

Damaliscus pygargus pygargus – Bontebok



Frans Radloff

Assessment Rationale

The Bontebok is a subspecies endemic to the East Coast Renosterveld bioregion within the Cape Floristic Region (CFR) of the Western Cape. It is an important South African conservation success story where a subspecies has been brought back from the brink of extinction in the 1830s by farmers in the Bredasdorp area. Currently (2014), the population estimate within the natural distribution range is 515 mature individuals (using a 75% mature population structure) on formally protected areas (including the Denel Overberg Test Range managed as an ecological unit within De Hoop Nature Reserve). Due to a lack of natural habitat availability within the natural range, the provincial conservation management authority, CapeNature, allows benign introductions of subpopulations outside of the natural range, in areas geographically adjacent to the natural range and possessing broadly similar habitat. Reintroductions into two such formally protected areas have been in place for at least five years with successful reproduction and these have increased the mature population to 664 individuals. Bontebok also exist on ranchlands and other private properties within the natural and benign introduction range. However, there are known incidences of intensive management and/or hybridisation with Blesbok within these subpopulations. Preliminary estimates of privately owned subpopulations nationally, suggest that only 33–39% of these subpopulations can be considered sufficiently wild to be included in this assessment. This adds between 118 and 1,272 individuals (by extrapolating this proportion to the private properties with the most or least abundant subpopulations respectively), which potentially increases the mature population size to between 752 and 1,618 individuals. However, the overall numbers of pure Bontebok within this population range and the intensity of management of these subpopulations are currently unknown.

Although Bontebok numbers within the benign introduction and extra-limital ranges are increasing, the core population within the natural range has not increased since 2004 (770 individuals in formally protected areas in 2004 compared to 686 individuals in 2014). Protected area expansion possibilities are limited within the natural range, thereby limiting core population growth. Currently, the extent of occurrence within the natural range is estimated at 8,779 km² and the current observed area of occupancy is 602 km². Including all known Bontebok-containing areas within both the natural and benign introduction ranges yields 1,453 km² of observed occupancy. We infer a continuing loss of suitable habitat from ongoing agricultural and urban expansion within the CFR (within the Western Cape, 107 km² land was converted to agriculture per year between 2006 and 2011, 31% occurred within Critical Biodiversity Areas; and there has been an 8.6% increase, from 1,029 km² to 1,118 km², in urban expansion between 2000 and 2013).

Given that the estimated mature population size (within the natural and benign introduction areas) ranges from 514 to 1,618 individuals, that numbers of hybrid animals

Red List status (2016)	Vulnerable B2ab(ii) + D1*†
Global Red List status (2008)	Near Threatened D1
Red List status (2004)	Vulnerable D1
Reasons for change	Non-genuine change: New information
TOPS listing (NEMBA) (2007)	Vulnerable
CITES listing (1981)	Appendix II
Endemic	Yes

*Watch-list Data †Conservation Dependent

The survival of Bontebok is due to a few prescient Cape farmers who, in 1837, set aside a portion of their farm to protect some 27 individuals. Adjoining landowners soon followed suit before the Bontebok National Park was proclaimed in 1937 (Bigalke 1955).

Taxonomy

Damaliscus pygargus pygargus (Pallas 1767)

ANIMALIA - CHORDATA - MAMMALIA -
CETARTIODACTYLA - BOVIDAE - *Damaliscus* - *pygargus* -
pygargus

Synonym: *Damaliscus dorcas dorcas* (Pallas 1766)

Common names: Bontebok (English), Bontebok (Afrikaans), Pitsi ya maronthwane (Sepedi), Inyamatane (Swati), Nglangu (Xitsonga)

Taxonomic status: Subspecies

Taxonomic notes: Van der Walt et al. (2013) argue that the matter of species versus subspecies status is far from resolved. Their genetic study, based on 34 Bontebok and 42 Blesbok (*D. p. phillipsi*) individuals, indicated that the classification of alpha taxonomy should be reconsidered in this genus and that management should seek to avoid hybridisation and sustain remaining diversity in the Bontebok.

Recommended citation: Radloff FGT, Birss C, Cowell C, Peinke D, Dalton D, Kotze A, Kerley GIH, Child MF. 2016. A conservation assessment of *Damaliscus pygargus pygargus*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

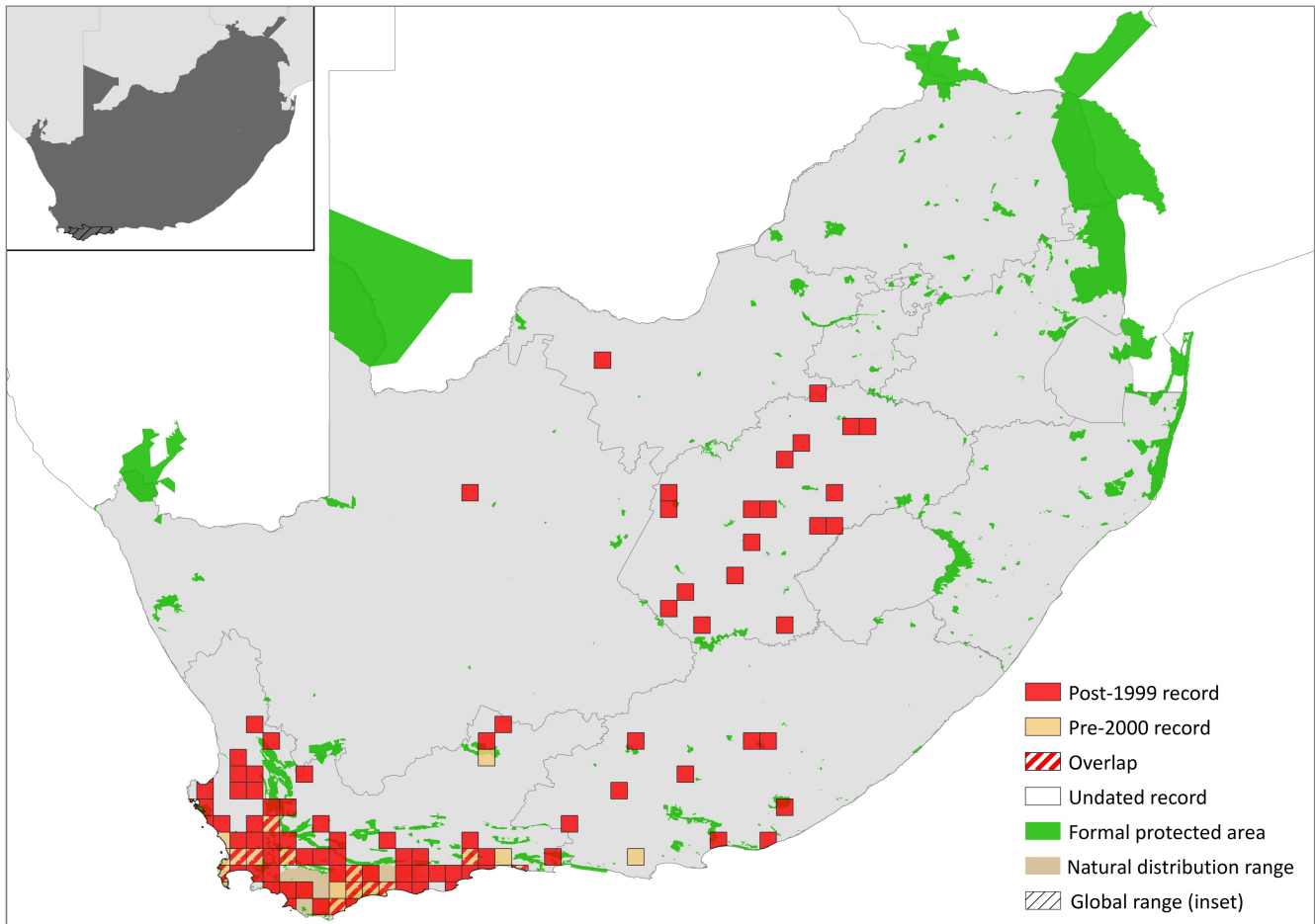


Figure 1. Distribution records for Bontebok (*Damaliscus pygargus pygargus*) within the assessment region

Table 1. Countries of occurrence within southern Africa

Country	Presence	Origin
Botswana	Absent	-
Lesotho	Absent	-
Mozambique	Absent	-
Namibia	Absent	-
South Africa: Western Cape	Extant	Native
South Africa: Eastern Cape	Extant	Introduced
South Africa: Northern Cape	Extant	Introduced
South Africa: Free State	Extant	Introduced
South Africa: North West	Extant	Introduced
Swaziland	Absent	-
Zimbabwe	Absent	-

are unknown, and that no long-term data from the private sector exist to prove that the population has passed the threshold for Near Threatened for five years, we take a precautionary purview and list Bontebok as Vulnerable D1. Additionally, because the upper estimate of the potential area of occupancy (AOO) is 1,453 km² and that there is continuing loss of suitable habitat that limits population expansion within both the natural and benign introduction range, as well as all subpopulations being fragmented by fencing with no metapopulation plan in place, Bontebok also qualifies for Vulnerable B2ab(ii).

The major threats to Bontebok are the uncertainty around the number of hybrids within the existing population, lack of habitat availability within its natural range (thus limiting population expansion), and the lack of a metapopulation plan to sustain genetic diversity. High incidences of hybridisation might render the majority of Bontebok subpopulations unfit for Red List inclusion and low genetic diversity may ultimately reduce the resilience of the subspecies. These threats should be counteracted through (1) the identification of all pure Bontebok subpopulations (and thus more accurate assessment of population size); (2) the development and implementation of an active metapopulation management plan for the pure Bontebok subpopulations to simulate gene flow, prevent inbreeding and to sustain a flourishing and resilient population; and (3) exclusion of Blesbok from core areas supporting Bontebok inside its natural range. Conservationists should thus incentivise landowners to become Bontebok stewards to expand the conservation estate for this subspecies within the natural and benign introduction range. Bontebok are able to use a variety of habitats, the key features being grassy landscapes and the availability of water. For example, they readily utilise short grass areas and transformed landscapes. This tolerance, and hence relative ease of management, together with their iconic status, facilitates stewardship prospects. This assessment should be revised when such data become available.

Distribution

Bontebok are endemic to the Western Cape, South Africa, although introductions have been made in most provinces

(Figure 1). Historically, they were confined to the coastal plain (60–200 m) east of the Kogelberg in the Western Cape where they are believed to have concentrated on the renosterveld areas (Boshoff & Kerley 2001; Skead 2011). Early settlers may have confused Bontebok and Blesbok, which overestimated the historical distribution of Bontebok. In reality, the subspecies were separated by at least 320 km at the time of European settlement (Skinner & Chimimba 2005; Boshoff et al. 2015) (Figure 2). Here, overhunting reduced it from locally abundant to the verge of extinction. It was saved from extinction in the mid-19th century by a few Cape farming families who protected the small remnant subpopulations. From a low of 22 animals in the original Bontebok National Park (established near Bredasdorp in 1931), the Bontebok population has gradually recovered (van Rensburg 1975). Translocated Bontebok from Bontebok National Park have formed the nucleus of reintroduced populations in other protected areas such as provincial and local authority nature reserves. The Bontebok National Park subpopulation is genetically pure (tested in April 2014).

Suitable natural habitat within the indigenous natural range (IDR) is limited to the remaining renosterveld patches and some grassy micro-habitat patches in the fynbos areas of the Overberg region. The extent of occurrence is estimated to be 8,779 km², of which 3,664 km² comprises remaining natural habitat (GeoTerralimage 2015), which can be construed as the maximum potential area of occupancy (AOO). However, only 623 km² of the preferred renosterveld habitat remains within the natural range, which closely matches the current estimated AOO within the IDR of 602 km². The latter may be an

overestimate because only approximately 12% of De Hoop Nature Reserve is actually used by Bontebok (Radloff 2008), and Agulhas National Park currently has very little renosterveld within it. Thus, the amount of utilisable or optimal habitat is both limited and fragmented within the natural range.

Preliminary genetic analyses indicate a low genetic variation within the IDR population (van der Walt et al. 2001, 2013). Within the IDR, the subpopulation is fragmented into small subpopulations restricted by fences. Habitat loss within the IDR has been so extensive that the area is estimated to be able to, at best, support 38% of the pre-transformation population potential (Kerley et al. 2003). The poor quality and limited availability of remaining habitat within the IDR necessitated the regulatory extension of their range, which we label here the benign introduction range (BIR) based on the latest Red List guidelines (IUCN Standards and Petitions Subcommittee 2014) (Figure 3). The AOO estimate increases to 1,153–1,453 km² depending on the inclusion of protected areas alone or private properties as well within the BIR. This range extension has been spatially modelled to include habitat aspects such as altitude, slope and major preferred vegetation types, within a range that had been demarcated for regulatory purposes, whereby translocations of the subspecies were permitted outside its natural range prior to 2012. The BIR has enabled additional utilisation of this subspecies by private land owners and the creation of a buffer population from which to augment subpopulations within the IDR. Both West Coast and Table Mountain national parks are located within the BIR. To date, however, no reintroductions into

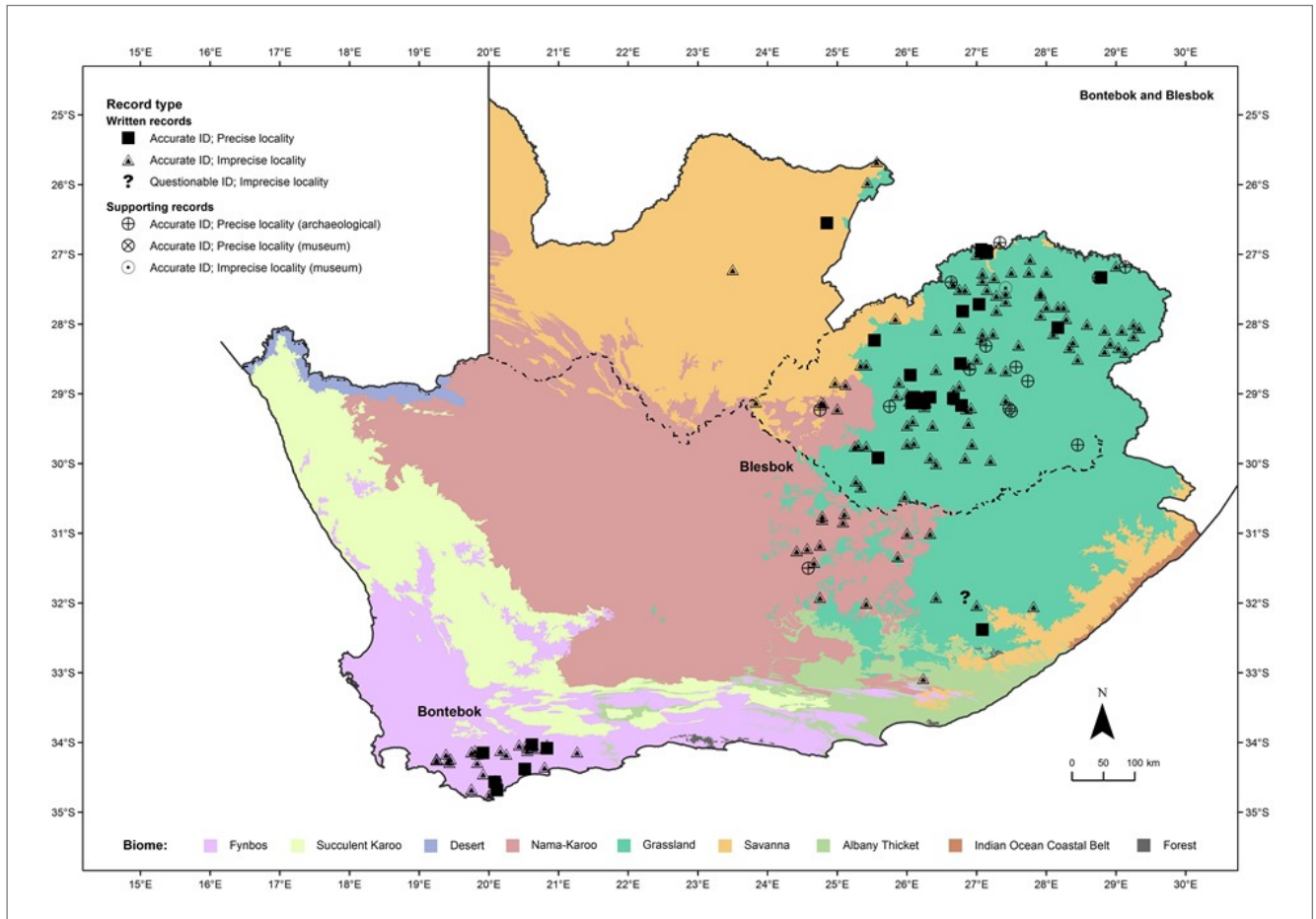


Figure 2. Historical distribution of Bontebok (*Damaliscus pygargus pygargus*) and Blesbok (*D.p. phillipsii*) within the assessment region (source: Boshoff et al. 2015); colour shading delineates biomes

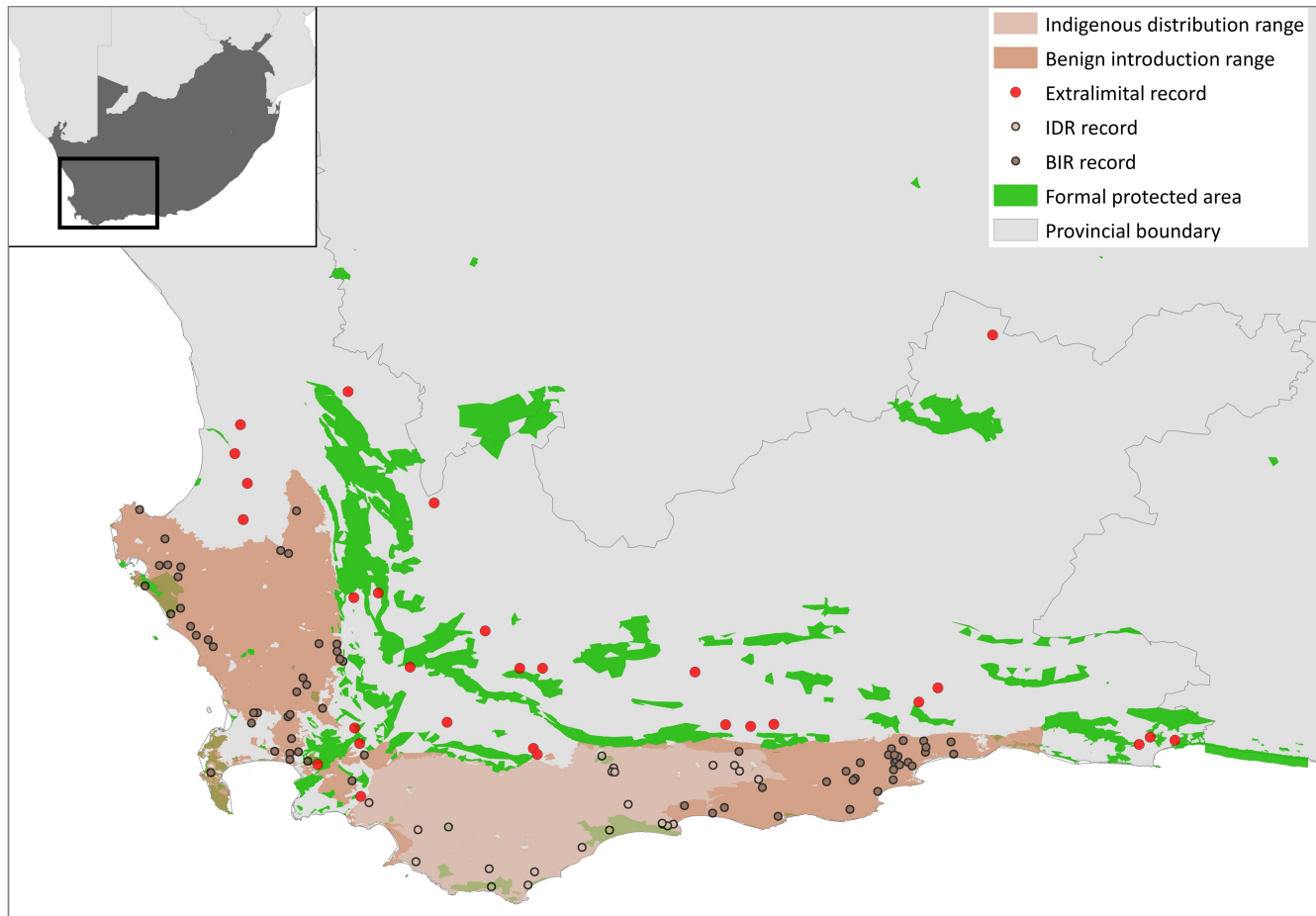


Figure 3. Distribution of Bontebok (*Damaliscus pygargus pygargus*) within the Western Cape, showing indigenous natural distribution range (IDR), the benign introduction range (BIR) and extra-limital subpopulations

IDR protected populations have occurred. For example, Agulhas National Park only has two Bontebok but the long-term plan is to source animals for future translocations from Table Mountain and West Coast national parks. All translocations in the Western Cape are subject to the CapeNature Bontebok Conservation, Translocation and Utilisation Policy (Birss et al. 2013), which requires all proposed Bontebok for translocation to be genetically tested and declared pure before release. Some Bontebok subpopulations in the BIR can be considered *ex-situ* conservation or benign introductions as they are within an environment that is reasonably close to the indigenous range and variables such as winter rainfall, disease, and habitat are considered similar enough to create comparable natural selection pressures. Additionally, this is a region where spatial separation from Blesbok is feasible, which has specific value in controlling the issuing of permits for Blesbok in this area. Importantly, the population within the IDR is <1,000 mature individuals and thus the BIR concept is a mechanism to support a viable population. However, at present, there is no metapopulation plan to connect subpopulations within the BIR to the IDR and thus the two populations are effectively isolated. Similarly, until genetic testing has been completed for both formally protected and privately protected subpopulations, it is uncertain which subpopulations should form part of the metapopulation. Thus, a precautionary approach is employed in including subpopulations.

Extra-limital subpopulations have been established on private farms or ranches in at least the Eastern Cape, Northern Cape, Free State and North West provinces

(Figure 1), and there is pressure to increase the extent of introduction (Power 2014). These extra-limital introductions could be detrimental to the subspecies because Bontebok are adapted to very unique habitat and climatic conditions: the East Coast Renosterveld bioregion receives some rain throughout the year but has a distinct peak during winter with about 65% of rain falling between April and October. These animals thus adapted over at least 20,000 years in isolation from the Highveld-bound Blesbok to a climate of wet and cold winters and warm and dry summers. This is opposite to the conditions experienced by Blesbok that experience warm and wet summers and very cold but dry winters.

Population

Due to its restricted range, habitat transformation for agriculture, competition with domestic grazers and over-hunting, meant the Bontebok population reached a critical low in 1931 when 22 animals were fenced into the newly proclaimed Bontebok National Park (van Rensburg 1975). Bontebok National Park was proclaimed in the Bredasdorp district with the specific goal of protecting a subpopulation of the subspecies (Barnard & van der Walt 1961). Population numbers increased, but remained below 100 individuals. It was then discovered that the animals at this site suffered from copper deficiency and high parasite infestation, specifically lungworm (*Protostrongylus* spp.). The park was also very small (6.8 km²) and was extensively covered (80%) by the unpalatable renosterbos (*Dicerothermus rhinocerotis*) (Barnard & van der Walt 1961). In 1960, the present site of Bontebok National Park was proclaimed close to

Swellendam and 84 Bontebok were translocated there, of which 61 survived (Penzhorn 1971). In the new area, numbers increased to 320 in 1981 with the current subpopulation maintained at around 250 and is currently 190 individuals after an annual off-take in 2014. The combined subpopulation for De Hoop Nature Reserve and neighbouring Denel Overberg Test Range, which is managed as an ecological unit, is currently estimated at 492 individuals, with a maximum of 526 individuals ever recorded. However, this subpopulation is prone to crashes if not managed correctly (Scott 1993). The current subpopulation size for Aghulhas National Park and Salmondsdam Nature Reserve is only two individuals, emphasising the urgent need for a metapopulation plan to create viable subpopulations.

Based on field surveys and censuses, we can determine the current number of Bontebok with reasonable accuracy. Within the IDR, there are 686 individuals in four formally protected areas (Table 2; we include the greater De Hoop Area that comprises De Hoop Nature Reserve and the privately owned Denel Overberg Test Range here). Subpopulation demographics from Bontebok National Park suggest a mature population structure of 75%, where a 1974 survey tallied 360 animals of which 71 were under two years of age and not deemed sexually mature (de Graaff et al. 1976). Using the figure of 75% thus implies that there are 515 mature individuals within the natural range. If the subpopulations existing on formally protected areas within the BIR are considered, the total mature population size may be considered to be 664 (Table 2). Additionally, there are an observed 219 individuals on 50 private properties within the IDR, which increases the mature population size to 679 individuals (Table 2), or 828 if we include the protected areas from BIR too. However, some of these subpopulations are intensively managed, or contain hybrids (Birss et al. 2013), and thus may not be eligible for inclusion (IUCN Standards and Petitions Subcommittee 2014). While both Bontebok National Park and Greater De Hoop Areas subpopulations have been genetically certified as pure, most private properties have not been tested and, of those tested, hybrids have been found (CapeNature unpubl. data). Ongoing testing will determine the number of

subpopulations on private properties that are pure and thus eligible for inclusion in the Red List. For the problem of intensive management, a preliminary analysis to determine which private subpopulations can be considered wild, revealed that 33–39% of private subpopulations are eligible for inclusion in the assessment (based on a sample of N = 18 private subpopulations from across the country, Endangered Wildlife Trust unpubl. data). Depending on whether we extrapolate this proportion to the private farms within the natural and benign introduction range (N = 141 properties) with the most or least abundant subpopulations yields an additional 118–1,272 individuals respectively, and thus 89–954 mature individuals. This increases the mature population range, including all formally protected areas and private subpopulations within both the IDR and BIR, to 752–1,618 individuals. However, it is important to note that this estimate does not include the serious threat of hybridisation which might reduce the number of eligible private subpopulations dramatically. The crux of Bontebok conservation is determining genetic purity of its subpopulations and the consensus among the assessors is that population size must be conservatively based on only genetically tested subpopulations that have been shown to be pure.

Overall, the core population within the natural range on protected areas has not increased since the 2004 estimate (Friedmann & Daly 2004), where the total population tallied to 770 individuals compared to 686 individuals in 2014 (Table 2). Outside of the IDR and BIR, however, Bontebok subpopulations are increasing. There are an observed 4,857 individuals (existing in extra-limital areas, which are not included in this assessment; IUCN Standards and Petitions Subcommittee 2014). This is probably an underestimate as not all information from the private sector is available. Extra-limital subpopulations are not considered to possess conservation value for reintroduction or supplementation in the IDR. For example, although the Tsolwana Nature Reserve, Eastern Cape, subpopulation was registered as pure Bontebok based on phenotypic, but not genetic, assessment (Fabricius et al. 1989), it is not considered an ideal source for reintroductions because the selection pressure outside

Table 2. Summary of population size estimates for Bontebok (*Damaliscus pygargus pygargus*) for both Formally Protected (FP) and Privately Protected (PR) areas inside and outside the indigenous natural range. Data represent minimum observed counts.

Province	Type	Inside natural distribution range	No of reserves/ properties	Subpopulation total (2013–2015)	Mature 75%
Western Cape	FP	Yes	4	686	515
Western Cape	PR	Yes	17	219	164
Western Cape	FP	No	2	199	149
Western Cape	PR	No	124	1,506	1,130
Eastern Cape	FP	No	1	181	136
Eastern Cape	PR	No	68	2,605	1,954
Northern Cape	PR	No	27	1,251	938
Free State	PR	No	22	812	609
North West	PR	No	1	8	6
Grand total	All	Both	266	7,467	5,601
Total natural range	FP	Yes	4	686	515
Total natural/benign introduction range	FP	Both	6	885	664
Total inside natural range	FP + PR	Yes	21	905	679

the natural range may differ significantly. Here, the number of years/generations since departure from the natural range will be important: if it is only a couple of years or generations since departure it might still be an acceptable source for reintroduction providing that the subpopulation was not subjected to selective breeding (Champagnon et al. 2012). Initial indications are that 116 extra-limital subpopulations are from herds that have been registered as pure based on phenotypic traits and another 229 are from herds that have been genetically tested (D. Dalton unpubl. data). These data still need more analysis, though, as there are a number of owners listed where numbers are not given and it is suspected that a greater proportion may also have been tested and or registered. However, these subpopulations, even if pure, are still of limited conservation value due to the problems associated with re-stocking from extra-limital subpopulations and outbreeding depression (Champagnon et al. 2012). Thus, extra-limital subpopulations of Bontebok, especially if maintained over several generations are of little to no value to Bontebok conservation.

A metapopulation management plan is desperately needed to sustain Bontebok genetic purity and diversity. Within the IDR, there are many small properties containing small subpopulations that cannot increase in size because they are limited by space. In the natural areas, there is also a space limitation due to extensive crop production. For example, the average subpopulation size on private properties in the Western Cape is 14 ± 20 individuals ($N = 127$ properties), compared to 38 ± 36 individuals in the Eastern Cape ($N = 69$ properties), 28 ± 31 individuals in the Free State ($N = 22$ properties), and 46 ± 49 individuals in the Northern Cape ($N = 27$ properties). Of 6,677 individuals estimated to have potentially occurred in the natural range before habitat transformation, only 2,544 individuals are estimated to be able to be supported now (Kerley et al. 2003). Thus, although there is still scope for the core population to increase (currently only 905 individuals in total within the natural range), protected areas and private conservation areas must significantly expand to create larger areas of natural habitat for the population and these should be connected to a wider metapopulation that includes the benign introduction range to become a resilient population.

Current population trend: Stable, but with ongoing habitat decline. Formally protected subpopulations maintained at ecological stocking rates.

Continuing decline in mature individuals: There is no observed decline. Within the natural range the population is regulated and stable. Outside the natural range, the population is increasing.

Number of mature individuals in population: 515–1,618 individuals, depending on inclusion of subpopulations within the benign introduction range.

Number of mature individuals in largest subpopulation: 295–344 individuals in the Greater De Hoop Area (De Hoop Nature Reserve and Denel Overberg Test Range).

Number of subpopulations: Within the natural range, there are only two formally protected subpopulations in Bontebok National Park and Greater De Hoop Area (Agulhas National Park and Salmondssdam Nature Reserve do not have viable subpopulations). There are an additional 17 private subpopulations. The total number of potential subpopulations within the natural range is thus 2–19.



Frans Radloff

Severely fragmented: Yes, at present, the dispersal of the Bontebok is restricted by fences and it is dependent on translocation for dispersal.

Habitats and Ecology

The historical distribution range of Bontebok is very closely associated with the East Coast Renosterveld bioregion, which comprises four different vegetation types: Western Rûens Shale Renosterveld (14% remaining), Central Rûens Shale Renosterveld (13% remaining), Eastern Rûens Shale Renosterveld (19% remaining) and Mossel Bay Shale Renosterveld (Mucina & Rutherford 2006).

Bontebok are almost exclusively grazers (Beukes 1984), with a preference for short grass and recently burnt veld (Beukes 1987; Novellie 1987; Kraaij & Novellie 2010). Water is an essential habitat requirement and they stay within 1.5 km from surface water during the dry season (van Zyl 1978; Luyt 2005; David & Lloyd 2013). Within their natural range on the coastal lowlands, grassy areas are predominantly found in the renosterveld areas but Bontebok also make use of small grassy microhabitats or recently burnt fynbos and strandveld habitats (Scott 1993; Radloff 2008). Suitable habitat for Bontebok is thus predominantly limited to the remaining renosterveld patches in the Overberg region. Fragmented subpopulations are currently found primarily in suboptimal habitat and old cultivated lands where they appear to do relatively well. Bontebok avoid tall woody vegetation with low visibility and areas with steep slopes, preferring open areas with low shrubs (Novellie 1987). Watson et al. (2011) showed that Bontebok are more closely associated with burnt veld than Cape Mountain Zebra (*Equus zebra zebra*) in Bontebok National Park. From 4–5 years post fire they no longer show interest in the burnt vegetation type and revert to grazing lawns of *Cynodon dactylon*.

A detailed 15-month study of Bontebok behaviour in Bontebok National Park during 1969 and 1970 revealed that the social structure comprises bachelor herds, nursery herds and territorial males (David 1973). Territories were found to be small in size and limited in number, leaving large areas where bachelor herds can roam with little or no harassment. Males defended their territories throughout the year through ritualised chasing but physical fighting was not observed. The average nursery herd size was three adult females with 1.5 lambs. De Graaff et al. (1976) found a similar figure of 3.0 ± 2.2 ($N = 18$ herds) females in a breeding herd. Bachelor herds consist of males of all ages older than one year, as well as yearling females (David 1973). Bachelor herd size

Table 3. Use and trade summary for the Bontebok (*Damaliscus pygargus pygargus*)

Category	Applicable?	Rationale	Proportion of total harvest	Trend
Subsistence use	No	Low incidence of illegal poaching.	Unknown, but small.	Stable
Commercial use	Yes	Trophy hunting and live sales.	All	Increasing
Harvest from wild population	Yes	Formally protected areas sell animals to the private sector.	Minority	Stable. However, the offtake includes translocations out of the natural range which may be higher than the increase in the population.
Harvest from ranched population	Yes	Extensive systems are used for trophy hunting and semi-intensive breeding.	Majority	Possibly decreasing due to the increased value of Bontebok, whereby they are increasingly now being confined in small camps and managed more intensively.
Harvest from captive population	Yes	Intensive breeding in captive environments for live animal sales at game auctions.	Minority	Possibly increasing due to their increasing commercial value (see above).

was 8.5 ± 6.3 (N = 12 herds) in the study of de Graaff et al. (1976); and David (1973) reported as many as 75 animals together. Young males and females leave the nursery herd on their own accord and can remain solitary but usually join bachelor groups (David 1973). Males do not seem to establish territories before the age of 5–6 years of age and return to bachelor herds once displaced from their territories (David 1973). Bontebok were found to be strong seasonal breeders with the main calving season being September–October and the rutting season from January to mid-March (David 1973).

Ecosystem and cultural services: Bontebok are a flagship subspecies of the Cape Floristic Region, particularly renosterveld, and can be used in ecotourism ventures. Rarity may increase its trophy hunting value, especially that of pure Bontebok.

Use and Trade

The horns and skins are traded as part of trophy hunts, and live animals are traded at game auctions (Table 3). Individuals are utilised from captive breeding, ranched (extensive) and wild (formally protected) areas. Activities on private land are mainly for ecotourism, trophy hunting and breeding of trophy animals. As such, the subspecies is widely hunted and traded outside of its natural range where it has increased dramatically in numbers but unfortunately have limited conservation value. The translocation of Bontebok and Blesbok outside their natural range is a significant threat to the continued existence of the two subspecies, as hybridisation takes place and becomes increasingly likely. Additionally, there is a concern that there is a net flow of individuals away from the natural range. Western Cape permit data for the last 10 years show that almost 600 animals have been translocated from the natural range and a further 200 from

the benign introduction range. Since hunting is not regulated through direct permitting, the number of hunted Bontebok is unknown. Bontebok is a subspecies listed on Certificates of Adequate Enclosures (CoAEs), which means that harvest/hunt/export is not regulated but exempted from separate applications and consequently there is limited regulatory control of subpopulations on private properties (Birss et al. 2013).

At present there has been no reported illegal offtake of Bontebok in any of the national parks or provincial parks where they occur. Given the limited genetic diversity of Bontebok, a strict control of live animal sales needs to be set in place to limit inbreeding in the long term. Additionally, exporting animals outside of the natural range can deplete the genetic pool of the core population and management plans should thus ensure that the translocation of animals, as part of a managed metapopulation, is kept between the natural and benign introduction range.

Farmers saved this subspecies from extinction but modern wildlife ranchers have ambiguous effects on Bontebok conservation (Table 4). Wildlife ranching is not prominent in the natural range and it appears as if the largely extra-limital industry is impacting negatively on landowners within the natural range who want to contribute to the conservation of the subspecies but increasingly cannot afford to buy and stock Bontebok. The value of the subspecies has increased in the last five years and there is an increasing demand for extra-limital introductions such as in the North West Province (Power 2014). Genetic testing for purity has increased the price and the demand for pure animals. This might act as an incentive to not only conserve the subspecies itself, but also its preferred habitat, the renosterveld, although there is no evidence that this is currently happening in its native

Table 4. Possible net effects of wildlife ranching on the Bontebok (*Damaliscus pygargus pygargus*) and subsequent management recommendations

Net effect	Unknown
Data quality	Inferred
Rationale	Private landowners have increased the numbers of this subspecies but may also be threatening its genetic integrity by hybridising it with Blesbok and/or intensively managing it to the detriment of the natural evolutionary process.
Management recommendation	Cooperate with provincial authorities in implementing a scientifically sound metapopulation plan aimed at creating a genetically diverse, pure and resilient population with the natural and benign introduction range.

range. Prudent veld management is needed in the native range where Bontebok do occur, as improving grass cover within renosterveld might result in the loss of plant species diversity, including species classified as rare or threatened (Novellie & Kraaij 2010). On the negative side, there is evidence that some private landowners deliberately hybridise Bontebok and Blesbok for trophy hunting purposes (Schmidt 1999), and artificial selection for colour morphs and exceptional horn lengths is suspected. The hybrid and artificial selection threat must be curbed through a management plan taken up and enforced by all participating landowners.

Threats

The major threats for this subspecies are hybridisation with Blesbok, the lack of available habitat within its natural range (thus limiting population expansion), low genetic diversity, which was probably the result of two bottlenecks caused by overhunting and disease (van der Walt et al. 2001) and poor gene flow between subpopulations. Habitat loss is severe and in some cases irreversible. Although the population size of what we hope is pure Bontebok has increased, it has remained relatively low compared to other ruminants (for example, Broders et al. 1999). The ultimate threat is the indiscriminate and uncontrolled movement of Blesbok, Bontebok and Blesbok/Bontebok hybrids across the country. As such, the exact status of Bontebok and the long-term security of the subspecies is still uncertain. Additionally, there is uncertainty over the impact climate change will have, especially in terms of the synergistic threat of habitat loss. The corresponding threats are (Table 5):

1. Habitat loss and consequent lack of available habitat, leading to fragmented and isolated subpopulations, which exist primarily on suboptimal habitat. Here Bontebok are currently managed as sources for properties outside the natural range for commercial gain, while comparatively little effort is being directed towards habitat rehabilitation and restoration to secure the future of the core Bontebok population within the natural range in the Western Cape. Currently, only 9–12% of renosterveld remains (Von Hase et al. 2003; Cowell & Birss 2013). The opportunity exists for fragmented natural areas to be linked via corridors to larger natural areas and to conserve more of the threatened renosterveld vegetation.
2. Low genetic diversity within the core natural range population and thus lack of resilience to environmental change. The historical bottlenecks are currently exacerbated by the fragmented and isolated nature of the subpopulations, which can lead to decreased genetic variation within individual subpopulations due to genetic drift. Additionally, biased selection pressures (for coat colour, pattern and horn sizes) further threaten the genetic integrity and viability of the population with inbreeding depression. The decision to translocate pure Bontebok, as part of a metapopulation should therefore not only consider the genetic purity of the subspecies, but also consider the genetic relationships among the subpopulations involved.
3. Hybridisation with Blesbok, which has been introduced into the Western Cape, may affect a significant number of subpopulations. Hybridisation

Table 5. Threats to the Bontebok (*Damaliscus pygargus pygargus*) ranked in order of severity with corresponding evidence (based on IUCN threat categories, with regional context)

Rank	Threat description	Evidence in the scientific literature	Data quality	Scale of study	Current trend
1	<i>2.1 Annual & Perennial Non-Timber Crops and 2.3 Livestock Farming & Ranching</i> : historical loss of habitat has led to small, isolated habitat patches and lack of available remaining habitat. Current stresses <i>1.2 Ecosystem Degradation, 1.3 Indirect Ecosystem Effects and 2.3.5 Inbreeding</i> : degradation and fragmentation of remaining ecosystems limits resource availability and subpopulation growth, contributing to continued loss of genetic diversity through inbreeding.	Von Hase et al. 2003	Indirect (remote sensing)	Regional	Only 9–12% renosterveld remains in natural range.
		Pence 2014	Indirect (land cover change from remote sensing)	Regional	Ongoing. Between 2006 and 2011, 107 km ² of natural habitat was lost per annum.
		GeoTerralmage 2015	Indirect (land cover change from remote sensing)	National	Ongoing. Between 2000 and 2013, 8.6% rate of urban settlement expansion.
		Van der Walt et al. 2001	Empirical	National	Greater genetic diversity found in Blesbok when compared to Bontebok.
2	<i>5.1.1 Intentional Use and 8.2 Problematic Native Species/Diseases</i> : historical overhunting and diseases outbreaks led to genetic bottleneck. Current stress <i>2.3.5 Inbreeding</i> : continued loss of genetic diversity through inbreeding.	Van der Walt et al. 2001	Empirical	National	Greater genetic diversity found in Blesbok when compared to Bontebok.
3	<i>8.1.2 Invasive Non-Native/Alien Species/Diseases</i> : intentional introduction of Blesbok into natural habitat of Bontebok. Current stress <i>2.3.1 Hybridisation</i> : deliberate hybridisation.	Van Wyk et al. 2013	Empirical	National	Hybridisation was detected in 33% (40 of 121) of the sampled individuals. Possibly increasing due to movement of subspecies across the country.

between the two has occurred due to human-mediated mixing of the separate subspecies. However, what is not known is the full extent to which hybridisation occurs. Preliminary research shows that a high proportion of Bontebok could be hybrids (van Wyk et al. 2013). Hybridisation was detected in 33% (40 of 121) of the samples with unknown purity. It is thus vital that hybridisation tests be expanded to include all regions in the natural and benign introduction ranges where potentially pure Bontebok subpopulations may be under threat. Negative consequences associated with hybridisation include reduction of fitness, alteration in the genetic structure of populations and the interference of locally co-adapted gene complexes (Allendorf et al. 2001). However, a study assessing body condition of hybrids in Oviston Nature Reserve, Eastern Cape, found that hybrid body condition was similar to Blesbok within their natural range and is probably adequately adapted to the Eastern Cape environment (Schmidt 1999). Further research is needed for subpopulations in the Western Cape. In the worst case scenario hybridisation might lead to the extinction of both the Blesbok and Bontebok subspecies, before the debate on the taxonomic status of the two subspecies/species has been resolved.

4. The overall management concern is the lack of a metapopulation management strategy for this subspecies, without which there is mismanagement and misunderstanding between stakeholders. The development of a strategic management plan that is aimed at ensuring the long term survival of Bontebok and uniting stakeholders is urgently required. Such a strategy should include incentives for landowners to continue managing and conserving Bontebok and it should build on the strengths of the previous success of saving this subspecies when only approximately 22 individuals remained in the 1930s.

Current habitat trend: There is an ongoing decline in natural habitat where agricultural expansion threatens to reduce the remaining renosterveld habitat on which this subspecies thrives. Pence (2014) calculated that between 2006 and 2011, 536 km² of land was converted to agriculture (107 km² / year) in the Western Cape. This is alarming since 31% of losses occurred within Critical Biodiversity Areas, which have been promoted in environmental decision-making as places within which losses should be avoided. Similarly, there has been an 8.6% increase (1,029 km² to 1,118 km²) in urban areas and development between 2000 and 2013 (GeoTerraImage 2015), which we infer to impact negatively on natural habitat. Subsequently, there is only about 9% of intact renosterveld left. However, Bontebok can survive on transformed land, as long as there is an adequate supply of short grass available, but that is far from the ideal situation (Cowell & Birss 2013). Additionally, the quality of remaining natural habitat may decline due to projected impacts of climate change (Midgley et al. 2002). Thus, securing remaining habitat, combined with habitat rehabilitation and sound management, is crucial.

Conservation

Currently, key protected areas include Bontebok National Park (genetically certified pure subpopulation within the natural range); Table Mountain National Park (genetically certified pure subpopulation within the benign introduction range); De Hoop Nature Reserve and Denel Overberg

Test Range (largest subpopulation within the natural range); and Agulhas National Park (potential for significant subpopulation growth within the natural range). Although subpopulations have exhibited positive growth rates, oftakes and translocations from within the natural range have suppressed overall population growth. Similarly, the lack of available habitat within the natural range has inhibited population expansion and an increase in area of occupancy. The net effect is that the core Bontebok population has not increased within the natural range since the 2004 assessment (Friedmann & Daly 2004).

To redress this, the main interventions should be the development and implementation of a Biodiversity Management Plan and metapopulation strategy, as well as the acquisition and connection of additional natural habitat within both the IDR and BDR.

Biodiversity Management Plan: Regulation of translocation is required to prevent hybridisation with Blesbok and Bontebok/Blesbok hybrids. Subpopulations within the natural and benign introduction ranges should be tested for purity and flagged as important subpopulations to potentially reintroduce or augment other areas. During a National Workshop on Bontebok Purity Testing and Management held in 2009, the National Zoological Gardens of South Africa was mandated to further develop a scientifically defensible genetic test for Bontebok and Blesbok hybridisation using microsatellite (DNA) markers. The genetic test developed is supported by peer-reviewed scientific publications and forms the basis for the updated CapeNature Bontebok Conservation, Translocation and Utilization Policy, as well as the national implementation of a standardised genetic testing protocol (Birss et al. 2013). Any animal which will be translocated must be tested and must be fitted with a microchip, and all test results are stored in a central database at the National Zoological Gardens. This information will inform metapopulation management, but will also flag properties where hybrids have been identified, which will allow conservation agencies to enforce regulations. It is foreseeable that collaboration between provinces will identify which subpopulations need to be targeted for further testing. Thus far, legislation appears to be working to prevent hybridisation. The CapeNature policy instructs that hybrids be destroyed within 48 hours of results being known and, until now, destruction orders have been carried out effectively. Once subpopulations have been identified that are eligible for inclusion in the Red List, a metapopulation plan should be employed to ensure translocations are used to sustain genetic diversity and increase the number and size of subpopulations within the natural and benign introduction ranges. The superior financial value of pure Bontebok subpopulations may be one mechanism to incentivise landowner participation.

Securing natural habitat: Conservancies and corridors must be created to conserve areas of suitable remaining natural habitat to ensure positive population growth for Bontebok in the IDR. For this to happen, the Biodiversity Management Plan currently being drafted must be adopted by public and private stakeholders, and biodiversity stewardship schemes should be strategically established. The importance of biodiversity stewardship is clear: currently, Agulhas National Park only has two Bontebok. However, 38 Bontebok from the Greater De Hoop Area were donated to the Nuwejaars Special Management Area (NSMA) in 2010. The NSMA is situated on the southern Agulhas Plain which includes a variety of

Table 6. Conservation interventions for the Bontebok (*Damaliscus pygargus pygargus*) ranked in order of effectiveness with corresponding evidence (based on IUCN action categories, with regional context)

Rank	Intervention description	Evidence in the scientific literature	Data quality	Scale of evidence	Demonstrated impact	Current conservation projects
1	<i>3.3.1 Reintroduction</i> : translocations and reintroductions regulated under a metapopulation strategy as informed by a Biodiversity Management Plan, including both private and formally protected areas.	-	Anecdotal	-	-	Biodiversity Management Plan currently being devised by SANParks and CapeNature.
2	<i>1.2 Resource & Habitat Protection</i> : biodiversity stewardship of renosterveld patches as potential reintroduction sites.	-	Anecdotal	-	-	CapeNature
3	<i>1.1 Site/Area Protection</i> : formal protected area expansion to create habitat corridors and conservancies to protect remaining renosterveld.	Kerley et al. 2003	Simulated	Regional	Sufficient remaining habitat to support 2,500 Bontebok in natural habitat if habitat connected and protected.	SANParks, CapeNature
4	<i>2.3 Habitat & Natural Process Restoration</i> : restore remaining renosterveld patches in within natural distribution range to increase areas for Bontebok reintroduction.	-	Anecdotal	-	-	-
5	<i>5.1 Legislation</i> : legislation designed to use biodiversity offsets to slow habitat loss within the natural distribution range.	-	Anecdotal	-	-	-
6	<i>6.3 Market Forces</i> and <i>6.4 Conservation Payments</i> : designing incentives for private landowners to participate in biodiversity stewardship and metapopulation management.	-	Anecdotal	-	-	-

threatened vegetation types, amongst which are Overberg Sandstone, Overberg Sand Fynbos, Overberg Dune Strandveld, Agulhas Limestone Fynbos, Elim Ferricrete Fynbos, De Hoop Limestone Fynbos and Central Rûens Shale Renosterveld. The NSMA consists of landowners who are committed to contributing to and pioneering this landscape conservation initiative, while maintaining their farming operations, and highlights the stewardship potential of private landowners for Bontebok conservation. Expansion of existing protected areas until sufficient habitat for at least 2,000 Bontebok has been achieved within the natural range and creating links between protected areas wherever possible, is recommended (Kerley et al. 2003). Conservationists and private landowners should also restore renosterveld areas in the natural range and promote other mechanisms of slowing land-use change in the area. For example, offsets can be put in place where new land is being farmed.

Bontebok conservation is primarily concerned with growing the population to achieve viability (Traill et al. 2007) through increasing available habitat, maintaining metapopulation processes to offset inbreeding and preventing hybridisation. Overall, more effort should be invested in connecting, rehabilitating and sustaining a resilient and genetically pure population within the natural range, which can then be used to seed private properties wanting to maintain pure subpopulations. Conservationists should concentrate on rehabilitating renosterveld habitat within the natural range (von Hase et

al. 2003; Cowell & Birss 2013), and incentivising landowners to become Bontebok stewards to expand the conservation estate for this subspecies in both the IDR and BIR. This subspecies evolved in an environment very different from the Highveld grassland conditions associated with Blesbok and has the potential to act as a flagship subspecies for the renosterveld, thus incentivising the conservation of this highly threatened veld type. Additionally, Bontebok are tolerant to human activities and adapt to changes in the landscape. They readily utilise short grass areas and transformed landscapes, thus facilitating stewardship opportunities.

We recommend that Bontebok outside the natural and benign introduction range should not be used to reintroduce or augment subpopulations within these ranges, and that conservation efforts should be focused on securing and growing the native subpopulations that have been experiencing the most natural selection pressures. Although Bontebok are genetically depauperate, genetic recovery through hybridisation is not recommended given the potential alpha level taxonomic distinction between the Blesbok and Bontebok (van der Walt et al. 2013). We recommend that the putative subspecies be managed as separate evolutionary significant units and that more research is undertaken to determine the taxonomic statuses of Bontebok and Blesbok.

Recommendations for land managers and practitioners:

- At present there is no formal management plan for Bontebok in any province and SANParks currently has no specific management strategy. Bontebok National Park, which was established to ensure the survival of Bontebok, has the largest subpopulation within SANParks and can no longer expand in size. The Agulhas National Park has been identified as ideal habitat to establish a subpopulation of Bontebok but the park currently has no fencing. Funding has been requested to erect fences and only then can Bontebok be augmented here. Conservation agencies must identify similar sites for subpopulation augmentation and incorporate the sites into a metapopulation plan. SANParks and CapeNature have initiated a process to develop a Biodiversity Management Plan (BMP) for Bontebok. The BMP will be aimed at ensuring its long term survival in the natural and benign introduction range. The management plan should prioritise the identification of pure Bontebok subpopulations and make recommendations for the alignment of existing legislation to achieve the desired outcomes of the BMP. National and provincial legislation must be aimed at policies that prevent the co-occurrence of Blesbok and Bontebok and the exclusion of Blesbok within the IDR of Bontebok. It should also provide guidelines concerning the keeping of Blesbok and Bontebok in close proximity to each other in extra-limital areas. Guidelines on the movement and mixing of subpopulations inside and outside the natural, benign introduction and extra-limital ranges should also be created and implemented.
- Genetic testing, using the microsatellite markers identified by van Wyk et al. (2013), must be completed for all putative metapopulation subpopulations within the natural and benign introduction ranges.
- Harvesting to prevent overstocking/grazing can help maintain the remaining renosterveld habitat. There is an opportunity to use Bontebok as a flagship subspecies for the conservation and rehabilitation of renosterveld. However, if Bontebok become common outside its natural distribution range, the financial incentive associated with its rarity will be lost and with it the opportunity to use the subspecies to promote renosterveld conservation. This emphasises the importance of implementing the BMP mentioned above.
- Extra-limital subpopulations are expected to have little conservation value due to the increased probability of hybridisation with Blesbok, as well as the very different environmental conditions, and consequent selection pressure, they are exposed to. Restocking or reintroducing individuals from such subpopulations into natural or benign introduction subpopulations could cause deleterious effects such as changes in behaviour, morphology and demography that could in turn erode local adaptation and decrease the fitness of the core population. Thus, reintroduction or supplementation of individuals from extra-limital subpopulations is discouraged.

Research priorities:

- It is of utmost importance that the taxonomic status of Bontebok and Blesbok, as either subspecies of each other or separate species, is resolved as a matter of urgency. The uncertainty around their status thwarts decision-making and consequent conservation efforts.
- The size, demography, location and health status of pure Bontebok subpopulations need to be identified so that a metapopulation management plan can be designed and implemented.
- A recent survey for farms which had Bontebok in the Western Cape in the past revealed that many properties no longer have Bontebok and anecdotal information suggests that animals die from contracting pathogens from domestic livestock (lungworms) and from poor habitat quality. Understanding which private properties have pure Bontebok with stable or increasing populations, and could be incorporated as core sites into the metapopulation, is crucial.

Encouraged citizen actions:

- Landowners should form conservancies within the natural and benign introduction ranges to support free-roaming Bontebok herds and keep their herds genetically pure or cooperate with provincial conservation authorities to translocate according to a metapopulation plan.

Data Sources and Quality

Table 7. Information and interpretation qualifiers for the Bontebok (*Damaliscus pygargus pygargus*) assessment

Data sources	Census (unpublished), field study (unpublished), indirect information (unpublished)
Data quality (max)	Estimated
Data quality (min)	Inferred
Uncertainty resolution	Maximum/minimum values
Risk tolerance	Precautionary

References

- Allendorf FW, Leary RF, Spruell P, Wenburg JK. 2001. The problems with hybrids: setting conservation guidelines. *Trends in Ecology & Evolution* **16**:613–622.
- Barnard PJ, van der Walt DK. 1961. Translocation of the bontebok (*Damaliscus pygargus*) from Bredasdorp to Swellendam. *Koedoe* **4**:105–109.
- Beukes PC. 1984. Sommige aspekte van die ekologie van die Vaalribbok (*Pelea Capreolus*, Forster 1790) in die Bontebok Nasionale Park. M.Sc. Thesis. University of Stellenbosch, Stellenbosch, South Africa.
- Beukes PC. 1987. Responses of grey rhebuck and bontebok to controlled fires in coastal renosterveld. *South African Journal of Wildlife Research* **17**:103–108.
- Bigalke R. 1955. The bontebok (*Damaliscus pygargus* (Pall.)) with special reference to its history and preservation. *Fauna Flora, Pretoria* **6**:95–116.

Birss C, van Deventer JD, Hignett DL, Brown C, Gildenhuis P, Kleinhas D. 2013. Bontebok conservation, translocation and utilisation policy. Version 1. Western Cape Nature Conservation Board, CapeNature, Cape Town.

Boshoff AF, Kerley GIH. 2001. Potential distributions of the medium-to large-sized mammals in the Cape Floristic Region, based on historical accounts and habitat requirements. *African Zoology* **36**:245–273.

Boshoff A, Landman M, Kerley G. 2015. Filling the gaps on the maps: historical distribution patterns of some larger mammals in part of southern Africa. *Transactions of the Royal Society of South Africa* **70**:1–65.

Brodgers HG, Mahoney SP, Montevicchi WA, Davidson WS. 1999. Population genetic structure and the effect of founder events on the genetic variability of moose, *Alces alces*, in Canada. *Molecular Ecology* **8**:1309–1315.

Champagnon J, Elmberg J, Guillemain M, Gauthier-Clerc M, Lebreton J-D. 2012. Conspecifics can be aliens too: a review of effects of restocking practices in vertebrates. *Journal for Nature Conservation* **20**:231–241.

Cowell C, Birss C. 2013. Resource Information for Bontebok (*Damaliscus pygargus pygargus*) in South Africa. CRC-11-2013. Cape Research Centre, South African National Parks, Cape Town, South Africa.

David JHM. 1973. The behaviour of the Bontebok, *Damaliscus dorcas dorcas*, (Pallas 1766), with special reference to territorial behaviour. *Zeitschrift für Tierpsychologie* **33**:38–107.

David J, Lloyd P. 2013. *Damaliscus pygargus*. Bontebok / Blesbok. Pages 496–501 in Kingdon JS, Hoffmann M, editors. *Mammals of Africa*. Volume VI: Hippopotamuses, Pigs, Deer, Giraffe and Bovids. Bloomsbury Publishing, London, UK.

De Graaff G, van der Walt PT, van Zyl LJ. 1976. Populasie-samestelling van die bontebok *Damaliscus dorcas dorcas* in die Bontebok Nasionale Park gedurende Januarie 1974. *Koedoe* **19**:67–74.

Fabricius C, van Hensbergen HJ, Zucchini W. 1989. A discriminant function for identifying hybrid bontebok x blesbok populations. *South African Journal of Wildlife Research* **19**:61–66.

Friedmann Y, Daly B, editors. 2004. *Red Data Book of the Mammals of South Africa: A Conservation Assessment*. CBSG Southern Africa, IUCN SSC Conservation Breeding Specialist Group, Endangered Wildlife Trust, Johannesburg, South Africa.

GeoTerraImage. 2015. Quantifying settlement and built-up land use change in South Africa.

IUCN Standards and Petitions Subcommittee. 2014. Guidelines for using the IUCN Red List categories and Criteria. Version 11. Prepared by the IUCN Standards and Petitions Subcommittee.

Kerley GIH, Pressey RL, Cowling RM, Boshoff AF, Sims-Castley R. 2003. Options for the conservation of large and medium-sized mammals in the Cape Floristic Region hotspot, South Africa. *Biological Conservation* **112**:169–190.

Kraaij T, Novellie PA. 2010. Habitat selection by large herbivores in relation to fire at the Bontebok National Park (1974–2009): the effects of management changes. *African Journal of Range & Forage Science* **27**:21–27.

Luyt ED. 2005. Models of Bontebok (*Damaliscus pygargus pygargus*, Pallas 1766) habitat preferences in the Bontebok National Park and sustainable stocking rates. M.Sc. Thesis. University of Stellenbosch, Stellenbosch, South Africa.

Midgley GF, Hannah L, Millar D, Rutherford MC, Powrie LW. 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography* **11**:445–451.

Mucina L, Rutherford MC. 2006. *The Vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria, South Africa.

Assessors and Reviewers

Frans Radloff¹, Coral Birss², Carly Cowell³, Dean Peinke⁴, Desire Dalton⁵, Antoinette Kotze^{5,6}, Graham Kerley⁷, Matthew F. Child⁸

¹Cape Peninsula University of Technology, ²CapeNature, ³South African National Parks, ⁴Eastern Cape Parks & Tourism Agency, ⁵National Zoological Gardens of South Africa, ⁶University of the Free State, ⁷Nelson Mandela Metropolitan University, ⁸Endangered Wildlife Trust

Contributors

David Mallon¹, Jeanetta Selier²

¹IUCN SSC Antelope Specialist Group, ²South African National Biodiversity Institute

Details of the methods used to make this assessment can be found in *Mammal Red List 2016: Introduction and Methodology*.

Novellie P. 1987. Interrelationships between fire, grazing and grass cover at the Bontebok National Park. *Koedoe* **30**:1–17.

Novellie P, Kraaij T. 2010. Evaluation of *Themeda triandra* as an indicator for monitoring the effects of grazing and fire in the Bontebok National Park. *Koedoe* **52**:1–5.

Pence GQK. 2014. Western Cape Biodiversity Framework 2014 Status Update: Critical Biodiversity Areas of the Western Cape. Unpublished CapeNature project report. Cape Town, South Africa.

Penzhorn BL. 1971. A summary of the re-introduction of ungulates into South African National Parks (to 31 December 1970). *Koedoe* **14**:145–159.

Power RJ. 2014. The Distribution and Status of Mammals in the North West Province. Department of Economic Development, Environment, Conservation & Tourism, North West Provincial Government, Mahikeng. South Africa.

Radloff FGT. 2008. The ecology of the large herbivores native to the coastal lowlands of the Western Cape, South Africa. Ph.D. Thesis. University of Stellenbosch, Stellenbosch, South Africa.

Schmidt AG. 1999. Body condition in blesbok x bontebok hybrids in the Oviston Nature Reserve, Eastern Cape Province. *South African Journal of Wildlife Research* **29**:145–147.

Scott HA. 1993. An investigation into possible reasons for a decline in numbers of bontebok *Damaliscus dorcas dorcas* (Pallas, 1766) in the De Hoop Nature Reserve, Southwestern Cape. M.Tech Thesis. Port Elizabeth Technikon, Saasveld School of Forestry, Port Elizabeth, South Africa.

Skead CJ. 2011. Historical Incidence of the Larger Land Mammals in the broader Western and Northern Cape, Second Edition (Boshoff AF, Kerley GIH, Lloyd PH, editors). Port Elizabeth: Centre for African Conservation Ecology, Nelson Mandela Metropolitan University.

Skinner JD, Chimimba CT. 2005. *The Mammals of the Southern African Subregion*. Third edition. Cambridge University Press, Cambridge, England.

Traill LW, Bradshaw CJ, Brook BW. 2007. Minimum viable population size: a meta-analysis of 30 years of published estimates. *Biological Conservation* **139**:159–166.

van der Walt JM, Nel LH, Hoelzel AR. 2001. Characterization of major histocompatibility complex DRB diversity in the endemic South African antelope *Damaliscus pygargus*: a comparison in two subspecies with different demographic histories. *Molecular Ecology* **10**:1679–1688.

van der Walt J, Nel LH, Hoelzel AR. 2013. Differentiation at mitochondrial and nuclear loci between the blesbok (*Damaliscus pygargus phillipsi*) and bontebok (*D. p. pygargus*): implications for conservation strategy. *Conservation Genetics* **14**:243–248.

van Rensburg APJ. 1975. Die geskiedenis van die Nasionale Bontebokpark, Swellendam. *Koedoe* **18**:165–190.

van Wyk AM, Kotzé A, Randi E, Dalton DL. 2013. A hybrid dilemma: a molecular investigation of South African bontebok (*Damaliscus pygargus pygargus*) and blesbok (*Damaliscus pygargus phillipsi*). *Conservation Genetics* **14**:589–599.

van Zyl LJ. 1978. Die waterbehoefte en drinkgewoontes van die Bontebok *Damaliscus dorcas dorcas* (Pallas, 1766) in die Bontebok Nasionale Park. M.Sc. Thesis. University of Stellenbosch, Stellenbosch, South Africa.

von Hase A, Rouget M, Maze K, Helme N. 2003. A finescale conservation plan for Cape lowlands renosterveld. Technical Report. Botanical Society of South Africa, Kirstenbosch, Cape Town.

Watson LH, Kraaij T, Novellie P. 2011. Management of rare ungulates in a small park: habitat use of Bontebok and Cape Mountain Zebra in Bontebok National Park assessed by counts of dung groups. *South African Journal of Wildlife Research* **41**:158–166.