quagga, Burchell's (plains) zebra, eland, black wildebeest, blue wildebeest, red hartebeest, blesbok and springbok. While there are probably several reasons for this, the following are believed to have been prominent (Skead, 2007, 2011; Boshoff & Kerley, 2013). First, these abundant animals were the main source of meat, skins and bones for the early European visitors and colonists, and were also frequently hunted for sport and commercial purposes during the mid to latter part of the 19th century, and this probably contributes to the relatively large number of records for them in the early literature. Second, the spectacle provided by the large to very large herds appears to have captured the imagination and wonder of many of the early chroniclers, thus prompting them to record their observations (Boshoff & Kerley, 2015).

On the other hand, the information in Skead (2007, 2011) and Boshoff & Kerley (2013) indicates that those ungulates (herbivores) that occur as singletons, pairs or small groups (<10 individuals), especially those that live mainly in hilly or mountainous terrain (e.g. mountain reedbuck, grey rhebok, oribi, klipspringer) or bushy areas (e.g. greater kudu, impala), all of which were largely inaccessible to early travelers on horseback and in wagons, or that were inconspicuous and easily confused with other, similar-sized and similar-looking species (e.g. klipspringer, grey rhebok, mountain reedbuck, southern reedbuck), tended to be relatively infrequently recorded. Furthermore, the members of the latter group of species appear to have been hunted mainly for the pot, and occasionally for their skins, and not for commercial or

recreational purposes; this possibly contributes to the general lack of records. The relative paucity of records for the latter group of species reduces the quality of the maps depicting their distribution patterns.

Of the seven carnivores covered by the study, lion and, to a somewhat lesser extent, spotted hyaena, leopard and African wild dog, were the most frequently and widely recorded by the early chroniclers, this despite the fact that spotted hyaena, lion and leopard are mainly active nocturnally (although spotted hyaena and lion readily reveal their presence by their characteristic nightly vocalisations). Many of the early literate travellers and settlers not only greatly admired the lion (the "King of Beasts"), especially, and the leopard but also feared that these large cats would physically harm or kill them or their livelihood-critical domestic stock (especially their horses, cattle and wagon-drawing oxen), and spotted hyaena and African wild dog were also feared as potent stock predators (Skead, 2007, 2011; Boshoff & Kerley, 2013). It is surmised that these issues contributed to the relatively frequent mention of these four species in the early literature.

The megaherbivores (African elephant, black and white rhino, hippo and giraffe) are all large and obvious species that were easily recognisable (although there was a tendency by early chroniclers to lump the two rhino species). Furthermore, these species, with the exception of the giraffe, all potentially represent a threat to man and his chattels. These species all also represent substantial resources, such as ivory (from elephant and rhino), skins or meat. This combination therefore renders these megaherbivores highly likely to have been observed, identified and recorded by the early chroniclers.

The above arguments support the proposition that the intrinsic features of a species influence the likelihood of it featuring in historical records. Thus, large, fierce, valuable and abundant taxa are more likely to be observed and recorded than small, non-threatening and sparse taxa. This hypothesis is supported by the analysis of current tourist game-viewing records, which show that tourists in protected areas are more likely to record such large and fierce taxa than those that do not fit this profile (Kerley *et al.*, 2003b). In addition, tourists are more interested in spending time observing these taxa (Maciejewski & Kerley, 2014). This concept provides a basis to predict which species may be underreported in historical records for other areas, and which species are likely to be well-reported.

Occurrence within broad habitat surrogates

By attempting to relate the estimated distributions of the various species to the biomes and their constituent bioregions that are represented in the study area (Figure 3 and the individual species distribution maps), the current work represents a first attempt to reconstruct the historical distribution patterns of southern African mammals against a biophysical background, rather than a geo-political one.

The spatial information provided, and taking into account patterns of early chronicler coverage (Figure 4), indicates that the occurrence of some species was limited to a specific part, or parts, of an individual biome or bioregion. The following examples illustrate this point (for the sake of brevity, these record-biome/bioregion associations are not mapped here):

Mountain zebra: in the Grassland Biome, the known written records are limited to only a relatively small area in the south-west.

Burchell's (plains) zebra: in the Dry Highveld Grassland Bioregion, the known written records are from only the part lying to the north of the Orange River.

Black wildebeest: in the Upper Karoo Bioregion, the known written records are from only the central and eastern parts, while in the Lower Karoo Bioregion they are from only the eastern part.

Blesbok: in the Upper Karoo Bioregion, the known written records are from only the eastern part, while in the Sub-Escarpment Grassland Bioregion they are from only the western part.

Mountain reedbeek: in the Upper Karoo Bioregion, the known written records are from only the eastern part.

Oribi: in the Eastern Fynbos-Renosterveld Bioregion, the known written records are from only the eastern part.

African buffalo, Burchell's (plains) zebra, black wildebeest, roan and impala: there is no evidence that these species occurred in the western part of the Savanna Biome, where it occurs to the north of the Orange River.

These examples illustrate the danger of assuming that because a species has been recorded in a part, or parts, of a biome or bioregion, that it automatically follows that it occurred throughout these units. This finding should be taken into account when using the written and supporting records to reconstruct the historical ranges of the larger mammals in southern Africa and elsewhere. In South Africa, the national Department of Environmental Affairs has produced a set of historical distribution maps for certain mammal taxa, for the purpose of informing provincial and national legislation concerning mammal translocation (see under "Distribution maps for mammals in South Africa" at <http://mapservice.environment.gov.za/tomviewer>). The value of the information on several of these maps is questionable, given the use of entire biogeographic entities as basic spatial mapping units in their compilation.

Possible effects of man's activities on early historical distribution patterns.

Based on current knowledge it is somewhat of an open question as to what extent certain activities conducted by indigenous humans prior to the onset of the colonial period influenced the broad zoo-geographical patterns presented here. This topic is briefly discussed below.

Competition with introduced livestock

Domestic livestock stock (here sheep, goats, cattle) was introduced by man to what is today called South Africa around 2000 years ago (Bousman, 1998). It is known that Khoikhoi groups, who lived mainly in the southern and western parts, and part of the west-central region, and who followed a nomadic lifestyle, maintained herds of livestock (Boonzaier *et al.*, 1996); herds of up to 20 000 animals have been recorded (Klein, 1983). Bantu language-speaking agro-pastoralists, who lived in the central, north-eastern and south-eastern parts, also kept herds of livestock (Maggs, 1984; Volman, 1984; Deacon, 1986; Thackeray *et al.*, 1990).

While competition for forage between indigenous and introduced herbivores undoubtedly existed, the extent, nature and consequences of this are not understood. It could certainly be expected that very large concentrations of the latter (cattle, sheep) would have possessed the ability to overgraze local areas (Kerley *et al.*, 2009). The impacts of domestic livestock have been implicated in the decline in the range of the blue

antelope, which showed a much wider distribution in the Last Glacial and early Holocene (Klein, 1974; Kerley *et al.*, 2009) than the historical distribution (Figure 31). Klein (1974) argues that the blue antelope suffered from competition with domestic livestock since about 1600 ybp, leading to a decline in the population and shrinkage of its range. However, more research is needed to test this hypothesis, and to assess how this activity may have affected other herbivores. For example, the blue antelope was already in terminal decline by the latter 1600s and the 1700s (Kerley *et al.*, 2009; Skead, 2011), whereas other indigenous grazers in the same region (e.g. red hartebeest, true quagga) did not exhibit a similar pattern of decline during that period (Skead, 2011).

We postulate that any competition for vegetal material from, and overgrazing and trampling by, herds of domestic stock would have been mainly of a local nature, being largely associated with temporary or permanent human settlements, and therefore they are unlikely to have affected the sub-regional distribution patterns of the indigenous ungulates and those carnivores that preyed or scavenged on them.

Alteration of vegetation communities through fire and overgrazing

There is little or no evidence that 1500 years of Khoikhoi pastoralism caused significant environmental degradation in the Fynbos Biome (Hoffman, 1997). In fact, one study maintains that the regular seasonal movements of the Khoikhoi and their livestock actually enhanced the condition of the vegetation and the livestock that utilised it (Smith, 1987). Similarly, some researchers maintain that historical stock-herding activities had little, if any, effect on vegetation communities in the eastern (Nama) Karoo up to the beginning of the 1900s (Avery, 1991). There is evidence of utilisation by domestic grazers and browsers in the Grassland and Savanna biomes in the pre-colonial and early post-colonial periods but there is no good evidence for this resulting in major transformation or degradation of the vegetation communities that occur there (Hoffman, 1997).

The role of fire in altering vegetation communities is well recognised, as is the practice of humans in using fire to manage habitats for the purpose of attracting game for hunting, or providing improved grazing conditions for livestock. Klein (1983) suggests that the Khoikhoi pastoralists would have practised large-scale burning to provide grassy habitats for their livestock. This would also have improved forage availability for indigenous grazers. This hypothesis also needs to be further explored before a robust understanding of how anthropogenic fires would have influenced the distribution of large mammals in the study area is achieved.

Hunting for subsistence and trade

It is well-known that the San, Khoikhoi and Bantu language-speaking peoples who occupied parts of southern Africa during the pre-colonial and early post-colonial periods obtained meat, skins, pelts and bones from wild animals for personal use, or for limited trade (e.g. skins and ivory, the latter for carvings, bangles etc.) (e.g. Maggs, 1984; Shillington, 1985, 2013; Maylam, 1986; Carruthers, 1995; Boonzaier *et al.*, 1996; Le Roux, 1999; Vinnicombe, 2009). However, it is not known whether the levels of utilisation were such that they influenced the overall population numbers and the estimated, regional, distribution patterns of the species that they hunted. It is considered by some researchers (e.g. Beinart & Coates,

1995; Carruthers, 1995) that the overall utilisation levels were low and were therefore unlikely to have been a factor in this regard.

Early anthropogenic impacts on the distribution of indigenous larger mammals clearly require further research. This issue is compounded by the fact that these impacts would vary in different biomes, as features of the plant communities influence, and respond to, the mechanisms of the impacts (fire, overgrazing, etc.). For example, it is well known that succulent Karoo and Albany thicket vegetation is not prone to fire, whereas fynbos, grassland and savanna vegetation burns readily (Mucina & Rutherford, 2006).

Expanded ranges during wetter climatic periods

While the general climate is considered to have been relatively stable during the later Holocene (see Introduction), it is known that some wetter periods occurred within this epoch (Deacon & Lancaster, 1988). This may explain why, in late pre-historical times, African elephant and hippopotamus occurred in areas which became unsuitable for them (presumably owing to a general lack of surface water) during the later part of the early historical period (i.e. from about 1850 onwards). This scenario is suggested by the presence of palaeontological records and the absence of written records, for these two megaherbivores, in certain areas (see the accounts for these two species).

Other possible impacts, if any, on the early distribution patterns of the larger mammals in the study area have not been adequately researched.

Emerging zoo-geographical issues

This compilation of historical distribution records, and the patterns that can be discerned from them, provide a number of emerging ideas regarding hitherto un- or under-recognised, broader, zoo-geographical patterns. These, which are briefly discussed below, all merit further investigation that is beyond the scope of the present study.

The Orange (Gariiep) River as a possible distribution barrier

Large rivers are known to serve as zoo-geographical distribution limits (barriers) (e.g. Wallace, 2011). The Orange River is a major feature on the landscape in the area covered here, and a number of authors (e.g. Smith, 1849; Skead, 2007, 2011) have stated, or implied, that it formed the southern limit of the distributions of some of the larger herbivores. Furthermore, d’Huart & Grubb (2001) suggest that this river may have separated the ranges of the Cape and common warthogs. The pattern of written records for the Burchell’s (plains) zebra (Figure 17), blue wildebeest (Figure 26), tsessebe (Figure 29), roan (Figure 30) and white rhino (Figure 13) could be interpreted as showing that it served as an effective southern limit to their distribution. Why these five species in particular show this pattern is not clear, as many morphologically and ecologically similar species were clearly able to disperse across this river. It is possible that the Orange is itself not a barrier, but rather coincides with major habitat features that define the ranges of these species. The five species (all grazers) are most commonly associated with savanna areas and, within the study area, the course of the Orange coincides closely with the boundary between the Savanna Biome, to the north, and the Nama-Karoo Biome, to the south; this lends support to the latter view.

The Cape Fold Belt as a range limit

It is known that high mountains with a west-east alignment tend to form boundaries of zoo-geographical regions and that they possess attributes for the evolution of clear distribution patterns for species (Löffler, 1984), i.e. that they may drive distribution patterns. A number of the species covered in the present study show a distribution pattern that suggests that the west-east trending axis of the Cape Fold Belt served as the southern boundary to their distribution area. These are the black rhino (Figure 14), true quagga (Figure 16), gemsbok (Figure 32) and springbok (Figure 36) (all herbivores), and possibly cheetah (Figure 8) (a carnivore). The mechanism behind this pattern is not clear. We speculate that the west-east running axis of this major mountain chain may have served as a barrier to the dispersal of these species, or alternatively, the habitat south of this range may not have been suitable for these species. The fact that the listed herbivores include both browsers and grazers suggests that this pattern is not simply a case of restricted forage availability in the area south of the Cape Fold Belt.

The Orange River as a corridor

Large rivers are known to form corridors that allow species to penetrate or traverse areas of otherwise unsuitable habitat (Naiman & Décamps, 1997; Vos *et al.*, 2002). The records presented here clearly show that the Orange River, a major physical feature in the study area (Figure 1), serves as a corridor through arid landscapes for certain medium- to large-sized herbivores, namely African elephant (Figure 5), hippopotamus (Figure 20), giraffe (Figure 21), African buffalo (Figure 22) and greater kudu (Figure 23). Along its western course the Orange River is flanked by the Desert Biome (Rutherford *et al.*, 2006), a landscape type that would not be able to support the forage, shelter or water requirements of these species. As indicated in these species’ accounts, it is hypothesised that riparian vegetation associated with the Orange River and the lower sections of its main tributaries, would have provided the resources for these species to be able to penetrate into this highly arid biome.

The Transkei “gap”

There are two species (black rhino – Figure 14, greater kudu – Figure 23) for which the absence of records (of any type) east of about 27° E and south of the Great Escarpment have been identified as representing a noteworthy distribution “gap” by Skead (2007), i.e. the so-called “Transkei gap”. These two species do occur east of the Tugela River, in central present-day KwaZulu-Natal Province (KZNP), indicating a 600 km gap between the respective populations. There is clearly suitable habitat for these two browsing species within this gap, so the explanation for this pattern must lie elsewhere.

Further evidence for this “gap” is provided by the blesbok (no records east of about 28° E – Figure 28) and the springbok (no records east of about 28°30’ E – Figure 36), south of the Great Escarpment. Both species formerly occurred south of this escarpment in KZNP (Rowe-Rowe, 1994; Skead, 2007), in an area approximately 400 km to the east of these longitudes, with apparently suitable habitat occurring within the “gap”.

The possible reasons for the apparent existence of a “Transkei gap” require further investigation.

Atypical distribution records

The distribution maps for the following species contain written or zoo-archaeological records, or both, that appear as outliers from the main concentrations of records: black rhino (Figure 14), mountain zebra (Figure 15), Burchell's (plains) zebra (Figure 17), African buffalo (Figure 22), blue wildebeest (Figure 26), tsessebe (Figure 29), roan (Figure 30), blue antelope (Figure 31), mountain reedbuck (Figure 34), impala (Figure 38). The reasons for these outliers, which present interpretational challenges, are believed to include one or more of the following:

- (i) The zoo-archaeological records may indicate a wider, earlier, distribution than is shown by the bulk of the records, with this reflecting local variation in the climatic regime that prevailed during the mid to late Holocene epoch
- (ii) Some of the zoo-archaeological records may derive from mis-identified bone and tooth material.
- (iii) Some records may represent vagrants or nomads.
- (iv) Some records may be linked to transhumance, or early, non-commercial, trade.

The atypical records do not influence the general distribution patterns of the listed species.

Seasonal range variation

It is emphasised that, because the distribution records are "telescoped" in time on the maps, no distinction can be

made between the seasonal ranges of species that may or do undertake seasonal, landscape-level movements, namely partial migrations, migrations or nomadic movements. The latter categories apply particularly to the equids, wildebeests, hartebeest, blesbok, springbok and possibly eland; all these taxa are known to, or suspected to, undertake such movements (Skinner & Chimimba, 2005; Skead, 2007, 2011; Harris *et al.*, 2009; Boshoff & Kerley, 2013). Therefore, the maps for these species estimate their overall year-round ranges. On the other hand, the estimated ranges for the species that are sedentary or only move locally are more likely to represent their year-round ranges; these taxa are the rhinos, pigs, hippo, reedbuck, grey rhebok, oribi, impala and klipspringer.

Comparison with Du Plessis (1969)

A simple, visual comparison of the estimated distribution patterns, for the same geographical area, obtained for the 27 species in the orders Perissodactyla (rhinoceroses and zebras) and Artiodactyla (hippopotamus, pigs, giraffe, African buffalo and antelopes) that are covered by both Du Plessis (1969) and the present study, reveals that while 10 species display similar patterns, there are detectable differences for the remaining 17 species; for eight species the present study shows a more restricted range and for seven species it shows a more extensive range, while for two species it shows a more restricted range in parts and a more extensive range in others (Table 2). Although the method of comparison is crude, it does indicate that the "individual record" approach

Table 2. Results of a visual comparison of distributional patterns from Du Plessis (1969) and from the present study, for larger mammals of the orders Perissodactyla and Artiodactyla.

Species	Present study indicates a		
	similar range	more restricted range	more extensive range
White rhinoceros		x	
Black rhinoceros		x	
Mountain zebra			x
True quagga	x		
Burchell's/plains zebra		x	
Bushpig			x
Warthog*		x	x
Hippopotamus			x
Giraffe	x		
African buffalo		x	
Greater kudu		x	
Common eland	x		
Black wildebeest		x	x
Blue wildebeest	x		
Red hartebeest	x		
Bontebok	x		
Blesbok	x		
Tsessebe	x		
Roan	x		
Gemsbok			?
Southern reedbuck		x	
Mountain reedbuck			x
Grey rhebok		x	
Springbok			x
Oribi	x		
Impala			x
Klipspringer		x	

*Neither study draws a distinction between the Cape and common warthogs.

followed in the present study provides a better resolution than the “broadbrush” approach followed by Du Plessis (1969). It is, however, emphasised that the latter study was conducted over 45 years ago and that since then some additional records, for some species, have come to light.

Some implications of using incomplete historical distribution data for zoo-geographical studies

The distribution maps provided in, particularly, Dorst & Dandelot (1970), Smithers (1983) and Skinner & Smithers (1990) and Skinner & Chimimba (2005), have frequently been used as the basis for zoo-geographical and conservation planning studies in Africa. Examples of such studies, relating to southern Africa that use post-anthropogenic impact distribution ranges include Siegfried (1989), Coe & Skinner (1993), Turpie & Crowe (1994), Gelderblom & Bronner (1995), Andrews & O’Brien (2000) and Fjeldsa *et al.* (2004). The implications of these data limits are that the ensuing zoo-geographical patterns or conservation plans may be incomplete or flawed, and should be treated with caution. We illustrate this here. An inspection of the maps in the listed publications indicates that, for the study area, they typically show a far more restricted range, for many of the species, than is apparent from the historical records presented here. These authors either explicitly state that their maps represent the current (at the time of their publication) distributions or are silent on the matter, but this aspect is not recognised in the listed zoo-geographical studies. This has substantial implications for our understanding of not only species-specific distribution patterns but also of the larger patterns of biodiversity. For example, Turpie and Crowe (1994: Figure 5, p. 26) indicate a nadir in ungulate diversity of less than 10 species in the south-western extremity of Africa, this coinciding with the south-western portion of the area covered by the present study. In addition, their next ungulate species isocline of less than 15 species encompasses the entire area of the present study. Using the historical records, however, shows that the first of these two regions includes not less than 24 species (19 species covered here plus the five ungulate species for which records were not adequate but which are recorded in this region (Skead, 2011)), i.e. more than double the richness mapped by Turpie & Crowe (1994). For their second region, the present study includes at least 28 species, nearly double the 15 species that they mapped. Thus, Turpie & Crowe (1994) failed to detect a peak in ungulate diversity that potentially rivals the well-recognised peak in East Africa. Zoo-geographical studies therefore need to include detailed historical distribution data to avoid overlooking such important patterns.

There is a real risk that the altered distribution patterns of a species become accepted as the norm, a phenomenon identified as the “shifting baseline syndrome” (Pauly, 1995). The implications of the bias against recognising the historical distributions of mammals are profound for conservation assessments. Thus, the various IUCN Red List categories reflect in part a measure of the decline in the range of a species. Failure to recognise how much of a species’ range has been lost in the historical period represents a failure to recognise the full extent of man’s impact on that species. The distribution records provided here offer a framework for the development of a more complete understanding of just how much species’ ranges have shrunk and hence how threatened such species really are, in the area in question.

Concluding statements

While the results of this study have advanced our knowledge on the topic in question, which in turn permits a re-assessment of the outcomes of earlier zoo-geographical studies within or including the region covered, they should be viewed as being of a preliminary nature, since the indicated patterns can be reinforced, and gaps filled, if and when new written records for the period under study are discovered.

There is now a need to extend the coverage achieved by this study to include the remaining approx. 30% of “South Africa”, i.e. the region incorporating the countries of South Africa, Lesotho and Swaziland, and also the area incorporated by Namibia, Botswana, Zimbabwe and Mozambique. This level of coverage will permit enhanced definition of sub-regional patterns for the larger mammals of the southern African sub-region. There is also a need to better understand the drivers, as well as the implications, of the observed changes in the distribution of the larger mammals since the start of the historical period.

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