Post-Late Glacial Maximum Palaeoecological Species Integrity, Phylogeography and Management of Bontebok (*Damaliscus pygargus pygargus*)

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Abstract Re-evaluation of bontebok following a multidisciplinary approach indicate its native habitat as the now submerged Palaeo-Agulhas Plain off the southern South African coast, and dominated by C₄ grasslands and savannah. Large grazer populations migrated across the plain and around the eastern end of the Cape Folded Belt into the Eastern Cape interior following climate oscillations and geographic-shifts of the winter-/summer-/all-year rainfall isohyets. Presently 77% of all bontebok are found on private farmland with grassland bioregions in the Eastern Cape, Free State and other. Bontebok showed enhanced performance in these grasslands if compared with poor performance on south-western Cape Lowland Renosterveld (SWC-LRV). Renosterveld (RV) was previously perceived as the bontebok's native habitat of origin. We argue that bontebok became trapped in RV due to sea-level rises and consequent multiple species congestion. Bontebok meta-population management on private farms showed significant species improvement when compared with government conservation actions in SWC-LRV. Geographic habitat constraints appear to have been the greatest factor limiting bontebok integrity. IUCN recognizes a global population size of 1,618 as reported by the Non-Detriment Finding of the Scientific Authority of South Africa, whereas actual population size is more than 7,000. We quantify post-1930s bontebok performance against phylogeographic and palaeoclimate proxies.

Keywords Bontebok, *Damaliscus pygargus pygargus*, Zoo-phylogeography, Palaeoecology, Game Farming, Genetic Integrity, Meta-population Management

1. Introduction

Species integrity [70,71,154] of the bontebok is in question following its IUCN (International Union for Conservation of Nature) status being stated as vulnerable and restricted to a pre-defined native location of geographic endemism, namely, the Lowland Renosterveld (LRV) [114] of the south-western Cape, South Africa [92,122]. Recent studies on palaeoenvironmental land change and global climate shifts [14,15,32-36,103] indicate periodic migrations of grazer animal populations [63,64,137-139,147] from predominant C₄ grassland plains of the currently submerged Palaeo-Agulhas Plain (P-AP) [1,38,74,78,104,136] to the C₄ and mixed C₄/C₃ grass habitats of the Eastern Cape (EC). Support for the migrations are found in fossils of large and medium sized C₄ grazers along the coastal belt including roan (*Hippotragus equinus*), blue buck (*H. leucophaeus*), giant wildebeest (*Megalotragus priscus*), longhorn buffalo (*Syncerus antiquus*), giant Cape zebra (*Equus capensis*), quagga (*E. quagga*) and the southern springbok (*Antidorcas australis*) [21,50,63,96,97,105,137,139].

Bontebok belongs to the genus *Damaliscus* with two species *D. lunatus* and *D. pygargus*. Both are grazers and considered large animals [46,63,74,140]. The latter species include two recognized subspecies *D. p. phillipsi* blesbok and, *D. p. pygargus* bontebok. Both are endemic to Southern Africa with an East African ancestral origin *D. hypsodon* [62,80,82,159]. Blesbok-like specimens have been reported from the late Pleistocene of Katanda in the Congo (as *D. dorcas*). These fossils overlap in time and space with *D. hypsodont* at Lukenya Hill (Kenya). There are dental similarities between the small *D. agelaius* from Olduvai Gorge (Kenya) and *D. niro* from Elandsfontein in the Western Cape (WC) and Florisbad in the Free State (FS) [24,81,98,144,145,161] – a 400-500 Ka turnover marking

the onset of a unique equatorial East African bovid community with *D. hypsodon* known only from this region. *D. niro* became extinct 600 Ka BP (before present). *D. hypsodont* evolved 420 Ka BP became extinct 10 Ka BP due to change from arid to moist grassland environments – thus raising question to the origin of *D. pygargus* [65,106,128,129].

Genetic studies indicate a natural geographic separation of a south-western group of blesbok [140,149-151] during a geomagnetic polarity reversal 1.19 Ma BP. Further reversals occurred 1.06 Ma BP, 900 Ka BP, 780 Ka BP (the Brunhes reversal), and 41 Ka BP (the Laschamp event) [28,131]. These events resulted in climate and vegetation changes [83] which consequently affected animal distributions.

It is likely that the blesbok split happened due to a major climatological and habitat change, unlike other post ice-age and 18 Ka BP changes [2,14,15,111]. Taking into account the speciation of black wildebeest (*Connochaetes gnu*) from blue wildebeest (*C. taurinus*) 1 Ma BP [13], which developed its present phenotypical appearance at only 10 Ka BP [21,22], it can be argued that the bontebok attained its present genetic difference to the blesbok after the post-LGM (Last Glacial Maximum) and Younger Dryas Cataclysm (YDC). The latter occurrence was a meteor shower impact 12.8 Ka BP resulting in a sudden short-term (2 Ka) world-wide cold-age and sea level drop.

In post-YDC history blesbok occurred in millions between the Winterhoek Mountains in the EC and the Magaliesberg 900 km to the North in Gauteng. Also, from the eastern Tugela River Valley in KwaZulu-Natal 800 km across to the western Karoo [34,46,74,138,140]. An area approximately 510,000 square km. This area contained open humid grassland and the former Karoo-wetland system, which was shared by Bond's springbok (*Antidorcas bondi*) and lechwe (*Kobus leche*) [21].

The bontebok was found by Europeans in the 1700s confined to grassy patches in the SWC-LRV to the south of the Cape Folded Belt (CFB) Mountains [104,105]. They occurred from the coastline to an altitude of 200 m against the southern mountain foot-slopes. In range, from George in the East to Elandsfontein (Langebaan) in the West (400 km across) – an area of approximately 25,000 km² [73,74,78,92]. The current natural barrier separating bontebok from blesbok is a mountain range (CFB) averaging 80 km in width and the 250-320 km unsuitable (<300 mm annual rainfall) Karroid-veld.

Bontebok were first sited in the Cape while blesbok were discovered 100 years later [140]. This created confusion and some authors believe the old geographic place name of "Bontebokvlakte" near Cathcart in the EC to rather refer to the blesbok [138]. This study indicates the name either referred to bontebok or hybrids of phenotypical bontebok. Bontebok are known to crossbreed and hybridize with blesbok producing fertile off-spring which threatens the genetic purity of both subspecies. Ever since its

classification the bontebok was perceived to be endemic and restricted to the SWC-LRV of the Cape Floristic Region (CFR) [73,140,150].

Bontebok numbers plunged to near extinction in the 1800s with less than 70 animals counted on private farms in the Bredasdorp area (south-western Cape) [126]. Conservation practices by government and successful meta-population management by the private game farming industry had saved the subspecies and enhanced the global population to beyond 7,000. The majority being on grassland in the EC and the FS.

IUCN Red List assessments at first listed bontebok in 1965 as 'Very Rare', up-listed to 'Vulnerable' in 1986, down-listed to 'Rare' in 1994, up-listed to 'Vulnerable' in 1996, further up-listed to 'Near Threatened' in 2008 [105] and down-listed to 'Vulnerable' in 2017. The 2017 down-listing is argued by government to have been done through lack of available data from the private farming industry [122]. The bontebok is also listed in Appendix II of the Convention on International Trade in Endangered Species (CITES), thus limiting international trade and import of bontebok products. This has negatively impacted private bontebok farming.

With the numbers included from the private game industry, the bontebok population has grown rapidly since 2008. Numbers are now beyond the status of 'Vulnerable' and heading towards the minimum level of 10,000, classed as 'Least Concerned'.

These above figures in conjunction with the study below, gives merit to the argument that bontebok should be downgraded from endangered.

2. Description and Methods

The study emerged from a request by the United States Fisheries Forestry and Wildlife Services (USFWS) towards the Eastern Cape Provincial Department of Environmental Affairs and Tourism (DEDEAT), following an application from a hunter in 2015 for the import of Threatened or Protected Species (TOPS), being bontebok trophies. At the time the IUCN recognized only 515 bontebok [123,134], whereas the private game industry subsequently managed more than 7,000 [73] raising question in relation to the 2015 NDF (Non-Detrimental Finding) report of the national Department of Environmental Affairs (DEA) [134].

The DEA claims that suitable natural bontebok habitat is limited to the remaining 623 km² of natural SWC-LRV and small grassy patches in the fynbos areas of the Overberg region [123] and, an additional 530-830 km² on private game ranches in the Western Cape (WC). This ignores more than 5,000 privately managed bontebok in other Provinces.

Bontebok reached a critical low in 1931 when 22 animals from three private farms were fenced into the

newly proclaimed 680 ha Bontebok National Park (BNP) near Bredasdorp [152] where 80% of the vegetation is comprised of unpalatable renosterbos (*Dicerothermus rhinocerotis*) [9,99]. Numbers increased but remained below 100 individuals due to poor nutrition, lack of grazing, copper deficiency, and subsequent poor resistance against parasite infestation, particularly lungworm (*Protostrongylus cf.*) [9,166].

In 1960 the BNP, with 84 bontebok, was moved to the present site near Swellendam, 61 survived [118] and by 1981 there were 320 animals. Since then numbers have fluctuated between 150 and 250 animals.

Following the genetic purity debate of DEA, the private bontebok farmers established an independent National Bontebok Advisory Committee in 2014 – later known as Bontebok Breeders South Africa (BBSA). The BBSA engaged with the genetic laboratory studies of the National Zoo in Pretoria [45], Wildlife Ranching South Africa (WRSA) and Provincial authorities developing bontebok metapopulation management strategies and protocols [10,18,79]. However, the numbers on private land outside WC are still denied by the NDF and the DEA [122,134].

In 2015, 2016 and 2017, in collaboration with BBSA, this study conducted national surveys by means of circulated questionnaires, telephonic calls and this was backed-up with DNA-certificates of purity. Also, the habitat behavior of 38 DNA-tested bontebok had been studied after their introduction in 2008 on the private farm Ubukhulu (1,000 ha) near Alexandria in the EC.

As part of the study, a comprehensive literature search (more than 400 papers) was conducted on the dynamics of palaeoclimate, palaeo-phylogeographic animal distribution and post-LGM vegetation, seeking reason for the post-LGM decline and recent poor performance of bontebok in the WC-LRV. A preliminary technical report was released in May 2016 [73] and further investigated as discussed below.

3. Results

3.1. Bontebok Meta-population Species Management (MPSM) and Recent History

Before European settlement in the 1600's bontebok became extinct to the west of the Bot River (80 km east of Cape Town) due to Khoisan cattle herding and hunting [139]. Increased European cattle and sheep farming challenged bontebok with regards to grassland-habitat niche and grazing pressure. This combined with hunting pressure attributed to the bontebok's near species extinction from the 1800s to 1939 [54,126,148].

In 1836 a government penalty of ZAR75.00 was enforced for the killing of a bontebok. In 1837 Mr Van der Byl, a farmer at Nacht Wacht near Bredasdorp, started

conserving 27 bontebok and later Mr. Van Breda (farm Zeekoevlei) with 20 animals. These subpopulations grew by 9% per annum to 180 animals in 1900. There were also 120 bontebok on the farm Zoetendalsvalley and 30 on the farm Bushy Park in the Bredasdorp area [126,139]. Parasite infections [9] reduced the total number of bontebok to 121 in 1927, with 77 animals remaining on the three Bredasdorp farms and, 44 on the Swellendam farms (owned by the families Albertyn, Van der Byl, Myburgh and Ohlsson). Due to governmental concern, Mr. Deneys Reitz was appointed in 1926 by Mr Piet Grobler (Minister of Lands) to investigate the bontebok status [126]. Reitz's journal states that (with underlying by the authors): "*In former years they roamed the coastal belt of the Cape Province in countless thousands, but they were by now so reduced in number as to be very near vanishing point.... This was largely due to indiscriminate hunting, but also to the fact that the bontebok die out if they have to share their grazing with domestic stock, and of late years sheep farmers had increasingly invaded their ancestral haunts. We examined the long strip of country that lies between Cape Agulhas and Algoa Bay, for in this area alone were a few of them said still to survive. ...after careful research we found that, all told, there were less than seventy bontebok left in the Union and therefore in the world. These were running in small groups mostly in the neighborhood of Cape Agulhas ... In the end I found a suitable tract of land in the district of Bredasdorp ... sixteen bontebok were with difficulty shepherded through a V-shaped approach and driven into the sanctuary*" The sanctuary refers to the BNP. From the less than 70 animals quoted by Reitz's it can be argued that 30-50 additional bontebok still remained on farms outside BNP.

The population in BNP grew by an average 57% per annum from 16 in 1931 [126], to 123 in 1939 when a rapid decline occurred. In 1939 Senator Hockley suggested some bontebok be moved to alternative land in the Eastern Cape forming a new breeding nucleus. Seven animals were translocated to Mr. Francis Bowker's farm Thornkloof near Grahamstown, with the proviso to later re-stock the BNP from this population. Two rams and three ewes survived the translocation [10,54] and they increased to 200 by 1960, an average annual growth rate of 138%. This was the **1st deliberate action of Meta-Population Species Management (MPSM) of bontebok.**

The habitat of the BNP became insufficient. Grazing deteriorated and 93 of the 104 bontebok in 1956 died from infections of conical fluke (*Paramphistomum cf.*), lung worm (*Protostrongylus cf.*), wireworm (*Haemonchus cf.*), brown stomach worm (*Ostertagia cf.*) and bankrupt worm (*Tirchostrongylus cf.*), as well as copper and vitamin-D deficiency [9,166]. No more than 12 animals on any farm survived in the WC. In 1960, 61 BNP bontebok were moved to better habitat near Swellendam. Simultaneously,

from the Thornkloof Ranch subpopulation in the EC, 16 animals were re-located back to BNP and 12 to the Cape Point Nature Reserve – the **2nd deliberate action of MPSM**. Many bontebok died from drought related stress in 1963 and 1969.

By 1978 the total global bontebok population (protected parks and private farms) had recovered to approximately 700 and by 1981 the BNP subpopulation was 320. The BNP bontebok later peaked at 400 and being managed sustainably at average 250 odd animals. In 1987, forty-seven years since the first translocation to the Eastern Cape, surplus rams from the WC were translocated to four farms including Thornkloof. This was organized by East Cape Game Management Association (ECGMA) – the **3rd deliberate action of MPSM** [10,54].

A significant localized decline happened when a herd of Cape mountain zebra (*Equus zebra zebra*) were introduced to BNP [162] and outcompeted the bontebok from the limital grass fodder of the RV habitat.

Between 1988 and 2008, when the DNA-analysis [45,155] was implemented, bontebok herds in the EC were photographed and registered by Jaap Pienaar, a senior official of DEDEAT, and certificates of purity issued in accordance to the approved photographic method developed [57]. In 1989 it was decided by Cape Nature (CN) and DEDEAT to spread the bontebok further, and certified subpopulations from BNP were introduced to the EC farms: Huntly, Glen and The Ruins in the Bedford area as well as Theafontein, Fabers Kraal, Hilton, Strowan, Shenfield and Thomas Bains Nature Reserve in the Grahamstown area and finally, The Glen near Somerset East area. This was the **4th deliberate action of MPSM**. Certified Bontebok were also exported from Thornkloof to Brennan Zoo, Catskill Mountain Zoo (New York), San Diego Zoo (California), Abudabi (Gulf Coast) and Leipzig Zoo (Germany) [10,54].

Bontebok numbers in 2017 were: 190 in BNP, 492 estimated accumulatively for De Hoop Nature Reserve

and Denel Overberg Test Range, 1,367 on private game ranches in the WC, and 4,298 elsewhere in South Africa.

The private numbers were not only ignored, they were excluded, by DEA [16] despite registrations and DNA-certifications of purity, and macro-genetic meta-population outbreeding [53,70-73,75-77] across more than 180 bontebok subpopulations (Figures 1-2). The DEA claims these private animals to be genetic hybrids and suffering detrimental species inbreeding [16].

Since 2008 bontebok are being privately translocated and genetically outbred (opposite of inbreeding) [53, 70-72,159-161] between private game farms (bontebok subpopulations). Private bontebok subpopulations numbered more than 6,200 in 2015 on more than 250 farms; 6,500 in 2016 on more than 181 farms; and more than 5,600 bontebok in 2017 on more than 157 farms (Tables 1-2 and Figures 1-2). It is important to note that 10.8% of the questionnaires sent to known registered bontebok farms in 2017 were not answered, hence this data is not incorporated. Since 2016, severe drought has also resulted in an estimated 10% decline from the 2016 bontebok numbers (Figure 3).

As precautionary protocol, every bontebok translocated in the private industry since 2014 is individually DNA-tested and certified by the genetic laboratory of the National Zoo, Pretoria [45,155]. In 2015 and 2016 at least 2,326 of the bontebok from 53 private EC subpopulations held certificates of DNA purity. From 29 subpopulations 1,128 bontebok had not been DNA-tested and 11 animals from one herd were hybrids, which means 67% of the private populations were pure. Likewise, 1,575 bontebok from 76 private subpopulations in the FS had certificates of purity while 116 bontebok from seven herds had not been tested and, 24 animals from one herd were hybrids. Thus, 91.8% of the private populations is pure. As for the 2017 survey, 2,651 of 4,230 bontebok from 103 herds (subpopulations) had been tested of which only 41 (1.55%) individuals were hybrids. That is 98.45% were pure.

Figure 1. Geographic distribution of bontebok numbers in protected Parks of WC, and on farms in: the WC, the EC, the FS, the Northern Cape, the North West and the Limpopo Provinces (years 2015, 2016 and 2017). Bontebok on 10.8% of private farms not included for 2017

Table 1. Surveyed and estimated bontebok population history since 1837

Year	Western Cape		Outside Western Cape	Total Population
	Protected Parks	Private Land		
1837	0	87	0	87
1900	0	330	0	330
1927	0	121	0	121
1931	16	<50	0	<66
1939	123	100 *	5	228
1960	61+11	60 *	200	332
1978	250 *	200 *	250 *	700
1982	320	300 *	400 *	1,020
1999	500 *	800 *	1,000 *	2,300
2008	600 *	900 *	2,000	3,500
2015	901	1,302	4,959	7,162
2016	548	1,102	5,399	7,049
2017	600 *	1,367	4,298	6,265

* Numbers simulated

Multiple translocations of bontebok between the private game ranches since 2008 created large scale macro-genetic outbreeding in subpopulations of purity. This was enhanced by the availability of ample C₄ grass

fodder, contributing the 5th action of MPSM.

Table 2. Bontebok subpopulations on private land per Province, surveyed in the years 2015-2017

Number of bontebok per survey per Province						
Year	WC	EC	FS	NC	Other	Total
2015	1,302	3463	991	500	5	6,261
2016	1,102	2,847	1,432	1,091	29	6,501
2017	1,367	2,855	1,060	372	11	5,665
Number of farms / breeders surveyed						
2015	51	81	85	32	1	250
2016	29	73	46	29	4	181
2017	31	68	34	23	1	157

WC – Western Cape, EC – Eastern Cape, FS – Free State, NC – Northern Cape. Data from 10.8% of registered farms not included for 2017.

Comparing bontebok growth from the geographic data sets in Tables 1-2 and Figures 2-3 and, with the dynamics of vegetation change and consequent palaeogeography species migrations below, it is noted that the 5th MPSM was the most important survival aid to date of the bontebok's species-integrity. It can confidently be accepted that privately farmed bontebok subpopulations, and the protocols set in 2014, has now resulted in more than 85% of all bontebok being pure.

Figure 2. Geographic dispersal of numbers of private farms with bontebok in South Africa, in relation to the number of protected parks with bontebok in the WC – for the years 2015-2017

Figure 3. Meta-population dynamics of bontebok numbers since 1837 in relation to geographic distribution: protected parks in the WC, private ranches in the WC, private ranches and parks rest of South Africa. Worst drought in 150 years recorded for 2016-2018 [133]. Bontebok from 10.8% of private ranches are not included for 2017

The individual areas (land sizes) of 58 private bontebok farms surveyed in the FS in 2015/2016 ranged from 100 to 5,800 ha with 60.3% being between 450 and 1,860 ha (Figure 4). The 140 ranches surveyed across all provinces in 2017 ranged from 18 to 27,000 ha with 62.9% being between 400 and 3,000 ha (Figure 5). Thus, more than 60% of private bontebok farms are at least equal to the average natural home range of 350–600 ha for bontebok [140].

Figure 4. Number of private game farms with bontebok subpopulations in the Free State per different land sizes (ha) – years 2015, 2016

Figure 5. Number of private game farms with bontebok subpopulations in all Provinces in South Africa per different land sizes (ha) – (2017 survey)

The initial BNP measured 680 ha, with 80% of the habitat being unsuitable renosterbos veld (RV) [99,152]. The BNP had been moved and enlarged in stepping-stages to its present 3,260 ha. Importantly, from the 140 private bontebok ranches surveyed 32 farms (22.9%), with a total of 1,841 bontebok are equal to or exceed the land area size of the present BNP. The bontebok on these ranches are not recognized as wild by IUCN listing or the DEA. In contrast, bontebok on smaller fenced-in government land (including BNP) are recognized [92,122]. Also not recognized are: (a) a subpopulation of 105 bontebok (45 tested as pure) roaming freely on a 23,000-ha private ranch; (b) 145 bontebok (no hybrids found) on a 27,000-ha private ranch; and (c) 11 private subpopulations (tested as pure) ranging from 114-240 individuals on ranches of between 716 and 7,907 ha (average 2,802 ha).

Private bontebok subpopulations surveyed in 2017 ranged from 2-240 (average 39) individuals – 98 (61.6%) were viable breeding herds of more than 20 individuals, 41 (25.8%) herds had more than 40 bontebok (Figure 6).

Figure 6. Frequency of herd size of 157 private bontebok subpopulations in all Provinces of South Africa (2017 survey)

Most importantly, 5,665 (90.4%) of the total global bontebok meta-population of 6,265 are privately farmed: 1,367 in the WC and 4,298 in other Provinces as seen in Table 1 and Figure 3.

3.2. Bontebok Performance in Relation to Habitat & Vegetation

The habitat of the present BNP is dominated by the Veld type named Swellendam Silcrete Fynbos (FFc1) having little grass [114]. As measured from Google satellite images, the BNP comprises less than 440 ha of suitable bontebok grazing, that is 13.5% of the Park's surface area – the rest being unpalatable fynbos and RV of little to no grazing value. The bontebok must share the limited grazing and compete against larger aggressive grazers including Cape mountain zebra, eland (*Tragelaphus oryx*), red hartebeest (*Alcelaphus buselaphus*) and black wildebeest [100,116,117]. This, in part, explains the bontebok's poor performance.

Figure 7. Vegetative habitats of the 1,000 ha Ubukhulu private game ranch in the EC, Alexandria, indicating renosterveld, C_4 grassland and savannah veld [69] of concern for a free roaming bontebok subpopulation

The Ubukhulu private ranch (1,000 ha) near Alexandria in the Eastern Cape comprises 16 vegetative habitats (Figure 7) of which 22.9% is RV on slightly undulating plains (Figure 8A), 13.9% is open C_4 grassland on flat old cultivated lands (Figure 8B) and 11.6% is mixed savannah on flat plains with C_4 grass. Ever since introduction in 2008, the bontebok has shown exclusive preference for the grasslands and avoided the RV habitats. Renosterbos, as at Ubukhulu, is an aggressive encroacher – only when mechanically cut and cleared (done once every few years depending on its regrowth, Figure 9A) and an abundance of grasses restored (Figure 9B) will the bontebok enter the habitat.

The average annual bontebok population growth in protected parks in the WC was 6.8% from 1931-2017 (86

years), these are dominated by CAM (Crassalacean Acid Metabolism) RV and fynbos. In comparison, private game farms with more C_3 and C_4 grasses in the WC showed a 15.3% growth. The latter performance, and the 55.8% growth since 1940 (77 years) on private farms, with more C_4 grasses, outside the WC (Table 1 and Figure 3), supports the argument that the SWC-LRV is not the original habitat of the bontebok.

The survey results proved that: allowing surplus bontebok numbers to be re-located from the protected parks in the WC to the private farming sector in other Provinces which have nutritious C_4 grass, would improve the poor 6.8% annual growth rate to an estimated 13.0% and more. This has the potential to secure the species' integrity.

(A)

(B)

Figure 8. Vegetative habitats of concern for 39 free roaming bontebok at Ubukhulu private game ranch, Eastern Cape, introduced in 2008 [69]: (A) 229 ha of 'renosterbos-veld' is completely avoided and (B) 139 ha of grassland on old cultivated lands is exclusively utilized

(A)

(B)

Figure 9. Only when, the RV at Ubukhulu private game ranch had been mechanically cut (A), and replaced with growth of *C₄* grassland (B), did the bontebok freely roam and graze the habitat [69]

Table 3. Population structure and performance of privately managed bontebok subpopulations as from the surveys for 2016 and 2017

Year		2016	2017
Number of herds (n)		181	157
Population size Number of Bontebok (n)	Male	2188	?
	Female	3875	
	Total	6501	5665
Breeding adults (n)	Male	1163	?
	Female	3345	
Birth-rate (%)	lambs/adult females	55,81%	?
Weaning rate (% of born lambs weaned)		59,57%	?
Mortality	Number (n)	968	566 *
	% of Population	14,9%	10% *
Hunted	International	241	?
	Local	43	
	Total	283	194
	% of Population	4,35%	3,42%
% Population loss (Mortality + Hunted)		19,24%	13,42%
Population annual growth rate (%)		18,34%	?

* Estimated after personal communication with registered breeders.

The population growth of the privately managed subpopulations for 2016 was 18.3%. Over and above this, the extreme drought (the worst in 150 years [133]) resulted in a natural mortality of 14.9% and a commercial harvest (hunting) of 4.4% occurred as shown in Table 3. Without harvesting the population growth would have been 22.7%, nearly double the long-term growth rate for the protected Parks in the SWC-LRV. These significant greater growth rate figures for privately managed bontebok support the discussion of post-LGM bontebok migrations below.

4. Discussion

Bontebok are almost exclusively grazers, with a preference for short grass and recently burnt veld [11,101, 108,115,140]. Water is an essential habitat requirement and they stay within 1.5 km of surface water during the dry season [46,47,107,156]. It prefers coastal lowlands but also utilize recently burnt fynbos, 'strandveld' habitats, old cultivated lands and lawns of *Cynodon dactylon* [123,135]. These areas have more abundant grass production than others of the SWC-LRV and the CFB. Bontebok avoid tall woody vegetation with low visibility and areas with steep slopes, preferring open areas with low shrubs and high abundance of nutritious grasses [115].

Figure 10. Native distribution range of bontebok and blesbok as claimed by DEA [122] from post-500 a BP travelers journals. Fossil sites: KR – Klasies River, PP – Pinnacle Point, SB – Still Bay, EF – Elandsfontein

Figure 11. Estimated historic bontebok and blesbok geographic distribution and the WEST and EAST Migration Portals of grazer animals. Fossil sites: KR – Klasies River, PP – Pinnacle Point, SB – Still Bay, EF – Elandsfontein.

Cape Nature and the DEA consider most of the RV to be threatened [41,158] and in need of protection from management practices that would allow grass production to increase. Greater grass production may result in a loss of fynbos plant species diversity [117] – such action is in direct conflict to the grazing needs of the bontebok. Low genetic diversity and poor species integrity, a bottleneck,

has created a lack of bontebok resilience to environmental change [151]. Bontebok survival has been challenged by livestock farming, grazing stress, poor resistance to parasite infections and historical overhunting. Lack of gene flow between current isolated subpopulations of the protected parks (which consist primarily of suboptimal habitat) with no frequent bontebok translocations (no

outbreeding), highlights the importance of the macro-genetic meta-population management (outbreeding) [7,102] and translocations since 2008 between subpopulations of private game ranches in other Provinces. The positive significance of MPMS and outbreeding of privately farmed bontebok to its species' enhancement is evident from the growth (performance) trends shown in Figure 3. The importance of DNA-testing protocols that ensures genetic purity of translocated animals must be stressed.

Government authorities perceive bontebok origin to be restricted to an area of SWC-LRV determined by its last 400 years distribution as noted in early travelers' journals crossing the country, indicated in Figure 10.

At the time of the Bontebok/Blesbok split, indications are of existing interior marshland conditions and of moist C₄ grassland habitats [21,25,90] dominated by large grazer animals including blesbok, hartebeest, roan, lechwe, blue buck, giant wildebeest, longhorn buffalo, quagga, giant Cape zebra, southern springbok and Bond's springbok [3,4,6,13,21,25,50,63,96,97,105,120,137,139]. This is now the location of the Nama Karoo desert of Northern Cape (NC), north-eastern WC and south-western FS.

The studies report that these and other animals migrated repeatedly between the hinterland described above and the southern coastal belt [58,59,61,63,64] of the frequently exposed Palaeo-Agulhas Plain (P-AP), now submerged

since between 9-7 Ka BP [30]. The P-AP area, when exposed, stretches 820 km from East London in the east to Cape Agulhas in the west, with varying width of 25–200 km (average 80 km) as shown in Figures 10-11. Apart from a single mountainous plateau far to the south of the present Cape Agulhas, more than 85% of the P-AP is a flat plain with a gentle downwards slope to the south [30,38,39]. The greater of the grasslands and savannah on the P-AP, where the grazers used to roam, occurred between the latitudes 21°00'E (south of Cape Infanta) and 26°30'E (south of Cannon Rocs). Recent studies on palaeoenvironmental land change and global climate shifts from 1.7 Ma BP to as recent as 700 a BP [2,15,32-36,103,112] indicate major animal species shifts, extinctions and periodic migrations [38,39] of grazer animal populations in eastern and southern Africa and in specific from C₄-dominated grassland plains [1,8,38,56,74,78, 87,104,136] on the P-AP, to the C₄ and mixed C₄/C₃ grass habitats of the EC [42,43,51,63,138,147]. This suggests some blesbok must have got isolated on the P-AP in the early Pleistocene and gradually developed into the bontebok. The P-AP habitat was reduced by a third over 300 years due to a rapid rise in sea-level. Also, rapid flooding may have increased human population density and competition on the southern coastal plains, with human now including marine resources and hunting larger animals including bontebok, in its diet [147].

Figure 12. Simplified present distribution of different vegetation veld types in the WC [67] and the estimated historical distribution range of the bontebok

Figure 13. Simplified present distribution of different vegetation veld types in the EC [67] and the estimated historical distribution range of the bontebok

Former DEA and Cape Nature opinion was that bontebok had adapted over time to the conditions of a unique habitat from 20 Ka BP, namely the SWC-LRV bioregion (Figures 12-13). Also the opinion that it happened in isolation from the interior Highveld-bound blesbok (Figure 10). This area, received rain all year round of which about 65% fell through the winter period between April and October [31,94,124,163,164]. With the last sea-level rise and closing of the EAST-Portal of the P-AP between 9-7 Ka BP [14,32-36,94,103] (Figure 11); came the last true isolation between the bontebok and the blesbok and the last P-AP migration of large grazers. Several significant post-LGM (LGM was 20-18 Ka BP) climate and vegetation changes happened after 20 Ka BP in the south-western Cape [27,37,143]. Grazers of *C₄* grasses such as bontebok and blesbok predominated in eastern and southern Africa during the LGM [17] and other similar periods of lowered sea-levels, as much as 120 m below the present level [40]. The migration portals shown in Figures 10-11 have been opened 24 times since the origin of the bontebok 1.2 Ma BP [15,91,103].

During these times of open portals bontebok and blesbok migrations would have come into contact in the areas close to and beyond the EAST-Portal of the present EC Algoa Bay with consequent hybridizing between the two subspecies. Scientific defining of genetic markers and macro-satellites for bontebok and blesbok [44,45,150,151] most certainly must be complicated by past natural

hybridizing [106].

Vegetation and palaeoclimate follow repetition cycles of change, affected by phenomena such as: (a) earth's rotation and orbital path, the Milankovitch Variation; (b) the passing of planet Sa.A.Mi. every 3.6 Ka; (c) the 23 Ka Precession Cycle, a 15% wobble of earth; (d) the 41 Ka Obliquity Cycle of axil tilt changing earth-surface sunlight by 22%; (e) the 100 and 413 Ka Eccentricity Cycle of orbit changing earth-surface sunlight by 30% [130]; as well as (f) sporadic polarity and magnetic shifts [28,131], volcanic activities and cataclysm asteroid impacts such as the recent YDC.

Most grazer animal species survived and out-lived the competitive pressures following the pre-LGM sea-level rises and submergence of the P-AP grasslands [90] which trapped the populations against the southern foot slopes and lowlands of the CFB Mountains, a land surface area 75% less than the P-AP grazing range. In difference, the post-LGM and post-YDC climate and vegetation changes and the last closing of the P-AP were most severe. Many large grazer species became extinct including the giant wildebeest, the longhorn buffalo, the southern springbok, the giant Cape zebra and more [6,21,25,63,90,95-98,109,120].

Subpopulations of many species with greater distributions to the north of the CFB such as waterbuck (*Cobus ellipsiprymnus*), gemsbok (*Oryx gazella*), roan (*Hippotragus equinus*) and reedbuck (*Redunca*

arundinum), died out along the southern Cape coastal belt. Roan, bluebuck, reedbuck and buffalo (*Syncerus caffer*) became extirpated on the Cape coastal belt between 1600 and 1800 AD, evidently the result of non-viable species diversity population size [6,127,160] being trapped in a limited geographic range [63,93,137]. The southern Cape bontebok population was one of few large grazer species to have survived in the SWC-LRV, but deteriorated into a genetic species integrity bottleneck.

The difference of the 24th (last) sea-level rise and EAST-Portal closure from the former 23 Portal closures since the first/original bontebok split (1.2 million years BP), was the now expanded human pressure herding more than 20,000 grazing cattle to the south of the CFB [155] adding more pressure to the trapped wild grazers and bontebok, contributing the many extinctions [58,59,63]. Humans concentrated on the submerged coastline since 60 Ka BP [50,52,58,132]. Palaeoclimate has had strong impacts on past biodiversity dynamics, driving range shifts and extinctions as well as diversification. Large grazing ungulates became rare owing to the limited availability and productivity of adequate grassland towards present [19].

Historic accounts and Holocene archaeological faunas show that the CFR is relatively poor in ungulate diversity, being dominated by a small number of small bodied browsing and mixed feeding taxa, such as duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), and Cape grysbok (*R. melanotis*) [61,95,139]. The loss of ungulate richness, particularly grazers, from the southern coastal regions of South Africa, clearly points to Post-LGM declining productivity and suitability of grassland habitats and shifts from C₄ to C₃ grasses [8,22-25,61,66].

Changes in ungulate diversity indicate that effective precipitation was highest during the LGM, corresponding with an intensified winter rainfall system which change to post-YDC greater summer rainfall shift [58,59]. Relative humidity in the southern Cape was generally out of phase with the interior of South Africa – the early Holocene following the YDC up to about 4,200 BP was relatively dry with a more open vegetation than that of the present, defined by *Vachellia karroo* savannah-trees [49] and considerable aeolian activity [5]. The period from 4,200 to 1,000 BP was apparently considerably wetter, with an increase in bush and forest. Thereafter the effects of drier conditions were enhanced by increasing interference by man [5].

5. Conclusions

Assessing all available research indicates that bontebok evolved on C₄ grassland and savannah thornveld in the 7.8-mil ha P-AP, an area with year-round rainfall now submerged off South Africa's southern coast. Bontebok, blesbok and other animal herds at present occur as isolated

populations in the interior, the southern Cape coastal plains and Eastern Cape regions. These populations periodically mixed during the Pleistocene when climatic fluctuations occurred. In the WC coastal and P-AP grassland areas migrations of large grazers such as bontebok, followed climate and geographic rainfall isohyet shifts, that affects grass production [109].

Increased competition due to a loss of land area as a direct result of sea-level rises was probably exacerbated by lower winter rainfall [36] and restricted migrations of large animal herds once the eastern migration portal had closed. The animal groups of animals who managed to change and increase the diversity of their native diet survived, such as bontebok. Animal populations living on the southern coastal P-AP grasslands consisted of those who moved (migrated) back into the interior before the closure of the eastern portal, such as roan, and others, such as bontebok that became trapped and isolated in the south-western Cape throughout the following interglacials [38]. Results indicate that ungulates spent most of their time on the P-AP and avoided dissected plains, foothills, and mountain habitats located more than about 15 km north of the modern coastline. Measured intra-tooth enamel strontium isotope fossil values [39] are also consistent with most areas of the now submerged P-AP. This suggests that the open-habitat fauna, such as bontebok, that dominates the Pleistocene assemblages on the south coast is derived from a population of animals largely restricted to the now-submerged P-AP. Given the specialized use of this plain, this animal community would have suffered catastrophic habitat loss when sea-levels rose during the Holocene and PLGM [39].

Bontebok split from the blesbok, a large C₄-grazer from a summer rainfall environment of 600-1,200 mm annual precipitation [140]. All indications are that the bontebok emerged and flourished historically pre-LGM in savannah and C₄ grassy environment on alluvial fertile soils along the floodplains and meander river crossings on the now-submerged P-AP. This environment was driven by low atmospheric CO₂ levels and intensified summer and all-year rainfall, >600 mm per annum, relative to modern times [6,8,61,87,104,136]. At that time, the winter rainfall isohyet had shifted to the far western edge of present WC, by the prevailing Agulhas Current [31]. The bontebok was one of few remaining large grazer species in the southern WC to have survived the post-LGM drying environmental shift 18–13 Ka BP and the cooling YDC (12.8 Ka BP) which was followed by successive climate oscillations after [86,164].

After the last sea-level rise and resultant closure of the migration portal south of present Port Elizabeth 9-7 Ka BP [94,163], the western bontebok population became trapped in the C₃/CAM winter-rainfall vegetation of the SWC-LRV [38]. These bontebok entered a bottleneck of long-term diversity decline [127] with the reduced C₄ grazing resources to the detriment of the species. In contrast the

eastern bontebok population's genetic diversity was lost through hybridization with the more diverse blesbok from the northern interior [127]. Hence the colonial name "Bontebokvlakte" near the town of Cathcart in the EC most likely refers to bontebok hybrids.

Conclusive evidence of migrating grazers passing through the Port Elizabeth portal in EC is evident from the remains of bontebok, hartebeest, wildebeest, long-horned buffalo, buffalo, quagga and blue buck in 126-100 Ka BP deposits in a cave at Klasies River, approximately 100 km west of the present city of Port Elizabeth [165]. There are also remains of roan antelope found at Nelson Bay Cave, Lake Pleasant, Melkhoutboom and Uniondale shelter, in the southern coastal region [60,97,96]. Bontebok remains were also found at Boomplaatz Cave and Nelson Bay Cave near George [62] confirming bontebok migrations.

Oldest blesbok fossils dates are 1.4 Ma BP found at Swartkrans Cave near Krugersdorp in Gauteng [142]. The earliest record of bontebok in the CFR dates to the end of the middle Pleistocene (151 Ka) at Pinnacle Point near George [126] coinciding with a marine regression. The evidence suggests that blesbok first emerged in the South African interior and later migrated into the CFR during a middle Pleistocene marine regression when reduced sea-levels and expanded grasslands, facilitated interchange between the CFR and the interior. Subsequent isolation during interglacial high-stands likely allowed allopatric divergence at the subspecies level [63]. The sub specific divergence of the bontebok from blesbok provides the only evidence for climatically driven allopatry leading to the emergence of a novel taxon. This can be attributed to migration of blesbok to the P-PA during an earlier marine regression, followed by geographic isolation in the CFR during the subsequent marine transgression, which promoted allopatric evolution of the two subspecies. This is roughly consistent with genetic evidence, which suggests the subspecies diverged at 250 Ka BP [55], whereas newer research indicate genetic split at 1.9 Ma BP [139,148-151]. The P-AP and CFR record shows that faunal turnover can occur over relatively short time periods. (100 Ka) [63].

Performance of bontebok on private game farms in the EC and FS has been measured against bontebok as conserved by government in marginal to unsuitable SWC-LRV with fragmented and isolated small populations.

The former, in contrast with the latter, has greater meta-population numbers in native habitats of natural savannah and C₄ grasslands with an annual all-year rainfall >600 which sustains genetic resistance integrity of bontebok against endo-parasites.

Endo-parasitism is the proximate cause of mortality [166] and population failure in the SWC-LRV and hence bontebok species diversity demise [127].

The study provides significant evidence for a mind shift by the DEA and the IUCN towards consumptive use conservation through private macro-genetic

meta-population management of species such as bontebok being practiced by private game farming since before 2008.

The black wildebeest / blue wildebeest split occurred in the same time frame as the bontebok / blesbok split and with consequent phenotypical appearance only after the recent YDC, though its phylogenetics are only now significantly described [84]. The phylogenetic description of the bontebok [45,154,155] are still vague and in need of further research pertaining to macro genetic meta-population long-term species proxy management [127], especially adaptive variation estimates of conservation genetics [157]. Thus, this requires closer collaboration between phylogenetic theoreticians and field biologists, animal managers and breeders. The efficient use of these results should be used to define conservation strategies that should influence policy regarding the privately farmed eastern bontebok subpopulation verses the south WC subpopulation.

Governmental (CN and DEA) bontebok conservation strategy is primarily concerned with growing the population to achieve viability [146] through increasing and rehabilitating RV and available SWC-LRV habitat [41,158] and maintaining meta-population processes to offset inbreeding and preventing hybridization [122].

Firstly: RV and fynbos in the WC is poor C₃/CAM fodder characterized by fine-leaved evergreen shrubs and bushes (*Restionaceae*) with limited C₃ grasses and few trees – different from the native C₄ grasslands and savannah of the P-AP of bontebok origin. Thus, in the WC, bontebok suffer malnutrition and consequently loss of resilience against endo-parasitism – the main cause of frequent past population plunges and near extinction turns in the WC.

Secondly: Private game farming is responsible for 77% of all bontebok meta-population outbreeding management since 2008 and has significantly enhanced species diversity and improved animal resilience success.

Government (CN and DEA) needs to engage with the private farming strategy to resolve the poor performance and inbreeding of its isolated WC subpopulations problem.

Thirdly: In contrast to former beliefs [122], bontebok evolved in an environment, not unlike the Highveld grassland conditions associated with blesbok. The unsuitable RV habitat cannot be taken as ultimate bontebok habitat. The core population within the WC has not increased since 2004 (770 individuals in formally protected areas in 2004 compared to 686 individuals in 2014) [122], whereas private bontebok have increased from five in 1940 to more than 6,501 individuals in 2016.

This study reveals major differences to the bontebok information submitted to the IUCN by the 2017-2 assessment [122] and, in contrast, supports a potential relieved listing to Least Concerned.

At present the bontebok is also listed in Appendix II under CITES, thus limiting international trade and import of any bontebok products and trophies. Private bontebok

farming has been proved to be the savior, the species extinction preventer, and the most successful species population enhancer of all actions to date. Trophy hunting has been a major incentive for this success. For future enhancement, hunting incentives need be further boosted by relieving regulation on import/export trade on bontebok products. Current DEA and CN legislation and regulation based on the IUCN assessment limits private bontebok farming and consequently the enhancement and genetic integrity of the subspecies.

All subpopulations of bontebok, both in protected parks and on private ranches, result in the species becoming fragmented by fencing. Government and the DEA claim not to have a metapopulation plan in place, though the constant trading and translocations between the private ranches result in highly successful meta-population outbreeding as seen from the results of enhanced bontebok performance outside the WC.

Examined hybridization rates between bontebok and blesbok reduced from 33% in 2013 [155] to 25% in 2016 [154] indicating enhancement of the species on private game farms and outside the WC. As a consequence of hybridization all translocations, as per Province, are subsequently subject to one of: (a) The CapeNature Bontebok Conservation, Translocation and Utilization Policy [16]; (b) The Norms and Standards for the Keeping and Management of Bontebok in the Free State [79]; (c) Operational Guideline of the Chief Directorate of Environmental Affairs, Eastern Cape, Bontebok Protocol [18], which requires all bontebok for translocation to be genetically tested and declared pure before release. As a result of this, more than 85% of current private bontebok are now pure. Subpopulations have been established on private ranches in the WC, EC, NC, FS, and NW provinces, and there is pressure to increase new areas of introduction [75,121].

SANParks and CapeNature have initiated a process to develop a Biodiversity Management Plan (BMP) for Bontebok. The BMP has aimed at ensuring long-term survival of bontebok in the SWC-LRV alone which has failed since the near extinction of the species in 1931. Future success is questionable for palaeoecological and species geographic reasons already described. The BMP needs be readdressed and take into consideration the enhanced species diversity success achieved from the continued macro-genetic meta-population management by private bontebok farming since 2008 and before [113]. Existing government legislation needs to be altered accordingly or risk future localized bontebok extinction due to subpopulation isolations and declining genetic diversity / integrity. Privately farmed subpopulations in the South African Game Industry at present fits the palaeoecological species traits of the bontebok and holds the conservational key of species enhancement and long-term survival of the bontebok.

Species are habitat specific and normally evolve

relatively slowly in ecological terms. As a result, they mostly respond by tracking environmental oscillations with their geographic distributions, rather than by evolving. The species stagnate when their distributions is isolated into 'islands', and expand again in synchrony with physical environmental changes [160]. The WC protected bontebok is seen as a specific population of the species, and the bontebok on private land as another population with species diversity relevance. As early as 1976 ecologists (Van Zinderen Bakker 1976), cited in [89], postulated that grassland expansion in southern Africa was a recurrent feature at a particular stage of each temperature-induced climatic cycle as happened with the YDC and carry with them animals with a preference for this kind of habitat. By definition, blesbok is a generalist species, while the bontebok has become a specialist sub-species by trapped-force, through restricted environmental conditions [89]. The turnover-pulse hypothesis [160] centers around the combined effects of late Quaternary climate change, sea-level fluctuations, and biogeographic barriers for large mammals. It is predicted [63] that the repative expansion and contraction of grassland habitats over multiple glacial-interglacial cycles, together with the isolation of grassland species on the P-AP during marine transgressions, should promote extinction and speciation in lineages (such as bontebok) adapted to open habitats. There are 39 bovid, equid, and suid taxa documented in the CFR over the last 600 Ka of which 16 became extinct [63]. This demonstrates conclusive evidence that climatic changes drive faunal turnover in the form of migration, dispersion and extinction. The biogeographic histories of bovids' along the southern Cape coastal belt suggest that geographic isolation and limited availability of grassy forage since the Pleistocene–Holocene transition contributed to a gradual decline of grazers well into the Holocene – diet does become a significant correlate of change, as in the bontebok decline.

The bontebok population dispute arose in a new era with changes of thought processes from biodiversity conservation towards consumptive use conservation with an emphasis on species integrity under the pressure of human growth and conflict [76,77,85,110,141]. Considering the dynamics of phenotypic development with explicit focus on sources of variations of a species, conservation could directly embrace the realities of populations living in changing environments [29]. The current situation, with reference to the game industry, is that leaders of the industry and in government, do not act in the interest of the industry. This is a direct result of a lack of an agreed collective vision. The process of assessment and certification can be a catalyst for knowledge sharing, trust building and learning, and can promote economic incentives for responsible management [26]. As a first step, a thorough review of current regulatory frameworks affecting the game industry is required to identify strengths and weaknesses, contradictions and incompatibilities.

Although the South African National Environmental Management Biodiversity Act (Act no. 10 of 2004) allows for co-regulation, government does not appear to have the capacity to put this into practice. A set of operational guidelines and codes of conduct therefore must be jointly developed by government, industry role players and independent specialists to put substance to the Act. Government needs to acknowledge the contribution of the industry and invest in it. Co-regulation requires the development of new mind-sets amongst all actors [88].

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