Genetic patterns in three South African specialist antelope species: Threats, conservation management and their implications

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Abstract

Genetic diversity is a fundamental measure of a populations ability to adapt to future environmental change. Subpopulations may carry unique genetic lineages that contribute to fitness and genetic diversity of species across their distribution range. Therefore, considerations, or lack thereof, of genetic diversity in wildlife management practices may result in either population persistence or extinction over time. Some management tools may pose a greater risk to a species’ survival than others when populations are impacted. In South Africa, there has been great interest to translocate animals, sometimes with little consideration to the potential impacts on the species and/or populations survival. Thus, there is a need to collate scientific information to better inform decision-making and review these management practices and their effects on populations. Here, we focus on three antelope species, the blue duiker (Philantomba monticola), oribi (Ourebia ourebi), and tsessebe (Damaliscus lunatus). We review the genetic status of each species across South Africa, with regards to taxonomy, genetic diversity and population structure, threats that may compromise the genetic diversity within species and across populations, conservation management actions and how they may compromise or benefit the genetic status and lastly make recommendations on possible alternative management actions and future research to inform conservation policy and sustainable management practice.

KEYWORDS
blue duiker, genetic integrity, oribi, translocation, tsessebe, wildlife management

1 INTRODUCTION

The 2020 evaluation by the International Union for Conservation of Nature (IUCN) of over 35,765 species across all taxonomic groups categorized approximately one-quarter of the world’s mammals (26%) as “Critically Endangered,” “Endangered,” or “Vulnerable.” In South Africa, while populations of some mammals are reported to be stable or increasing, a significant number of species, especially habitat specialists, are experiencing population declines and/or...
range contractions (Chirima et al., 2018; Seydack et al., 2012; Skowno et al., 2019). Of the 331 known mammal species, 56 (17%) are threatened with extinction (www.ewt.org.za; Skowno et al., 2019) and one species, the blue antelope (Hippotragus leucophaeus), has been declared extinct (www.ewt.org.za; Kerley et al., 2009). It has thus become increasingly axiomatic that targeted conservation management efforts are imperative to halt population declines. There is evidence that with timely and efficient management practices, projected extinctions may be reversed (e.g., Moodley et al., 2017). In addition, wildlife conservation measures should not only be maintaining effective population size but also ensuring that there is adequate genetic diversity to enable these populations to adapt in a rapidly changing environment impacted by anthropogenic-induced stressors and climate change (Supple & Shapiro, 2018).

In South Africa, wildlife management in the past has been largely based on broad or lucrative management practices (Taylor et al., 2016; van Vuuren et al., 2017). These have included agricultural-style land ecological engineering, translocations and reintroductions and culling of excess individuals or removal of unwanted species (Carruthers, 2008). However, the conservation gains made from these efforts and their long-term success has been debated in literature (Chirima et al., 2018; Grey-Ross et al., 2009a; Taylor et al., 2020, 2021). Focusing on short-term management goals can lead to detrimental and irreversible long-term negative effects. Van Vuuren et al. (2017) conceded that while conservation action should be based on sound research, often necessity requires that action be taken before the availability of scientific knowledge. As a result, these actions may not lead to the best outcomes but lead to unexpected complications that may be irreversible. Thus, it is important that priority areas of research be undertaken on species of conservation interest prior to management actions. Furthermore, these efforts may need to be reviewed periodically as new scientific evidence becomes available.

In this article, we aim to synthesize available literature on the genetic status of the three species, the blue duiker (Philantomba monticola), oribi (Ourebia ourebi), and tsessebe (Damaliscus lunatus), the threats facing them, as well as management actions and the implications of these for their genetic diversity, population structure and integrity. Various recommendations have been put forward for the three species but have not yet been implemented. For example, it has been suggested that previous intervention success and the development of a metapopulation plan is needed for the blue duiker to guide translocations and reintroductions (Venter et al., 2016). It has also been recommended that plans to guide translocations for the oribi is needed (Shrader et al., 2016) or a Biodiversity Management Plan (BMP) should be developed to combat hybridization risk. Lastly, there is a need to assess the risk of hybridization between tsessebe and red hartebeest (Nel et al., 2016). Furthermore, farmers in South Africa have expressed an interest to translocate blue duiker and oribi to new farms, providing species diversity for hunters (Pers. Comm J Selier), and currently all three species are hunted for subsistence and as trophies (Van der Merwe & Saayman, 2003). The current review will form a strong basis for actioning the above listed recommendations, as well as bring to light knowledge gaps key to responsible decision-making for conservation of the three species.

2 TAXONOMY AND POPULATION STRUCTURE

Species are basic units of biodiversity and have evolved over time into niches where they function as part of the ecosystem’s ecological dynamics. Their delineation is
crucial for policy and for the implementation of appropriate conservation management actions (Groves et al., 2017; Mace, 2004; Thomson et al., 2018). However, species or subspecies delimitation is challenging and requires a multidisciplinary approach that uses morphological, genetic, and ecological data. Furthermore, species may consist of populations that represent evolutionary significant units (ESU) requiring specific conservation effort. In the absence of these data, a species-level blanket taxonomy may be applied, which could potentially threaten the existence of ESUs, subspecies and/or species (Groves et al., 2017; Mace, 2004). Below, we review the progress of taxonomic research and state of knowledge with regards to genetic diversity in the three species, the oribi, blue duiker, and tsessebe. All three species have wide distribution ranges across sub-Saharan Africa, overlapping in eastern and central Africa (Kingdon & Hoffmann, 2013). In South Africa, the species’ distributional ranges overlap largely in the eastern and southeastern regions (Figure 1) occurring in protected areas, communal areas and private land with varied occupancy and abundance levels (Figure S1).

### 2.1 Oribi

Oribi is polytypic, with 11 extant subspecies recognized and occurring in southern coastal regions of Africa (O. ourebi ourebi), south-eastern Africa (O. o. hastata), south-west of central Africa (O. o. rutile), central-eastern Africa (O. o. masakensis, O. o. goslingi and O. o. aequateria), eastern Africa (O. o. cottoni, O. o. haggard, O. o. gallarum and O. o. montana) and West Africa (O. o. quadriscopa) (Brashares & Arcese, 2013). A 12th subspecies (O. o. kenyae) is considered extinct, having previously occurred in a restricted range on the lower slopes of Mount Kenya (Hillman, 1988; Shrader et al., 2016). The current taxonomy is based on size and color variation, although Brashares and Arcese (2013) noted that the validity of these subspecies requires further molecular examination. Only one subspecies, O. o. ourebi, is located within South Africa (Brashares & Arcese, 2013). Molecular genetic investigations on O. ourebi have largely focused on the phylogenetic placement of the species within the Antilopinae subfamily (Bärmann et al., 2013; Cernohorska et al., 2015; Ghassemi-Khademi, 2017). The taxonomy of the species is not without controversy. On one hand, O. ourebi is currently accepted as a single species with its own unique genus and tribe, being the sister taxon to all other antilopines (Shrader et al., 2016; Zurano et al., 2019). On the other hand, some authors suggest that two subspecies in East Africa may not be conspecific with O. o. ourebi, thus highlighting the need to reassess oribi taxonomy (Cotterill, 2003a; Van Vuuren et al., 2017). Thus far, only two published studies, Van Vuuren et al. (2017) and Dalton et al. (2020), have reviewed the genetic diversity within O. ourebi. Van Vuuren et al. (2017) explored the phylogeography of oribi in South Africa and reported high genetic diversity but lack of phylogeographic structure and differentiation due to historic translocations and suggested that these populations are panmictic. They also performed a phylogenetic analysis based on two mitochondrial regions and one nuclear intron to investigate the phylogenetic relationship of the South Africa subspecies (O. o. ourebi) against the geographically closest oribi subspecies (O. o. hastata), using the steenbok (Raphicerus campestris) as an outgroup. The authors suggested that the two subspecies were too divergent for conspecific entities, with over 13% sequence divergence in the mitochondrial cytochrome b (Cyt b) gene region between the subspecies while sequence divergence was only 0.8% within O. o. ourebi across the distribution range in South Africa. On the other hand, Dalton et al. (2020) observed 2.7% Cyt b divergence within O. ourebi, although these sequences had little geographic information. Thus, these studies highlight those relationships among oribi species should be further investigated and a precautionary treatment of the South African subspecies as a distinct evolutionary lineage is valid.

### 2.2 Blue duiker

The blue duiker (Philantomba monticola) is polytypic with 13 subspecies currently recognized, divided by Hart and Kingdon (2013) into three lineages: (1) a “southern” lineage occurring from the Congo River and Angola southward into the Western Cape Province of South Africa (P. monticola monticola, P. m. anchetae, P. m. bicolor, P. m. defriesi, P. m. hecki and P. m. simpsoni), (2) a “northern” lineage occurring in central to eastern Africa (P. m. congicus and P. m. muscolides), and (3) a “montane” lineage occurring in mountainous regions of Tanzania (P. m. lugens and P. m. schusteri) and insular forms occurring on the islands of West (Bioko) and East Africa (Mafia, Pemba, and Zanzibar) (P. m. melanorheus and P. m. sandevali, respectively). The taxonomy is based on the variation in leg color and geographic distribution (Hart & Kingdon, 2013). Two subspecies are found within South Africa, P. m. monticola and P. m. bicolor, with the former being endemic to South Africa (Hart & Kingdon, 2013). Data from the Global Biodiversity Information Facility (GBIF; gbif.org) indicate that there is geographic discontinuity between the two subspecies, with P. m. monticola occurring in the Western Cape and western regions of the Eastern Cape and P. m. bicolor occurring in
Kwa-Zulu Natal and the eastern regions of the Eastern Cape. A number of studies have largely focused on species delineation (Akomo-Okoue et al., 2015; Bowkett et al., 2013; van Vliet et al., 2008). Studies that appraised species of the genus Philetantomba have highlighted the presence of possible cryptic speciation. Colyn et al. (2010) performed craniodental comparisons between the blue duiker, Maxwell’s duiker (P. maxwelli) and a newly sampled population from the Dahomey Gap in West Africa, subsequently concluding that the new population represented a new species, P. walteri. DNA barcoding studies reported that the cytochrome oxidase c subunit 1 (COI) did not meet the DNA barcoding criteria for delineating the blue duiker from other duiker species, including the closely related sister species, Maxwell’s duiker (Dalton et al., 2020; Inoue & Akomo-Okoue, 2015). To date, no study has incorporated the recently discovered P. walteri, while neither Dalton et al. (2020) nor Inoue and Akomo-Okoue (2015) included Maxwell’s duiker in their studies. Failure to meet the DNA barcoding criteria in delineating a species may imply that the taxonomy of the species is not sufficiently resolved, there is insufficient sampling, incomplete lineage sorting or interspecific hybridization (Dalton et al., 2020; Ermakov et al., 2015). It is currently unknown if any of these factors are contributing to failure to delineate species of blue duiker. Insights into the phylogeographic structure of blue duikers in central and western Africa have been provided by Ntie et al. (2017), who found a high level of spatial genetic structure. Their analyses also revealed that environmental heterogeneity, and not riverine systems, provided the basis for genetic structuring among geographical regions. Therefore, while literature indicates that molecular species identification has been validated for blue duikers, it would be beneficial to conservation management efforts to investigate genetic variation within blue duikers in South Africa to confirm species boundaries, as well as assess potential hybridization between the two subspecies. To date, there is no phylogeographic or population genetic study published for southern African duikers.

2.3 | Tsessebe

Several antelopes across Africa have been assigned the D. lunatus species name, namely, tsessebe (D. l. lunatus), coastal topi (D. l. topi), tiang (D. l. tiang), Bangweulu tsessebe (D. l. superstes), korrigum (D. l. korrigum) (korrigum) and topi (D. l. jimela) (Cotterill, 2003b, 2003c). Arctander et al. (1999) explored the phylogeography of three Alcelaphini species, including D. lunatus, using mtDNA displacement loop (D-loop) and established that there is a north–south split in D. lunatus with high genetic diversity within and between the two lineages. This north–south split was later adopted by Cotterill (2003b, 2003c) who hypothesized that D. lunatus is a species complex with two geographically delineated species, based on biogeographic and morphometric analysis. The author hypothesized that only populations from central and southern Africa should, besides D. l. superstes, be considered as D. lunatus proper while the rest should be considered as a separate species, named D. korrigum (Cotterill, 2003b, 2003c). Arctander et al. (1999) and Cotterill (2003b, 2003c), however, did not include specimens or samples from South Africa, the type locality of the species, or West Africa, the distributional range of D. l. korrigum. Later texts make a distinction between D. lunatus and D. korrigum (Djagoun et al., 2020) and this implies that the distributional range and population numbers of the tsessebe are smaller than previously established. Incorporating molecular data into a comprehensive taxonomic review of the D. lunatus complex will add value to the conservation management of the species by not only helping to validate whether southern African tsessebe and the other “subspecies” are conspecific but also determine whether there are distinct genetic lineages among the southern African tsessebe. Currently, the species is listed as Least Concern globally due to its wide geographic distribution and global population numbers. However, the identification of a species complex will require a reassessment of the conservation status of unique lineages of D. lunatus, which may have narrow distribution ranges and small population sizes.

3 | CONSERVATION STATUS AND MANAGEMENT

Regional conservation assessments for tsessebe (Nel et al., 2016), oribi (Shrader et al., 2016) and blue duiker (Venter et al., 2016) have been undertaken. The three species are listed in the IUCN Red List category of Least Concern globally, due to their wide distribution across Africa. In South Africa, however, the three species are at risk of extinction in the wild, primarily due to low and declining population numbers. Of the three species, only the status of tsessebe has recently been revised from Endangered to Vulnerable due to increasing population numbers in the private game ranching sector (Nel et al., 2016). The blue duiker and the oribi represent endemic subspecies in South Africa, while the tsessebe represents a distinct lineage (D. l. lunatus) endemic to southern Africa. Thus, the populations of the three species in South Africa represent unique evolutionary lineages. The three species are threatened by illegal hunting as well as habitat loss, degradation and transformation, which exacerbate population losses and extinction risks (Table 1).
3.1 Threats to the species

3.1.1 Habitat loss, degradation, and transformation

All three species are habitat specialists. The oribi and tsessebe thrive in flat grassland, although both tree and bush cover in these habitats may vary (Bennit et al., 2019; Brashares & Arcese, 2013). The blue duiker is an obligate browser that prefers forest habitats with high wood cover and simultaneous high canopy and floor cover and has been shown to avoid habitats that lack one of these (Ehlers-Smith et al., 2017; Gagnon & Chew, 2000). It may still use habitats that are adjacent to forests, such as coastal scrubs, thickets, and plantations (Lloyd, 2000; Shrader et al., 2016). The grassland and forest biomes are heavily transformed in South Africa, with 63% of thicket forest and over 60% of grasslands used for anthropogenic activities (Shrader et al., 2016; Stickler & Shackleton, 2015). The grassland is the most endangered biome, while coastal forest coverage has shrunk by up to 94% and both are highly fragmented (Ehlers-Smith et al., 2017; Olivier et al., 2013). Furthermore, both habitat types make up a very small portion (combined 2.2%) of available land for conservation purposes in South Africa (Carbutt et al., 2011; Ehlers-Smith et al., 2017).

These three species are found on private land, as well as formally protected land (Shrader et al., 2016; Venter et al., 2016). An estimated 22% (ca. 270,000 km²) of land in South Africa is utilized for wildlife conservation, with approximately 8% set aside as public protected land and an additional 16% is used for wildlife ranching (Skowno et al., 2019; Taylor et al., 2016). O'Connor (2005) maintains that land set aside for conservation and wildlife purposes may undergo drastic changes due to climate change, and wildlife may need accommodation in rangelands and other open habitats that are currently undergoing transformation. Thus, the ideal habitats of these species have become increasingly threatened. The formally protected populations of tsessebe inside its natural distribution range are approximately 1642 individuals in 15 reserves, with 46%–87% of tsessebe subpopulations being privately owned, while the blue duiker has been confirmed in only 36% of the 92 protected areas (including coastal forests) in South Africa (Nel et al., 2016; Shrader et al., 2016; Venter et al., 2016).

3.1.2 Illegal hunting

Antelopes make up a significant proportion of demand and supply in African bushmeat markets (36%–95% across Africa) and trophy hunting, suggesting that antelopes may be the most hunted species (Crosmary et al., 2013; McNamara et al., 2016). While motivations...
for hunting may vary, from subsistence to income generation and recreation, it can be broadly categorized into illegal and legal hunting (Di Minin et al., 2021). Although blue duiker, oribi, and tsessebe do not constitute a substantial part of the formal and regulated game meat market (Johanisová, 2020; Taylor et al., 2016), they make up a substantial part of the supply-demand dynamics in the unregulated, illegal and informal bushmeat market, as they are either more preferred than other species due to larger biomass and more majestic appearance (tsessebe) or cost less energy and resources to hunt than other species (such as blue duiker and oribi) (Martin et al., 2013; Martins & Shackleton, 2019; Schilling et al., 2020). In South Africa, the blue duiker and the oribi are impacted by indiscriminate illegal hunting not only for sustenance and trade but also for recreational purposes including sports (Manqele et al., 2018).

The consequences of hunting pressures on genetic diversity of ungulates have been investigated for regulated hunting. Harris et al. (2002) summarizes that gene flow among hunted populations may be hindered (e.g., decrease in number of dispersing sex) or promoted (e.g., breakdown of territorial structure and decreased competition for mates between populations) because of hunting pressure, and these changes may be parallel to natural responses of the populations to drastic changes. The authors indicated that hunting may lead to increased genetic drift in smaller populations, greater selection pressure and subsequent loss of desirable alleles and increase of undesirable alleles. Information on the genetic consequences of unregulated hunting is sparse for antelopes. Studies in other mammal groups indicate that unregulated indiscriminate hunting can lead to increase in inbreeding, hybridization due to decreased availability of mating partners, as well as reduction in reproductive potential (Allendorf et al., 2008; Moura et al., 2014). Hunting when excessive or selective can also introduce skewed sex ratios into populations of species with sexual dimorphism and therefore alter gene flow rates in ungulates (Harris et al., 2002; Marealle et al., 2010).

### 3.1.3 Low and declining populations

Population reduction has been known to negatively impact the genetic diversity and integrity of species (Grobler et al., 2018). A small population size has in one instance led to the complete extinction of antelope species, the blue antelope (Kerley et al., 2009). While some subpopulations of the three species are experiencing growth, the overall population numbers of each species are decreasing locally (Table 2) (Nil et al., 2016; Shrader et al., 2016). Furthermore, some subpopulations of these species across their historical distribution ranges in South Africa have gone extinct (Dunham et al., 2004; Hill, 2009; Shrader et al., 2016). Shrader et al. (2016) report that the population estimates for the blue duiker are difficult to determine due to the species' secretive nature, as well as the variable population densities in different habitats (as such, they are not included in Table 2). However, Shrader et al. (2016) estimated that the blue duiker population size across its distributional range in South Africa may be between 5716 and 27,621 mature individuals. They also estimated that approximately 42% of subpopulations have experienced unknown or negative growth rates. The populations of both the oribi and the tsessebe are smaller, with the largest subpopulation of each species less than 300 individuals.

| Population               | Oribi (Shrader et al., 2016) | Tsessebe (Nel et al., 2016) |
|--------------------------|-----------------------------|-----------------------------|
| Eastern Cape             | 1155 (83)                   | 0 (0)                       |
| Free State               | 154 (7)                     | 844 (37)                    |
| Gauteng                  | 13 (1)                      | 45 (1)                      |
| Kwa-Zulu Natal           | 1429 (100)                  | 103 (3)                     |
| Limpopo                  | 8 (1)                       | 1048 (22)                   |
| Mpumalanga               | 337 (38)                    | 66 (1)                      |
| North-West               | 2 (1)                       | 672 (34)                    |
| Northern Cape            | 0 (0)                       | 925 (11)                    |
| Western Cape             | 0 (0)                       | 0 (0)                       |
| Private                  | 114<sup>a</sup>             | 2166<sup>a</sup>            |
| Public                   | 34<sup>a</sup>              | 1537                        |
| No. of subpopulations    | 231                         | 109                         |
| Min subpopulation        | 1                           | 19                          |
| Max subpopulation        | 416 (250)<sup>b</sup>       | <250                        |
| Ave. size per locality   | 13.4 (13.5)<sup>c</sup>     | 34                          |
| Total                    | 3098                        | 3703                        |

Note: The values in brackets indicate number of localities in each province.

<sup>a</sup>Indicates that Eastern Cape has been excluded and ranches have been included.

<sup>b</sup>Indicates possible multiple subpopulations (estimate).

<sup>c</sup>Indicates that Gauteng, Limpopo and North-West Provinces have been excluded.
(Table 2; Venter et al., 2016). Furthermore, the largest populations of the two species are found in specialized habitats, grassland biome for oribi (<99%) and savannah for tsessebe (76%). Nel et al. (2016) suggested that good quality habitat may boost population growth in tsessebe as low survival rates in adults and calves have been observed in poor quality habitats. The average population size of the oribi per locality is low (average 13.4 individuals) particularly in localities outside their natural habitats, suggesting that these peripheral populations may not fully contribute to the overall genetic diversity of the species. On the other hand, tsessebe occur in relatively larger numbers (average 34 individuals) across their recorded range. However, the average number of individuals per locality for both oribi and tsessebe fall below the recommended minimum of 50 (Allendorf et al., 2012) and an average of 90 individuals suggested by Coverdale et al. (2006) to maintain genetic viability. The genetic diversity of these species is therefore potentially threatened by local extinctions. While it is generally assumed that sex-biased polygamous mating populations will most likely have small effective sizes, factors that are unique to each population can variably influence the relationship between effective sizes of populations and census size. Moreover, both oribi and tsessebe may exhibit plasticity in their social structure. It is thus difficult to make predictions regarding their effective population sizes outside of directly assessing the different populations. For example, in a study by Greyling (2007) of two populations of buffalo, the difference in the ratio of the effective sizes to the census sizes of the populations was rather large (i.e., \( N_e/N = 0.79 \) in Kwa-Zulu Natal and \( N_e/N = 0.15 \) in Kruger National Park).

### 3.1.4 Hybridization

The genetic integrity of the three species may also be threatened by hybridization. Hybridization is generally defined as mating of two individuals from genetically distinct populations across any taxonomic rank (Allendorf et al., 2012; Chan et al., 2019; Stronen & Paquet, 2013). Hybridization can have both negative and positive outcomes (Allendorf et al., 2012; Chan et al., 2019). On one hand, hybridization can enhance the heterozygosity of a population and increase its adaptive potential (Chan et al., 2019). On the other hand, hybridization can also promote homogeneity and reduce overall fitness, outcompete parent genotypes through hybrid vigor and lead to reproductive dead-ends (Allendorf et al., 2012; Seehausen, 2004). Anthropogenic activities are accelerating the breakdown of natural barriers directly by translocation, as well as destruction of eco-geological features and indirectly through range shifts caused by climatic pressures (Crispo et al., 2011; Stronen & Paquet, 2013). In South Africa, wildlife has been translocated using the best practice management of the time (Carruthers, 2008).

Translocation may enable the relocation of animals into more suitable habitats, as well as the facilitation of gene flow among subpopulations across both man-made and natural barriers (Jahner et al., 2018; Miller et al., 2020). However, this has also led to species and populations being introduced outside their natural ranges (Carruthers, 2008; Lloyd, 2000). Case studies have shown that hybridization and genetic introgression is widespread among South African ungulate species that have been translocated in the past (Grobler et al., 2018; van Wyk et al., 2019). Interspecific hybridization is suspected among different duiker species (Akomo-Okoue et al., 2015; Johnston & Anthony, 2012). However, the genetic status of these suspected blue duiker subspecies and the potential hybridization among them where their populations overlap have not been explored. For the oribi, phylogenetic analyses have revealed that the homogeneity of oribi populations in South Africa may be a result of historical translocations (Van Vuuren et al., 2017).

### 3.2 Management practices

Wildlife in South Africa exists mostly on state protected areas and private land, with wildlife management being based mainly on the right of ownership by communal and private landowners or the state (Taylor et al., 2016). Game numbers have increased over the past 30 years with private game reserves and wildlife ranches growing significantly (5%–20% annually over the last decade) as landowners have shifted from agriculture to game ranching (Taylor et al., 2016). Van der Merwe and Maia (2019) highlight various aspects of conservation management actions undertaken by private land managers; these include managing the availability and positions of water sources, range management (natural and invasive plant life), infrastructure such as fencing, direct intervention such as breeding, as well as disease control. The authors did not discuss how these management practices may affect different animal species. Below we review various management actions employed and how these may affect South African antelopes, with emphasis on the blue duiker, oribi, and tsessebe.

#### 3.2.1 Land management and habitat availability

In South Africa, the conservation model involves the reservation or protection of land where these animals can be
accommodated (Carruthers, 2008; Child et al., 2013). Legislation in South Africa such as the Game Theft Act of 1991 (No. 105 of 1991; as amended in Acts 18 of 1996 and 62 of 2000) has enabled privatization of wildlife, providing incentives and conditional ownership of wildlife to private landowners which directly or indirectly contributes to conservation efforts and generating income (Blackmore, 2020; Taylor et al., 2016). As such, the nature of wildlife conservation in South Africa prioritizes availability of land for wildlife management. However, the availability of land is a challenging issue as it impacts not only stakeholders in wildlife conservation and industry but also adjacent communities, agriculture, and urban development (Luvuno et al., 2018; Spierenburg & Brooks, 2014). Costelloe et al. (2016) maintain that rather than making land available for conservation, management strategies within already available land should be improved to increase efficiency of wildlife management. There is little or no planning for land management practices and generalized methods are applied regardless of the species composition (Child et al., 2013; von Solms & van der Merwe, 2020). These land management practices generally favor species of greater economic interest and because these species are mostly generalist species, this has led to unsuccessful introductions of specialist species, as well as extirpation of other specialist species in the past (Child et al., 2013; Curveira-Santos et al., 2021). It is crucial that current and past management practices be scrutinized for their impacts on the species within their boundaries.

The first of these practices is the management of different species within a management area (i.e., “stock” management). Multiple species are often managed together in confined areas, chiefly due to limited available land and the need to diversify products to maximize profit (Child et al., 2013; Lindsey et al., 2007). Generalist herbivorous species, such as wildebeest (Connochaetes), buffalo (Syncerus caffer) and zebra (Equus), have been shown to have strong competitive effects on the populations of tsessebe, as these generalist species have wider home range preferences and greater adaptability (Bennit et al., 2019; Child et al., 2013; Grant et al., 2002; Pacifici et al., 2015). These generalist species are coincidentally preferred by wildlife farmers and as such are introduced across a majority of private wildlife land (Taylor et al., 2016).

The management of water sources is another practice, and it includes building and maintaining artificial water sources (Guldemond et al., 2017; van der Merwe & Maia, 2019). Artificial water sources provide surface water for a wide variety of ungulates (Grant et al., 2002; Guldemond et al., 2017). However, artificial water points can adversely affect certain species such as the tsessebe, as well as the utilization of the surrounding habitat. The presence of competitive species was correlated with artificial water points in various studies, with waterpoints attracting generalist water-dependent species such as zebra and larger browser species like elephants, which may lead to degradation of essential grass for specialist grazers (Bennit et al., 2019; Muposhi et al., 2017). This is especially true during the dry season when surface water is limited and these waterpoints are the most accessible to all species, with specialist species becoming most susceptible to extirpations during these dry months (Bennit et al., 2019; Chirima et al., 2018).

Fire management has been used as a habitat management tool (van Wilgen, 2009) with various parks using different burning techniques and practices (van Wilgen, 2013). Fire policies have evolved over time with accumulation of knowledge on fire ecology (van Wilgen, 2013). The motivations for fire control and management also differ. For example, fires lead to the decrease in bush and tree cover and an increase in available grass for foraging (Pacifici et al., 2015). On the other hand, fire can promote the growth of invasive plant species (van Wilgen, 2013) thereby impacting foraging and habitat suitability. Pacifici et al. (2015) demonstrated that different fire management strategies affect specialist grazer antelopes (tsessebe, roan, and sable antelope) differently, with both the sable and the tsessebe benefitting greatly from shorter fire intervals compared to roan antelope. Chirima et al. (2018) demonstrated that the availability of foraging material correlates with the presence of specialist grazers such as the tsessebe, with a decrease in quality and quantity of grazing material leading to range contraction, fragmentation, and extirpation of populations. Both the oribi and the tsessebe prefer shorter and greener grass, and as such, fire management is crucial for their diet. For example, the oribi has shown a high preference for burnt areas toward the end of winter (Tekalign & Bekele, 2011). These burnt areas, however, do not provide cover, and species avoid such areas during the peak birth months as females need cover to hide themselves during gestation or their young during the preweaning (Brashares & Arcese, 2013; Jongejan et al., 1991).

While conservation efforts of the two species that prefer habitats dominated by grass, the oribi and tsessebe, can be summarized in conjunction with the other charismatic antelope that prefer grass-like habitats, the same cannot be said of the blue duiker. This may be primarily due to the small size of the forest biome in South Africa (0.4%). Although there are a high number of threatened animal species that are forest dependent, historically there has been little systematic planning for the conservation of this biome (Berliner, 2009). Forest-type habitats
currently enjoy the greatest amounts of protection in terms of legislation; however, there has been a lack of enforceable conservation efforts (Berliner, 2009; Watts, 2006). Various management strategies have affected species differently among various forest types. For example, Ehlers-Smith et al. (2017) observed that occupancy levels of the blue duiker and its cephalophine relative, the gray duiker (Sylvicapra grimmia), differed considerably among forest types, as well as vegetation cover. Hayward et al. (2005) observed differences in ungulate relative abundance and occurrence between differently managed forests in the Eastern Cape, that is, nature reserve management strategy (South Coast Forest) versus state forest management strategy (Afromontane Forest and Pondoland coastal forest). Due to the highly fragmented nature of forest habitats and their small core areas, it is critical to consider the genetic impacts on populations of blue duikers in their management plans.

Lastly, we focus on the management of the livestock–wildlife interface. Currently 82.2% of land in South Africa is used for agriculture (Dry, 2011; Taylor et al., 2016). About a third (3000 out of over 9600) of the wildlife ranches practice a mixed-ranch system where both wildlife and livestock are farmed (Dry, 2011; von Solms & van der Merwe, 2020). Furthermore, contact between livestock and wildlife has been documented indicating that the current management practices in South Africa do not, or cannot, effectively prevent interactions between wildlife and livestock (Brahmbhatt et al., 2012; Jori & Etter, 2016). The oribi has been recorded to select low-quality grass alternatives during periods of great competitive pressures from livestock in rangelands (Stears & Shrader, 2020).

Another factor of concern regarding the livestock–wildlife interface is disease transmission (Bastos et al., 2000; Weny et al., 2017). The blue duiker, oribi, and tsessebe have been previously shown to harbor blood-borne pathogens, notably *Trypanosoma* and *Theileria* species (Boundenga et al., 2016; Brothers et al., 2011; Hamilton et al., 2009). There is currently insufficient literature on surveys of pathogens in South Africa. This may indicate that there is little disease monitoring in the management of the three species and potential threats of zoonotic transmission at the human–livestock–wildlife interface. Alternatively, it may suggest that there have not been interesting results among South African populations of the blue duiker, oribi, and tsessebe (i.e., positive detections of pathogens).

### 3.2.2 Fencing

Conservation management efforts must account for human–wildlife conflict by protecting humans from wildlife and wildlife from humans. Furthermore, the nature of the South African wildlife industry and the conditional ownership of game has led to landowners protecting their land and animals as valuable resources (Carruthers, 2008; Curveira-Santos et al., 2021). Fencing is widely utilized as it aids in curbing the transmission of disease, may keep out and mitigate human–wildlife conflicts and might curb illegal harvesting and hunting (Jori & Etter, 2016; Taylor et al., 2016). Thus, in South African wildlife exists mostly in fenced areas on a continuum from intensive to extensive areas (Child et al., 2019; Nel et al., 2016; Taylor et al., 2016). According to Taylor et al. (2016), one of the requirements for prospective game ranchers is provision of proof of adequate enclosures around ranches; this is indicative that farmed wildlife is ubiquitously kept behind fences due partially to state-sanctioned wildlife management policy and thus reducing mobility of farmed wildlife. Despite the highlighted benefits of fencing around wildlife, the reality is that fencing around these areas poses major challenges as impermeable fences constitute barriers for species, hampering gene flow through dispersal and migration (Hayward & Kerley, 2009). Thus, measures to mitigate the negative effects of putting these species behind impermeable fences should be deliberated.

Conservancies have emerged in the private conservation sector as one of the ways to mitigate effects of fencing and human–wildlife conflicts. For example, to the west Kruger National Park borders a network of small and large conservancies, with a total area comparable to that of the park (Child et al., 2013). As with all other privately owned wildlife management areas, these conservancies are considered integral to achieving conservation targets. However, these areas are likely to be economy-intensive and thus detrimental to specialist species, as well as the local habitat (Child et al., 2013; Curveira-Santos et al., 2021). Wildlife corridors allow for the movement and migration of animals across various man-made structures, and these have been proposed and applied in various countries across Africa (Cushman et al., 2018; Schüßler et al., 2018). While the concept of corridors has been applied in the Western Cape forests (www.capenature.co.za/corridors), the nature of South African legislature, law, politics, and socioeconomic dynamics make the implementation of wildlife corridors challenging (Curveira-Santos et al., 2021; Sinthumule, 2017). To date, translocation has been the most viable option to facilitate gene flow between populations within private and public areas.

### 3.2.3 Translocation

Translocation has been used as a conservation tool to reintroduce populations and supplement low population sizes (Jahner et al., 2018; Miller et al., 2020).
Translocation, however, is a complex solution where the short-term benefits, may not always outweigh long-term unintended harmful consequences (Van Vuuren et al., 2017). For example, in the private sector, translocations have been used to maximize economic benefits using species desired by clients (Taylor et al., 2016) including the introduction of animals to habitats that are unnatural to them (Child et al., 2013; Lloyd, 2000). When translocation is to a new habitat, the introduced “alien” species can have a considerable impact on the genetic integrity and population viability of both the introduced and native species within the introduced area (Harrington et al., 1999; Lloyd, 2000). The most obvious and widely studied negative consequence of translocation on antelopes is hybridization (Dalton et al., 2014; Grobler et al., 2018; van Wyk et al., 2019). Translocation can also facilitate spread of disease and even introduce novel diseases to naive habitats (Glover et al., 2020; Lloyd, 2000; Smith et al., 2019). In antelopes, pathogen transmission from introduced wildlife may devastate adjacent livestock, and the reverse is also true (Glover et al., 2020). Translocation as a conservation tool, when preceded by scientific evidence and good knowledge on candidate populations is useful and successful (Miller et al., 2020; Van Wyk et al., 2013).

Blue duiker, oribi, and tsessebe have been historically translocated across South Africa, including to areas outside their natural distribution range (Dunham et al., 2004; Reilly et al., 2003; van Vuuren et al., 2017). Little monitoring and research have been published regarding the status and populations dynamics of the translocated animals. In an investigation of two translocation operations of oribi, Grey-Ross et al. (2009a, 2009b) observed two opposite levels of success, in which one operation failed and the other succeeded. The authors attributed the contrasting levels of success to the levels of care and suitability of the habitats, access of hunters to the released animals, the investment and energy the managers put into the care of the animals, as well as the origin of the animals themselves (captive-bred vs. wild) (Grey-Ross et al., 2009a, 2009b). Conflicting results from translocation operations have also been reported for the tsessebe. While initial attempts at introducing the tsessebe into the Kruger National Park region (Grant & van der Walt, 2000) showed promise, follow-up research indicated that the tsessebe, together with other habitat specialist species, were declining in numbers and locally extinct in other areas (Child et al., 2013). On the other hand, van Houtan et al. (2009) investigated the translocation success and found that the majority of the translocations were successful and achieved positive population growth despite many starting with fewer than 15 individuals. They noted that the effects of environmental stochasticity on population growth could not be eliminated entirely. This highlights the need for prior research such as habitat viability analysis and individual genetic integrity or purity before translocation of individuals. To date, the genetic consequences of translocation have not been assessed for the blue duiker, oribi, and tsessebe.

### 3.3 The role of the private wildlife industry in genetic management

Krug (2001) outlines the shortfall of publicly protected land for conservation, including limited space, poor ecological boundaries and high levels of fragmentation. Privatization of wildlife has long been considered an alternate solution to limited land and financial resources for conservation (Child et al., 2013; Clements et al., 2019). Private land, with twice the capacity of state land, makes up a great proportion of the wildlife estate in South Africa, with less than 50% of blue duiker, oribi, and tsessebe populations occurring outside private properties. The private wildlife industry is a potentially profitable land-use option that can provide conservation benefits by providing both protection and suitable habitat for antelopes (Krug, 2001; Taylor et al., 2016) when sustainable management practices are applied. There are approximately 8979 wildlife ranches across South Africa ranging from small properties to in excess of 50,000 ha (Taylor et al., 2016). Game ranches partake in various wildlife-based activities, including breeding, recreational hunting, live trade, and can have a direct impact on the genetic diversity of wildlife. In their review, Russo et al. (2019) highlight the dearth of genetic monitoring and appreciation of genetic consequences in game populations among wildlife ranchers, despite evidence of activities that may genetically affect the concerned populations in the industry. Recreational or trophy hunting is used as an option to manage population numbers and curb illegal hunting, as well as provide incentives to private landowners and state entities to participate in wildlife conservation (Di Minin et al., 2021). The main income stream for many sampled game ranches in the study by Taylor et al. (2016) were live sales, with hunting and breeding as close second and third, respectively. Krug (2001) observes that game farmers are likely to choose species to keep or introduce onto their ranches based on market preferences. Other surveys record introduced game animals in areas where they had not previously occurred (Ehlers-Smith et al., 2017; Zungu et al., 2020) because of these perceived benefits. Game farmers in South Africa have in certain cases deliberately promoted interspecific and intraspecific hybridization to obtain rare phenotypes or color variants (Lindsey et al., 2007; Russo et al., 2019;
Selier et al., 2018). Furthermore, certain traits may be favorable (Taylor et al., 2016), and farmers may be selectively breeding for these and in doing so reduce the genetic variation within populations through artificial selection (Lindsey et al., 2007; Selier et al., 2018). There has however been no reported evidence of artificial selection and/or hybridization for the three species described in this review to date.

4 | CONSERVATION MANAGEMENT PLANNING

In this review, we conducted an assessment of the biodiversity status of three South African antelope species: blue duiker, oribi, and tsessebe and further summarized key scientific findings. Currently, management of species in South Africa is directed by National and provincial policies based on the best available science. Based on the high-level panel of experts for the review of policies, legislation, and practices on matters of elephant, lion, leopard and rhinoceros management, breeding, hunting, trade, and handling (https://www.dffe.gov.za/sites/default/files/reports/2020-12-22_high-levelpanel_report.pdf), there are several inefficiencies in governance of the wildlife sector such as (1) outdated provincial legislation that is in some instances inconsistent and conflicting and requires extensive review. (2) Concurrent legislative mandate that is held by national and the nine provinces, which creates division between conservation authorities due to poor understanding of roles and responsibilities, duplication in management structures and confusion among clients with regards to issuing of permits. This system if further inefficient as it is paper-based, nonintegrated, and nonaligned. (3) Lastly, this sector is underfunded and requires consolidation of resources to ensure capacity for compliance and enforcement.

In addition, antelope species worldwide are generally relegated to footnotes in conservation considerations and thus there are several gaps in our knowledge and more species-specific research is needed to inform and improve conservation efforts and management plans. Various aspects of fundamental research that is needed include (1) taxonomic revision, (2) habitat assessments (3) assessments of threats, (4) identifying the evolutionary significant units (ESU) or management units among populations, (5) investigation of current and historic population distribution, (6) assessment of genetic diversity, and (7) assessing disease and pathogen risk (Figure 2). Here, we further identified several factors that may threaten the long-term survival of these antelope. These species are found in specialized, fragmented habitat with small and/or declining subpopulations. While South Africa practices an area-based management style, this review supports the argument for facilitated metapopulation management of the species to halt further declines in genetic diversity. Metapopulation management can be achieved through either developing/protecting corridors ensuring natural movement between subpopulations or facilitated through translocation. However, as species may respond differently to such management practices and there is a need for wider
taxon-specific metapopulation management strategy to complement existing practices and maximize sustainable conservation management efficiency. In addition, management plans should be adaptive in order to deal with challenges faced by species due to climate change.

An additional factor that should be considered is that most antelope species in South Africa are largely distributed in the private wildlife sector. Management, economic, and social aspects within this sector with land being twice the capacity of state land therefore have great consequences for the genetic diversity of most species where distributions are fragmented. There is a need for a metapopulation approach in the management of these antelope species to ensure that demographic and genetic stochastic processes continue to operate (Hanski, 1998) by simulating natural social mechanisms that have broken for the survival and persistence of species. Artificial or “managed” metapopulations have been proposed for various predator species in South Africa (Miller et al., 2015). Due to the current wildlife management landscape in South Africa, many populations are in fragmented and enclosed/fenced habitats (Child et al., 2019; Miller et al., 2015) be it private or national reserves, leaving translocation as the most viable option for maintaining genetic diversity of metapopulations. The importance of pretranslocation and posttranslocation studies of antelope species has been stressed by Grey-Ross et al. (2009a, 2009b) and van Vuuren et al. (2017) and should not be ignored in this approach. Translocation can potentially lead to hybridization and indiscriminate translocation of other antelope species has left some irreversible genetic consequences and the extents of these are currently inadequately known (van Wyk et al., 2013, 2019). However, there is limited data available on the translocations that have already occurred locally among reserves. Metapopulations are defined by dynamic processes that vary temporally and spatially, falling on a continuum of patch size and patch isolation such that a single model may not describe a species’ metapopulation structure (Aycrigg & Garton, 2014). Miller et al. (2015), suggested that the South African landscape (based on historical management) and definitions of Aycrigg and Garton (2014) may have two types of metapopulations among reserves, those that fit a more (1) patchy metapopulation structure (have mixed genetic provenances) and those that fit a more (2) nonequilibrium metapopulation structure and have maintained their original genetic provenance. Therefore, local and regional metapopulation plans may need to be formulated for the three species to guide management taking into account the natural distributions or gene pools of the different subspecies while accounting for all previous historical translocations. To conserve not only the populations of the species but also their genetic diversity, there is also a need for raising awareness among private landowners, as well as adjacent communities and nature conservation of the value of connectivity for the long-term survival of species. This is a critical step and there may be need for incentives (be it costs or other benefits of these antelope species) or governing policy to private landowner and other stakeholder groups that favor sustainable utilization of natural resources rather than policy restrictions on resource use. This would be to promote meaningful metapopulation practice on a broader scale for each species to maximize their conservation value. The underlying value of promoting the survival and persistence of these species should offset unfavorable exploitation or management of their populations. Lastly, capacity and resources are needed at the local, provincial, and national level to implement metapopulation plans and guide translocations based on sound knowledge of the genetic structure of the antelopes. It will also be vital to ensure that any genetic management approach should ensure that measures are put in place that are practical and cost-effective for governments or the private sector to implement and for mainstreaming. These should be guided by area-specific land-use objectives as defined by 2030 Biodiversity Framework (Milestone A.3) to ensure “genetic diversity of wild and domesticated species is safeguarded, with an increase in the proportion of species that have at least 90% of their genetic diversity maintained.”

**AUTHOR CONTRIBUTIONS**

Mamadi Theresa Sethusa conceptualized the research and led the discussion among co-authors. Methlolo Andries Phukuntsi conducted data analysis for the review and wrote the initial draft of the article and contributed to subsequent drafts of the article. Desire Lee Dalton, Monica Mwale, Jeanetta Selier, Thando Cebekhulu, and Mamadi Theresa Sethusa collaborated in reviewing different drafts of the article. All authors contributed to conceptual development, as well as discussed and contributed ideas for the article.

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**CONFLICT OF INTEREST**

The authors declare no conflict of interest.

**DATA AVAILABILITY STATEMENT**

All data are presented in the article or the supplemental materials.
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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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