

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

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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 The sources of these records comprise mainly published or unpublished letters, journals, diaries or books written by literate pioneers - notably various missionaries, explorers, travellers, naturalists, military personnel, big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 subregion, 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

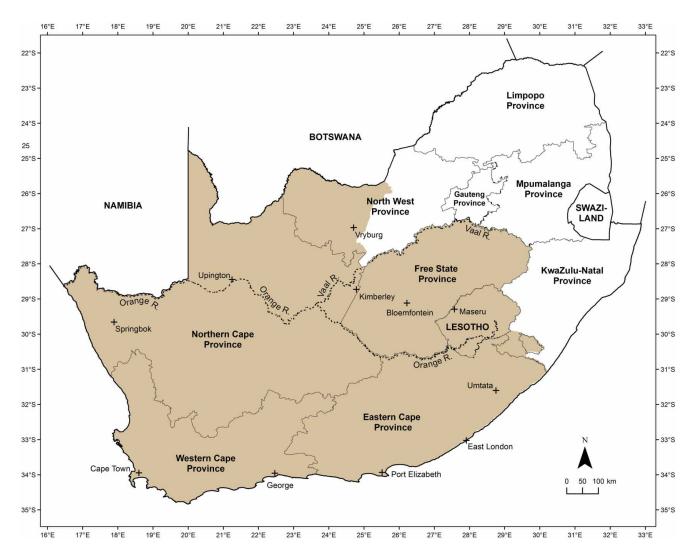


Figure 1. The nine provinces of the Republic of South Africa and the kingdoms of Lesotho and Swaziland. The study area is shaded.

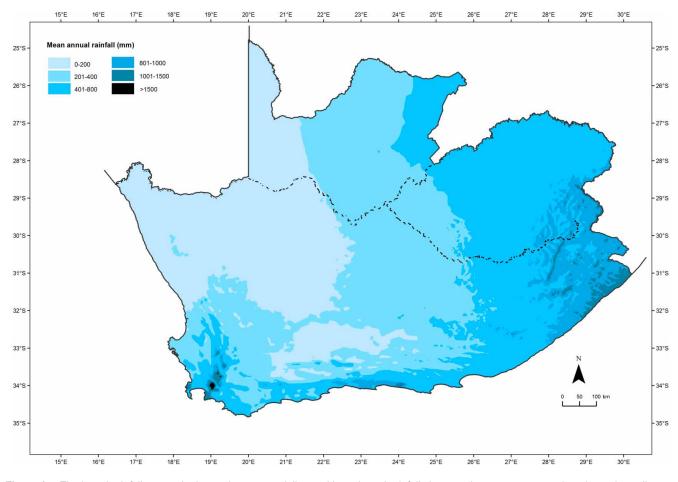


Figure 2. The broad rainfall pattern in the study area, as delineated by selected rainfall classes, shows east-west and north-south gradients.

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 datasets 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 zooarchaeological 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".

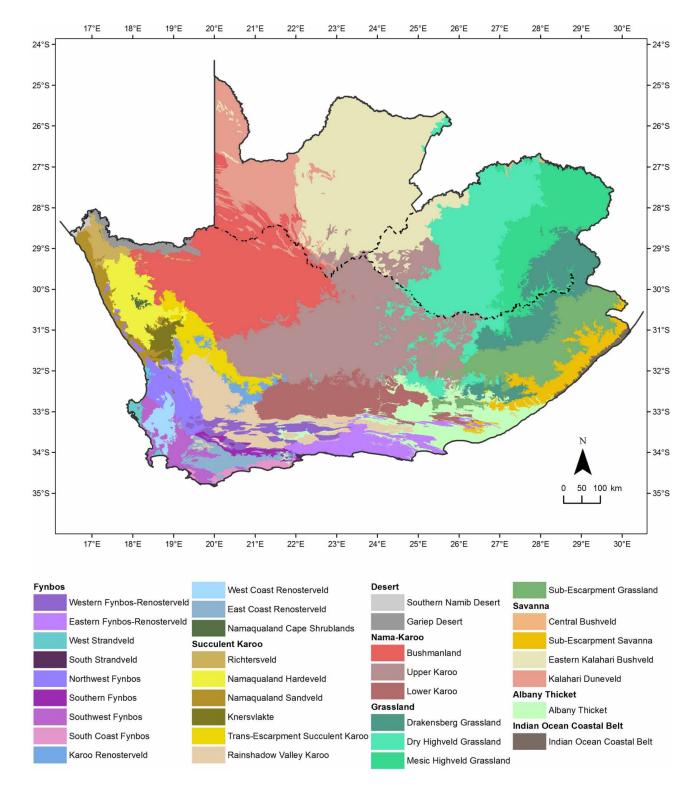


Figure 3. The bioregions, listed according to parent biome, that fall within the study area. Adapted from Rutherford et al. (2006).

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)

DISTRIBUTION RECORDS

Written records in Cowan (1808), Moodie (1838), Skead (2007, 2011) and Boshoff & Kerley (2013), together with selected supporting records in Klein & Cruz-Uribe (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

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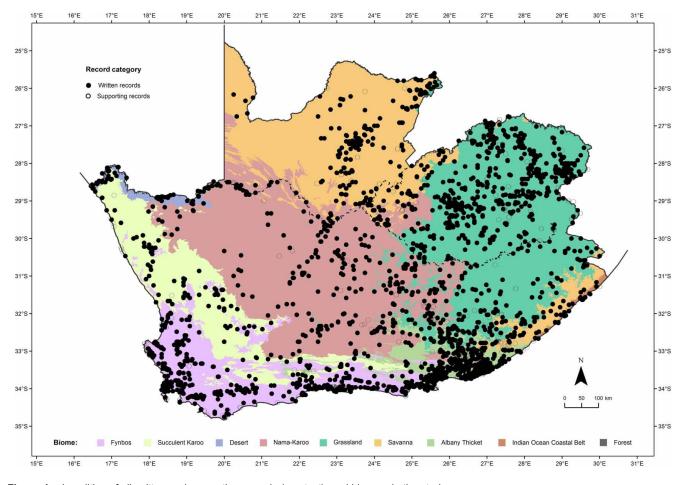


Figure 4. Localities of all written and supporting records (see text), and biomes, in the study area.

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 Gariep 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 chronicler 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 chronicler 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 chronicler 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

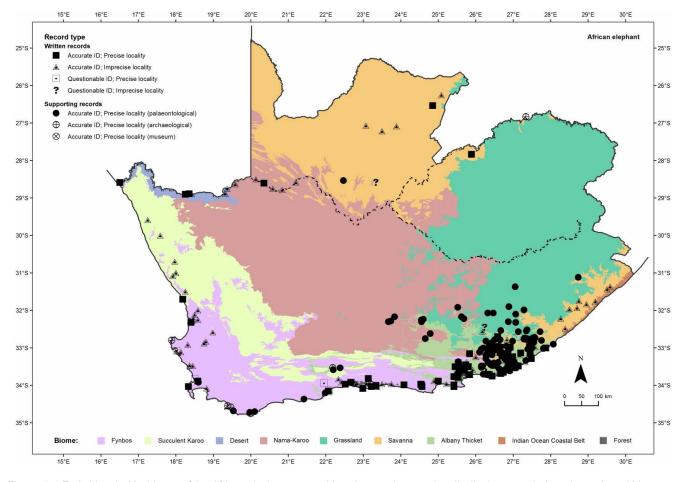


Figure 5. Early historical incidence of the African elephant: mappable written and supporting distribution records (see the text), and biomes.

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

	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.

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).

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 chronicler 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 northwest 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 longdistance "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 BRUINHIËNA/STRANDWOLF Parahyaena brunnea (Thunberg, 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 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.

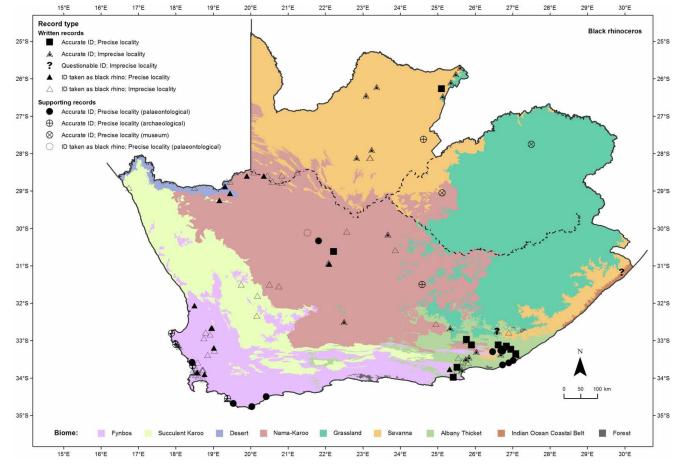


Figure 14. Early historical incidence of the black rhinoceros: mappable written and supporting distribution records (see the text), and biomes. Owing to the absence of confirmed records of white rhino to the south of the Orange River, all "rhinoceros – species indeterminate" records from that region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

(2013), together with selected supporting records in Klein & Cruz-Uribe (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 Gariep 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

- 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 subcoastal 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

BERGSEBRA

Equus zebra (Linnaeus, 1758)

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