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APPLICATION ESSAY

'Intentional Genetic Manipulation' as a conservation threat

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Abstract
Wildlife ranching including the hunting, collection, sales and husbandry of wild animals in captivity, is practised worldwide and is advocated as an approach towards the conservation of wild species. While many authors have explored the biological impacts of intensive wild population management, primarily with respect to disease transmission (especially in ungulates and fish), the evolutionary and demographic effects of wildlife ranching have been examined less intensively. We discuss this issue through the case of intensive wildlife management in southern Africa. The genetic consequences of this global practice, with an emphasis on Africa, were addressed by a motion passed at the 2016 IUCN World Congress- 'Management and regulation of intensive breeding and genetic manipulation of large mammals for commercial purposes'. Here, we highlight concerns regarding intensive breeding programs used to discover, enhance and propagate unusual physical traits, hereafter referred to as 'Intentional Genetic Manipulation'. We highlight how 'Intentional Genetic Manipulation' potentially threatens the viability of native species and ecosystems, via genetic erosion, inbreeding, hybridisation and unregulated translocation. Finally, we discuss the need for better policies in southern Africa and globally, regarding 'Intentional Genetic Manipulation', and the identification of key knowledge gaps.

Keywords Genetic erosion · Hybridisation · Inbreeding · Wildlife · Selective breeding · Small populations · Southern Africa · Translocation

Introduction

Wildlife ranching entails the utilisation of non-domesticated animals in captivity or in larger fenced areas (Nogueira and Nogueira-Filho 2011). The industry's value to conservation, along with its ecological sustainability and profitability, is highly debated among conservationists (Nogueira and

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Nogueira-Filho 2011). The wildlife industry has grown rapidly over the past 10 years due to the high economic value of wild animals across the globe, which includes sport hunting in Europe, commercial ranching and the sales of American bison (*Bison bison* Linnaeus, 1758) and ostrich (*Struthio camelus australis* Gurney, 1868) in North America, ranching for horn production in black and white rhinoceros (*Diceros binornis* Linnaeus, 1758 and *Ceratotherium simum* Burchell, 1817), the trade of illegal bush meat in West Africa, and legal trading in antelope since European settlers arrived in Africa. In many regions, affected species once had vast, inter-connected ranges. However when kept in enclosed wildlife ranches, such species experience issues including small population size, hybridisation, artificial selection and breeding to create or enhance particular phenotypic traits (see Fig. 1). These practices potentially threaten the integrity and viability of native species and ecosystems.

Here, we define wildlife ranching as the maintenance and management (monitoring, feeding, culling, and translocation) of native/non-native animals within fenced land for breeding, sales, hunting or wildlife viewing. Although the ecological, evolutionary and economic risks associated with an intensifying wildlife industry have been identified in southern Africa by institutions such as the South African National Biodiversity Institute (SANBI 2007), there are few policies in place to regulate or mitigate them. Adherence to best practices among wildlife ranchers seems to be patchy (Dugmore 2013), while conservation agencies, tasked with assessing the potential risks of selective breeding and trade of wildlife resources, have voiced concerns about the genetic integrity of individuals, populations and species (Nel 2015).

Here we focus on southern Africa due to recent and large scale changes in practice in this region. Breeding operations in southern Africa have mainly focused on previously unmanaged species such as Cape buffalo (*Syncerus caffer* Sparrman, 1779), blue wildebeest (*Connochaetes taurinus* Burchell, 1823), black wildebeest (*Connochaetes gnou* Zimmerman, 1780), blesbok (*Damaliscus pygargus phillipsi* Pallas, 1767), impala (*Aepyceros melampus* Lichtenstein, 1812) and sable antelope (*Hippotragus niger* Harris, 1838). Legislative changes such as the private ownership of wildlife in several African countries since the 1960s have resulted in an increase in wildlife ranching, moving away from traditional livestock farming (Lindsey et al. 2009). These changes occurred in Namibia (1967), Zimbabwe (1960 and 1975) and in South Africa at different times depending on the province (Lindsey et al. 2009). Recently, the 2016 IUCN World Congress passed a motion focusing on 'Intentional Genetic Manipulation', which was precipitated by the case of southern Africa, but highlights the global scope of this issue (https://portals.iucn.org/congress/motion/016). With advances in biotechnology, intensification of land use, and continued use of wildlife for viewing, breeding and hunting, the issue of genetic manipulation of wildlife can be expected to be increasingly raised in other countries around the world.

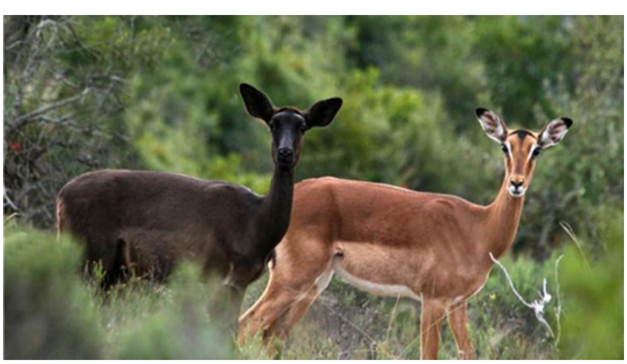

Fig. 1 A black (left) and common impala on the right. Picture: Agriconnect. (Color figure online)

Here we (1) summarise the historical situation and current 'Intentional Genetic Manipulation' practices in the southern African wildlife industry, (2) describe the novel challenges posed by these practices with examples, including parallels with the related practice of aquaculture and (3) discuss potential decisions-making processes to ensure the future sustainable use of wildlife resources. We focus primarily on genetic concerns but recognise that non-genetic analyses are important (e.g. Cloete et al. 2015), since there are many aspects of wildlife ranching that may raise concern.

While many genetic concerns have been described (Lindsey et al. 2006) in aquaculture (Lafferty et al. 2015), evolutionary implications of wildlife ranching (including changes in effective population size, inbreeding, rapid spread of novel alleles, sterility of hybrids, inbreeding, and outbreeding depression) have received less attention but remain crucial factors in conservation. We evaluate the current status of wildlife ranching in southern Africa as an example to highlight these concerns. We include a description of the industry and relevant legislation in South Africa for context, as this case is well-documented and timely, but where appropriate we highlight global connections and implications.

South Africa

South Africa, as a signatory to the Convention on Biological Diversity (CBD), has committed to implement reasonable measures for achieving biodiversity conservation and sustainable use of wildlife resources. The South African Constitution mandates the government to develop and implement legislative measures for environmental protection. Close to 9% of the country's land is included under terrestrial protected areas. However, much of South Africa's semi-natural land is under private ownership with approximately 9000 properties covering an area of more than 170,000 km^2

(Taylor et al. 2016). Approximately 20% of South Africa's land (~ 1,220,000 km^2) is used for wildlife activities including hunting, ecotourism and live trade (Taylor et al. 2016), of which 6% is used for intensive breeding. The majority of South Africa's 'biodiversity estate' is not secured in formally protected areas. For example, protected areas within the historical distribution of bontebok (*Damaliscus pygargus pygargus* Pallas, 1767) contain fewer than 500 individuals, whereas several thousand individuals are under private ownership (Radloff et al. 2015; Fig. 2). South Africa is not unique in this regard, for instance in the USA there are currently around 500,000 American bison in captive commercial populations on about 4000 privately owned ranches of which only 4% (20,000) are in conservation herds (Hedrick 2009).

The total turnover of the wildlife industry in South Africa was estimated at USD 8.1 billion in 2015 including USD 119 million from wildlife auctions (Janovsky 2015). The World Tourism Organisation (WNWTO) has reported that global wildlife tourism is growing at a rate of about 10% per year. Individual animals can be extremely valuable, recently a kudu bull (*Tragelaphus strepsiceros* Pallas, 1766) was sold for USD 629,800, a sable antelope for USD 1,809,000, and a roan antelope (*Hippotragus equinus* sp. Saint-Hilaire, 1803) for USD 636,500 (Table 1). These prices seemingly reflect an increasing demand for 'quality animals' with exceptional morphological features including horn length, body size, coat colour and coat pattern (Cloete et al. 2015) and the willingness of wildlife ranchers or investors to pay these prices.

Some wildlife owners have recently been deriving a large proportion of their income from unusual colour and other morphological variants (Nel 2015). Sophisticated marketing strategies are employed to highlight 'quality' gene-pools (see http://www.studgamebreeders.co.za). Animals are now regarded as a financial investment, stimulating the establishment of new wildlife ranches every year (Cloete et al.

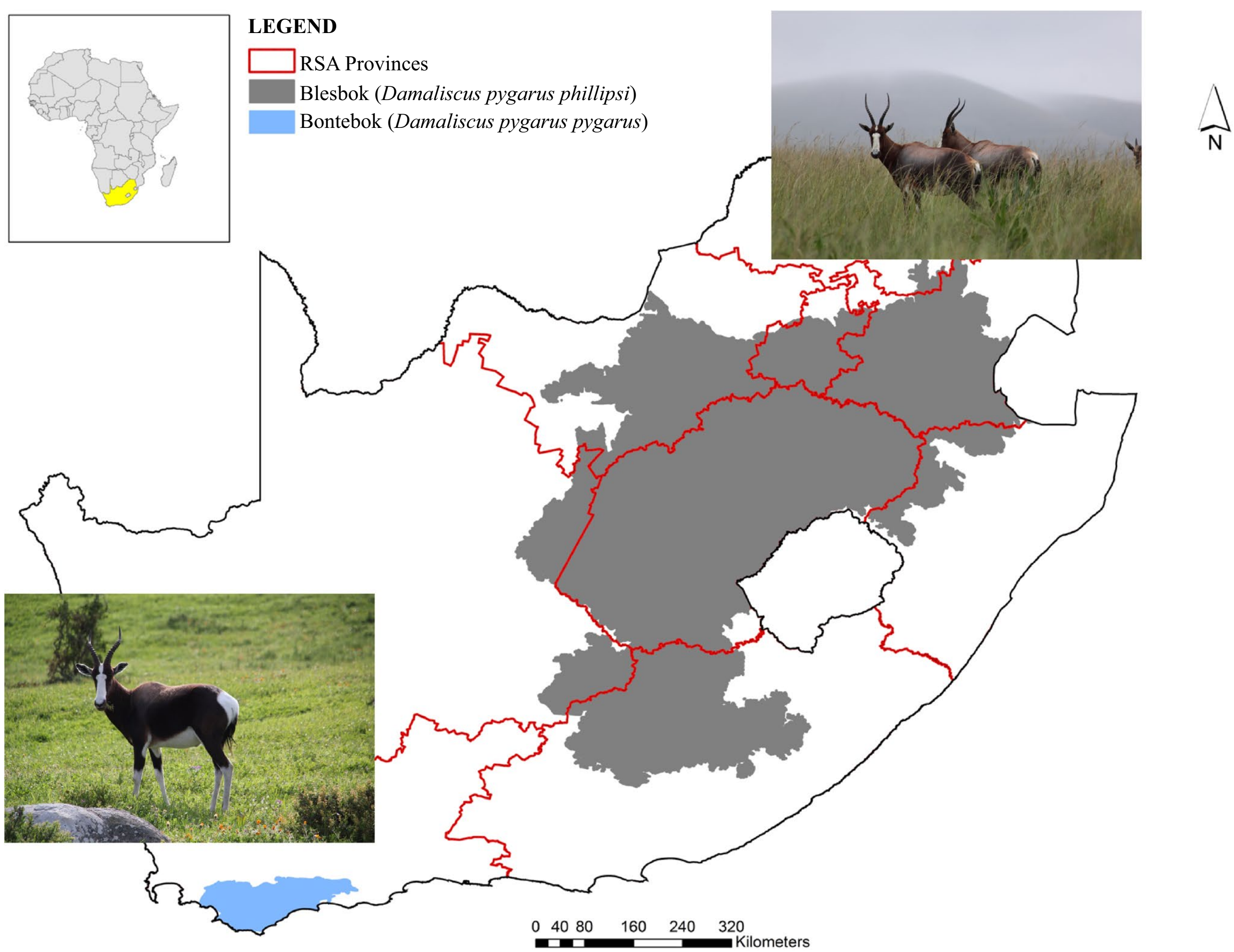

Fig. 2 Historical ranges of bontebok (light blue) and blesbok (grey) in South Africa. Red lines indicate provincial boundaries. Data represent known species distributions as of 30 March 2017 (Birss et al. 2017). (Color figure online)

Table 1 Average price trends and record wildlife auction prices for commonly traded species (most prices reflect adult bulls) adapted from Cloete et al. 2015

Wildlife species	Price trend 2013–2015	Record price	Wildlife species	Price trend 2013–2015	Record price
Blue wildebeest	234–348	16,750	Kudu	737–4020	629,800 (66″)
Golden blue wildebeest	38,190–67,000	180,900	Kudu/black	15,410–100,500	100,500
King blue wildebeest	167,500	871,000	Gemsbok	361–455	2680
Cape Buffalo	20,100–134,000	11,792,000 (55″)	Red Gemsbok	24,120–268,000	636,500
East African Buffalo	134,000–187,600	670,000	Roan	24,120–37,520	636,500 (31″)
Blesbok	107–234	670	Sable	2747–6231	154,100
Blesbok/white	187–710	–	Sable (Zambian)	67,000–154,100	1,809,000
Blesbok/white saddlebacked	–	281,400	Springbok	127–147	871
Blesbok/yellow	3819–67,000	100,500	Springbok/black	368–670	2412
Impala	107–589	60,300 (27.5″)	Springbok/coffee	–	174,200
Impala/black	16,348–46,900	214,400	Springbok/Kalahari	388–1407	8713
Impala/saddle-backed	46,900–284,750	502,500			

Values in parentheses refer to horn length in inches for the animals that were sold for these record prices. Prices are given in US Dollars (USD) using an exchange rate of 14.92

2015). Trophy hunting also drives markets (and is linked to evolutionary changes) in other parts of the world, where individuals of a certain coat colour, trophy size or shape are more likely than others to be removed from the population (Allendorf and Hard 2009).

South Africa currently has an estimated 20 million head of game on private land, whereas 50 years ago, a census of all game numbered approximately 575,000 (Oberem 2015; Taylor et al. 2016). Therefore, numerically there is currently more wildlife in SA than there has been since the large-scale exterminations by outbreaks of bovine pleuropneumonia (1850), rinderpest (1896), and hunting by explorer-hunters/settlers (Bond et al. 2004). Parallel increases in wildlife population size have been observed in many parts of the world (e.g. Henrruzo and Martinez-Jauregui 2013). This increase in numbers, however, does not necessarily contribute to biodiversity/conservation. The Red List of South African mammals highlighted this issue where many mammal populations are not 'wild' and therefore do not contribute to the IUCN criteria, and thus would not receive the same protection as wild populations (Taylor et al. 2016). Populations containing inter and intra-specific hybrids (as are increasingly appearing on wildlife ranches) are also not given equal protection in many countries including the US Endangered Species Act (Allendorf et al. 2004).

The role of legislation

Legislation on nature conservation and wildlife management is often locally devolved, as it is in South Africa, where it has been developed and implemented at both national and provincial levels. Legislative standardisation can thus prove challenging: conditions under which species may be translocated, released and bred may differ among regions, and in general, breeding under intensive conditions is poorly regulated. In South Africa, State owned protected areas capture and sell excess animals, so wild animals can sometimes be bought to bring new genetic material to breeding ventures. In addition, protected areas may have their own breeding projects focusing on conservation breeding principles [e.g. the disease-free buffalo project of the South African National (SAN) Parks], and these animals may also enter into private ownership.

In South Africa, recent government-initiated stakeholder forums have emphasised the importance of the wildlife economy and resulted in a recent policy shift where game ranching is now recognised as both legitimate and an important driver of the country's agricultural economy and future wellbeing. Consequently, the Department of Agriculture, Forestry and Fisheries (DAFF) recently amended the Animal Improvement Act of 1998 (SA Government Gazette 2016) to include 12 wildlife species in addition to domestic species, confirming that game ranching is nationally supported. This amendment was published without any consultation with major role players in the wildlife industry as required by law (Naude 2016). Further discussion around the implications of the new legislation and expansion of the wildlife economy for long-term biodiversity management and conservation is therefore needed between all parties involved. In a similar vein, ostrich has been recognised as a domestic species by the USDA (United States Department of Agriculture) and has been included in the Agriculture Census since 2002 (https://www.ostriches.org). The global implications of legislation and expansion of the wildlife economy for biodiversity management therefore needs careful consideration.

Examples from the wildlife industry

Wildlife breeding has recently focused on finding and perpetuating rare or novel morphs or forms (for example, black vs. common impala; see Table 2; Fig. 1). These morphs or forms do not confer any selective advantage on the individuals, and are highly likely to have negative consequences at the individual and population level (Hetem et al. 2009). Rare colour morphs may have a recessive or epistatic nature such that the morph will not be observed in 'carriers' (Anderson et al. 2009).

The interface between farmed and natural land is very likely to be porous since biosecurity in wildlife ranches is not 100% effective (e.g. Grobler et al. 2011) and as such, alleles at high frequencies in ranched animals could potentially circulate undetected in natural populations, especially if recessive. Selection against desirable phenotypes (unnatural selection) may decrease survival in the wild (Allendorf and Hard 2009). For example, the colour and structure of an animal's pelt are associated with adaptation to the thermal environment. Hetem et al. (2009) reported that black springbok forage less in winter because the metabolic cost of homeothermy is lower, but may be disadvantaged during hotter periods. In contrast, white springbok will be more protected from solar heat load but less able to meet the energy cost of homeothermy in winter (Hetem et al. 2009). Metabolic costs may therefore partially explain the rarity of springbok colour morphs in the wild. Colouration in mammals is especially important in crypsis, in which (1) the body colour resembles or matches the natural background of the environment that varies with season and age or (2) where colour patterns on the body match patterns of light and dark in the surrounding habitat (Hetem et al. 2009). In a more recent example, two independent loss-of-function mutations in a Wrangel Island mammoth at the locus of FOXQ1 have been observed (Rogers and Slatkin 2017). These independent mutations confer a satin coat phenotype which result in translucent fur but normal pigmentation (Rogers and Slatkin 2017).

Challenges and potential decision-making processes

Selective breeding

Challenge

Ranchers are increasingly carrying out 'Intentional Genetic Manipulation' for desirable traits such as larger horns for trophies, colour morphs and bigger animals for meat production. There has been much interest in the production of game meat in South Africa and Namibia over the last 50 years (Taylor et al. 2016) with 1350 tonnes of game meat consumed (Taylor

Table 2 Known desirable colour variants and other variants of 'wild-type' animals which have been sold at recent auctions

Species	Colour variants	Other variants
Blesbok	Apache, bronze, coffee, copper, curly hair (woolly), skilder, red, speckled, top deck, dappled, masked, painted, saddle-backed, silver, white, white saddle-back, yellow	–
Buffalo	White	Disease free buffalo, east African, east African × southern African, horn and body size
Eland	King cape, white, skilder	Cape eland, Livingstone's, horn length and number of stripes
Impala	Black, black-backed, black-nosed, grey, midnight, royal, saddle-backed, white, white-flanked, white painted	East African × southern African impala (horn length)
Lechwe	Red, yellow	Horn length, cross with waterbuck
Kudu	Black, brown, white, zebra-striped	Horn length, cross with nyala
Nyala	–	Cold adapted nyala, horn length, cross with kudu
Gemsbok	Dappled, golden, ivory, red, white, yellow, skilder, cardinal, scimitar	Heartwater gemsbok, Kalahari, horn length
Reedbuck	–	Horn length
Roan	–	Western Africa × southern Africa roan (horn length)
Sable	Golden	Malawian sable, Matetsi Tanzanian, Zambian, West Zambian, various crosses, horn length
Springbok	Black, blue, coffee, copper, cream, damara, dappled, king, ivory, painted, royal, white	Heartwater springbok, Kalahari
Blue Wildebeest	Gold with markings, golden (tuli), king (including marking variants), golden king	–

et al. 2016) and 450 tonnes of wild meat exported annually during the early 2000s (National Agricultural Marketing Council, NAMC 2006). 'Intentional Genetic Manipulation' can lead to genetic erosion due to founder effect, genetic drift and inbreeding, potentially resulting in the fixation of deleterious alleles that may be co-inherited with anthopogenically-desired traits (Frankham et al. 2010). Loss of heterozygosity and allelic diversity may impact on a species' evolutionary potential and the reproductive potential of captive stock. Some of these traits such as coat colour may be genetically linked to behavioural changes (Jacobs et al. 2016). Genetic exchange between farmed and wild populations could result in substantial alteration of local allele frequencies in natural populations, decreasing short-term fitness and long-term evolutionary potential as shown in Atlantic salmon (Perrier et al. 2013). Unintentional selection is also likely to occur on wildlife ranches due to the absence of predators, the practices of supplementary feeding and water provision, and the provision of veterinary care. The diminution of natural selection may encourage traits or behaviours that are maladaptive in the wild (Frankham et al. 2010). In both plants and animals, managed populations have converged on a 'domestication syndrome', featuring sets of traits that may be beneficial in captivity (Wright 2015).

Decisions

Management decisions include the implementation of barriers or buffer zones between ranched and wild populations as seen in the case of buffalo and cattle and monitoring of both gene pools using molecular markers (Hansen et al. 2012). Guidelines for breeding, population isolation and translocation should be developed after scientific investigation and determination of their feasibility, social acceptability and effectiveness. Small scale implementation of trial management plans could be performed or an adaptive management approach could be taken to establish which practices best conserve genetic variation and fitness. The fisheries industry often performs careful evaluation of the genetic status of their stock and of the genetic contact between stocked and wild populations (Begg et al. 1999).

Sound policy must be underpinned by scientific information. There is an urgent need to understand the underlying genetic basis of the traits that are currently being selected on wildlife ranches and to determine how allele frequencies differ between ranched and wild populations. This knowledge can be achieved through analysis of candidate genes, experiments and/or by using shared records on breeding outcomes from the ranchers, though we recognise that the genetic basis of some traits will be more difficult than others to document (Hoban et al. 2016). There is now a broader knowledge base on the genetic underpinning of coat colour in wild and domestic animals (e.g. Anderson et al. 2009), which can be expanded upon. Additional data regarding colour genes are given in the Supplementary materials. For an illustration of four different colour gene types and a description of the primary colour genes in horses see Supplementary material 1 (Table 1) and 2, respectively. Policy needs to be co-developed in an open, transparent, and fair fashion. This should include the development of regulatory frameworks to find the right balance between biodiversity and economic interest (Cook et al. 2013).

Small populations

Challenge

Effective management of small or disconnected populations has been identified as a core problem in conservation biology since the inception of the discipline. In addition to genetic issues, small populations often feature breakdown of normal behaviours, and demographic instability with high extinction potential. Small populations on wildlife farms are also subject to the frequent removal of individuals for hunting or breeding. In such populations, a few males may dominate reproduction within a population or several subpopulations via the deliberate use of stud animals (Garnier et al. 2001). Such issues are likely to be especially problematic in many southern African wildlife species, regardless of whether they are found on wildlife ranches, since many of these species have historically featured very large populations distributed over vast areas (see Figs. 2, 3; Birss et al. 2017).

Decisions

Traditional approaches include well-planned breeding and translocations in addition to keeping detailed records (studbooks) which include genetic data e.g. results from parentage analyses (Leus et al. 2011). For example, translocation records have enabled better management of Alpine ibex (*Capra ibex* Linnaeus, 1758) populations (Biebach and Keller 2009). Genetic monitoring can be performed to establish status and trends and help decide when to bring in animals from other populations (e.g. Iyengar et al. 2007). A private reserve of scimitar-horned oryx (*Oryx dammah* Cretzschmar, 1827) in the United Arab Emirates has recently been evaluated for its genetic importance to the whole species (El Alqamy et al. 2012). Population viability analysis can be coupled with monitoring to help model, understand and predict the future consequences of different management strategies (Pierson et al. 2015). Software that combines elements of natural population simulations (e.g. Vortex; Lacy 2000) and population management (e.g. PmX; Lacy et al. 2012) can also be applied. Several online data recording systems now exist to help with these efforts:

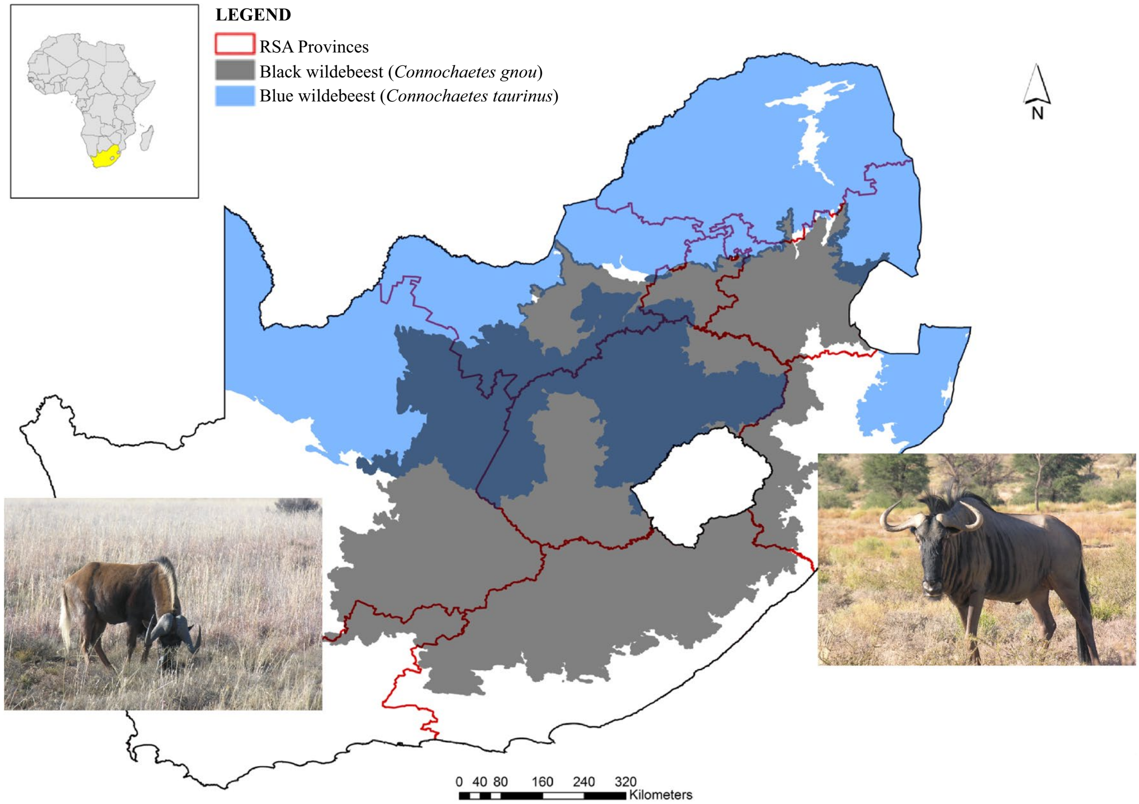

Fig. 3 Historical distribution ranges of blue (light blue) and black wildebeest (grey). The overlap between blue (right) and black (left) wildebeest distributions is indicated by the darker blue colour. Red lines indicate provincial boundaries. Data represent known species distributions as of 30 March 2017 (Birss et al. 2017). (Color figure online)

for example, the South African Stud Book and Animal Improvement Association (http://www.logix.org.za), and the Independent Wildlife Registering Authority system (http://ws2.co.za/about-us/).

Policy and guidance is needed to develop and promote best practices for sustainability, similar to goals for zoo populations (Lacy et al. 2012). Zoo populations are carefully managed to alleviate small population problems, with frequent transfer of individuals for mating (Lacy 2013). Scientists and wildlife ranchers should be encouraged to co-develop metapopulation and population management plans for each species, as has been done for wild dogs, lions and other predators (Miller et al. 2015). This may, for example, include guidelines for the number of individuals needed to be translocated to maintain genetically healthy populations after taking into account the costs and benefits. Another way to alleviate negative effects in small/fragmented populations, especially populations that have been strongly reduced by anthropogenic activities, may be to allow managed gene exchange between two or more closely related populations or even, in extremis, subspecies (Frankham 2015; Frankham et al. 2017). There are numerous arguments for and against this approach and each case should be evaluated on its own merits. General considerations include (i) limiting gene exchange to within the same taxon, (ii) considering whether exchanging populations are adapted to similar environments, (iii) testing whether the populations have fixed chromosomal differences and (iv) evaluating whether gene flow has occurred between the populations within the recent past (500 years has been suggested; Frankham et al. 2011). Conservationists and scientists should therefore attempt to evaluate the risks of outcrossing for the species of interest. Data from previous studies showed that 93% of such events resulted in fitness benefits (improved growth rates, fertility, and survival) for the outcrossed population. Only nine cases showed deleterious effects and one study showed mild outbreeding depression (Frankham 2015).

Hybridisation and translocation

Challenge

Hybridisation can and does occur in nature between closely related species (e.g. black wildebeest and blue wildebeest; Grobler et al. 2011), subspecies (bontebok and blesbok, *D. p. phillipsi*; Van Wyk et al. 2013) or genetically differentiated populations. Human-mediated hybridisation may occur due to changes in the distribution and abundance of a species, removal of landscape or behavioural barriers, or introduction of non-native species (Allendorf et al. 2001). Between 130,000 and 167,000 animals (http://www.wtass.org/Default.aspx; Dry 2013) are estimated to be translocated annually in South Africa but these numbers may be underestimates (Taylor et al. 2016). Due to the rapid rate of ongoing translocations in wildlife farming, documentation is scarce.

Hybridisation may be deliberate, accidental or both. Deliberate hybridisation is known between greater kudu (*Tragelaphus strepsiceros* Pallas, 1766) and nyala (*T. angasii* Angas, 1849), waterbuck (*Kobus ellipsiprymnus* Ogilby, 1833) and lechwe (*K. leche* Gray, 1850) and southern-western sable (*Hippotragus equinus equinus* Saint-Hilaire, 1803) and roan (*H. e. koba*, Gray 1872). The historical distribution of black and blue wildebeest overlapped but hybridisation may have been prevented by the presence of plentiful con-specific mates and no restriction to movement (Fig. 3; Supplementary material 3). However, farming both species on the same land with few or no con-specific mates may encourage hybridisation (Grobler et al. 2011; Dalton et al. 2014) and this is a general risk of game farming (e.g. Blanco-Aguiar et al. 2008). Hybridisation can have positive effects such as heterosis (hybrid vigour) and genetic rescue of inbred populations. Crossing closely related species/subspecies may be a solution for taxa that have been reduced due to human impact (Frankham et al. 2017). However, negative effects of hybridisation include loss of local adaptations and unique traits, reduced fertility and offspring viability which can lead to extinction (Wolf et al. 2001), and outbreeding depression which has, for example, been documented in southern Africa (e.g. greater kudu-nyala; Dalton et al. 2014). Furthermore, species are routinely introduced beyond their historical distributions (different climatic conditions/vegetation/ecosystems), e.g. black wildebeest in Namibia (Lindsey et al. 2006) and Botswana (I Rushworth, personal communication, Ezemvelo KZN Wildlife). We therefore propose that the climate requirements of the focal species should be understood and matched to current/future climate at the translocation site by measuring key climate parameters (see the IUCN Guidelines for Reintroductions and Other Conservation Translocations).

Decisions

In order to conserve biodiversity by safeguarding the genetic integrity of each species/subspecies (*sensu* the Convention on Biological Diversity's Aichi Target 13, http://www.cbd.int/sp/targets/), national and provincial policy needs to clarify which species may be kept on the same land, for example prohibiting co-enclosure of closely related species/domesticated relatives to prevent hybridisation events (Hedrick 2009; Grobler et al. 2011, see Supplementary material 3 and 4). Other decisions include isolating suspected hybrid groups in adequate, regularly inspected enclosures. When hybridisation is deemed detrimental, no translocations should be allowed until reliable genetic tests to screen for hybrids have been conducted. If hybrids are found in a population, and sufficient genetic variation exists in non-hybrid populations, owners may be encouraged to remove all unwanted animals with compensation from the government (see wolf-dog hybridisation; Vilà et al. 2003). Another option is to incentivise or mandate wildlife ranchers to register populations of species where the taxonomic integrity of that species has been preserved (based on management history and genetic tests) and to tightly control introductions into and translocations from these populations. In contrast, some may argue that actions such as deliberate admixture by introducing individuals from related subspecies may be necessary to recover population fitness even though the taxonomic integrity of a species may be temporarily disrupted (Stowell et al. 2017). This issue of genetic rescue to prevent species from extinction is debated in the literature (Frankham 2015; Stowell et al. 2017). However, here we refer to the issue of deliberate subspecies admixture where there is no threat of extinction or reduced population fitness to either of the subspecies. Therefore we do not recommend this as a first course of action for viable species/subspecies unless a risk assessment has been carried out to assess the likelihood of outbreeding depression.

Data should be maintained for each individual and all actions (for example, translocations) should be recorded. It is also important to conduct educational campaigns for landowners and officials on genetic principles/issues such as hybridisation.

Genetic techniques and software tools can help to identify hybrids and determine the extent of hybridisation in order to inform policy makers (Supplementary material 3 and 4). Local molecular genetic facilities in countries such as South Africa, Botswana and Namibia are readily available but the methods carried out should be standardised and laboratories should be encouraged to exchange baseline reference data where mutually beneficial. Such services are increasingly available worldwide.

A crucial need is to establish and agree upon the 'natural' ranges (including historical, current and translocated ranges) of wildlife species and the genetic variants (including subspecies) within them. Genetic and other data within species need to be available to identify evolutionarily significant units (ESUs) and management units (MUs) which allow for the preservation of genetic variation within species. It is also important to identify the appropriate units for conservation in order to maintain ecological and evolutionary processes (Funk et al. 2012). For example, the South African Department of Environmental Affairs (DEA) is producing range maps for all indigenous species (e.g. Birss et al. 2017) and this activity is ongoing worldwide in pursuance of Article 7 of the Convention on Biological Diversity. Ecological and genetic information should be integrated into range definitions, as well as historical distributions. Combining range maps and current knowledge of breeding outcomes can inform the level of translocation that may be considered detrimental to the species and this knowledge may improve decisions regarding translocations.

Future technologies

Given new technologies such as CRISPR/CAS9 gene editing, it is possible that genetically modified organisms will soon appear in the game ranching industry, as it has already in aquaculture (Howard et al. 2004). A regulated approach needs to be formulated for the implementation of these methods since genetically modified genetic material could thus enter wild populations, via unintended consequences. For example, in Howard et al. (2004) it has been reported that genetically modified male medaka fish have an overwhelming mating advantage while their offspring suffer from a survival disadvantage relative to the wild type. This mechanism will ultimately lead to population extinction because of the viability disadvantage. More recent examples of genetic modification involve CRISPR and eradication of invasive species such as rats (Owens 2017). Potentially any species could be subject to CRISPR modification, though it is not clear when it may be applied to large mammals.

Conclusions

In summary, we suggest the following key steps for this industry:

1. New guidelines, policy and legislation, informed by scientific evidence and expert wildlife ranching knowledge, should be developed and enforced globally, including in southern Africa, via collaboration between wildlife ranchers, scientists, community members, government, and management authorities.
2. A lack of evidence remains in key areas such as the genetic basis of commonly selected traits, knowledge of range distributions, species' boundaries, impact of unintentional selection, and the required effective population size to manage wildlife species. Partnerships between scientists and ranchers, individually and on large scale through shared, open data, can help to obtain such knowledge. Scientists also need to develop and broadcast case studies of representative outcomes.
3. Specific recommendations based on the long-term monitoring of genetic effects within intensively managed populations are needed.
4. Educational/outreach material is needed on the conservation, environmental, social, and economic dimensions of 'Intentional Genetic Manipulation', including online educational resources (Hoban et al. 2013).
5. Open recording of animal breeding and movement across all wildlife ranches and other conservation areas with the integration of genetic tools should be encouraged to track translocations and provide knowledge on stock genetic diversity and species' divisions.
6. Yearly forums for involved stakeholders should be held to share information, facilitate communication, and host training sessions.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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References

Allendorf FW, Hard JJ (2009) Human-induced evolution caused by unnatural selection through harvest of wild animals. PNAS 16:9987–9994

Allendorf F, Leary RF, Spruell P, Wenburg JK (2001) The problems with hybrids: setting conservation guidelines. Trends Ecol Evol 16:613–622

Allendorf FW, Leary RF, Hitt NP, Knudsen KL, Lundquist LL, Spruell P (2004) Intercrosses and the U.S. Endangered Species Act: should hybridized populations be included as westslope cutthroat trout. Conserv Biol 18:1203–1213

Anderson TM, Candille SI, Musiani M, Greco C, Stahler DR, Smith DW, Padhukasahasram B, Randi E, Leonard JA, Bustamante CD, Ostrander EA (2009) Molecular and evolutionary history of melanism in North American gray wolves. Science 323:1339–1343

Begg GA, Friedland KD, Pearce JB (1999) Stock identification and its role in stock assessment and fisheries management: an overview. Fish Res 43:1–8

Biebach I, Keller LF (2009) A strong genetic footprint of the reintroduction history of Alpine ibex (*Capra ibex ibex*). Mol Ecol 18:5046–5058

Birss C, Rushworth I, Collins N, Peinke D, Buijs D (2017) Inferred natural distribution ranges of certain large mammals in South Africa. Unpublished GIS coverage

Blanco-Aguiar JA, González-Jara P, Ferrero ME, Sánchez-Barbudo I, Virgós E, Villafuerte R, Dávila JA (2008) Assessment of game restocking contributions to anthropogenic hybridisation: the case of the Iberian red-legged partridge. Anim Conserv 11:535–545

Bond I, Child B, de la Harpe D, Jones B, Barnes J, Anderson H (2004) Private land contribution to conservation in South Africa. In: Child B (ed) Parks in transition. Earthscan, London, pp 29–61

Cloete PC, Van Der Merwe P, Saayman M (2015) Game ranch profitability in South Africa. ABSA, CTP Printers, Cape Town

Cook CN, Mascia MB, Schwartz MW, Possingham HP, Fuller RA (2013) Achieving conservation science that bridges the knowledge—action boundary. Conserv Biol 27:669–678

Dalton DL, Tordiffe A, Luther I, Duran A, Van Wyk AM, Brettschneider H, Oosthuizen A, Modiba C, Kotzé A (2014) Interspecific hybridisation between greater kudu and nyala. Genetica 142:265–271

Dry G (2013) Wildlife ranching in perspective. http://africanindaba.com/2013/02/wildlife-ranching-in-perspective-february-2013-volume-11-1/. Accessed 20 July 2016

Dugmore H (2013) The wildlife industry rises to the challenge. Farmer Weekly, 22 April. http://www.farmersweekly.co.za/article.aspx?id=38412&h=The-wildlife-industry-rises-to-the-challenge. Accessed 20 July 2016

El Alqamy H, Senn H, Roberts M-F, McEwing R, Ogden R (2012) Genetic assessment of the Arabian oryx founder population in the Emirate of Abu Dhabi, UAE: an example of evaluating unmanaged captive stocks for reintroduction. Conserv Genet 13:79–88

Frankham R (2015) Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. Mol Ecol 11:2610–2618

Frankham R, Ballou JD, Briscoe DA (2010) Introduction to conservation genetics, 2nd edn. Cambridge University Press, Cambridge

Frankham R, Ballou JD, Eldringe MDB, Lacy RC, Ralls K, Dudash MR, Fenster CD (2011) Predicting the probability of outbreeding depression. Conserv Biol 25:465–475

Frankham R, Ballou JD, Ralls K, Eldridge M, Duhash MR, Fenster CB, Lacy RC, Sunnucks P (2017) Genetic management of fragmented animal and plant populations. Oxford University Press, Oxford

Funk WC, McKay JK, Hohenlohe PA, Allendorf FW (2012) Harnessing genomics for delineating conservation units. Trends Ecol Evo 27:489–496

Garnier JN, Bruford MW, Goossens B (2001) Mating system and reproductive skew in the black rhinoceros. Mol Ecol 10:2031–2041

Grobler JP, Rushworth I, Brink JS, Bloomer P, Kotze A, Reilly B, Vrahimis S (2011) Management of hybridisation in an endemic species: decision making in the face of imperfect information in the case of the black wildebeest—*Connochaetes gnou*. Eur J Wildlife Res 57:997–1006

Hansen MM, Olivieri I, Waller DM, Nielsen EE, GeM Working Group (2012) Monitoring adaptive genetic responses to environmental change. Mol Ecol 21:1311–1329

Hedrick PW (2009) Conservation genetics and the North American bison (*Bison bison*). J Hered 100:411–420

Henrruzo C, Martinez-Jauregui M (2013) Trends in hunters, hunting grounds and big game harvest in Spain. For Syst 22:114–122

Hetem RS, De Witt BA, Fick LG, Fuller A, Kerley GIH, Meyer LCR, Mitchell D, Maloney SK (2009) Body temperature, thermoregulatory behaviour and pelt characteristics of three colour morphs of springbok (*Antidorcas marsupialis*). Comp Biochem Phys A 152:379–388

Hoban S, Arntzen JW, Bertorelle G, Bryja J, Fernandes M, Frith K, Gaggiotti O, Galbusera P, Godoy JA, Hauffe HC, Hoelzel AR, Nichols RA, Pérez-Espona S, Primmer C, Russo IM, Segelbacher G, Siegismund HR, Sihvonen M, Sjögren-Gulve P, Vernesi C, Vilà C, Bruford MW (2013) Conservation genetic resources for effective species survival (ConGRESS): bridging the divide between conservation research and practice. J Nat Conserv 21(6):433–437

Hoban S, Kelley JL, Lotterhos KE, Antolin MF, Bradburd G, Lowry DB, Poss ML, Reed LK, Storfer A, Whitlock MC (2016) Finding the genomic basis of local adaptation: pitfalls, practical solutions, and future directions. Am Nat 188:379–397

Howard RD, DeWoody A, Muir WM (2004) Transgenic male mating advantage provides opportunity for Trojan gene effect in a fish. PNAS 101:2934–2938

IUCN/SSC 2013 Guideline for Reintroductions and Other Conservation Translocations. Version 1.0. Gland, Switzerland: IUCN Species Survival Commission, viiii + 57 pp. ISBN: 978–2-8317-1609-1

Iyengar A, Gilbert T, Woodfine T, Knowles JM, Diniz FM, Brenneman RA, Louis EE, Maclean N (2007) Remnants of ancient genetic diversity preserved within captive groups of scimitar-horned oryx (*Oryx dammah*). Mol Ecol 16:2436–2449

Jacobs LN, Staiger EA, Albright JD, Brooks SA (2016) The MC1R and ASIP coat colour loci may impact behaviour in the horse. J Hered 107:214–219

Janovsky E (2015) Wildlife industry expected to continue to grow. ABSA report 1–3

Lacy RC (2000) Structure of the VORTEX simulation model for population viability analysis. Ecol Bull 48:191–203

Lacy RC (2013) Achieving true sustainability of zoo populations. Zoo Biol 32:19–26

Lacy RC, Ballou JD, Pollak JP (2012) PMx: software package for demographic and genetic analysis and management of pedigreed populations. Methods Ecol Evol 3:433–437

Lafferty KD, Harvell CD, Conrad JM, Friedman CS, Kent ML, Kuris AM, Powell EN, Rondeau D, Saksida SM (2015) Annu Rev Mar Sci 7:471–496

Leus K, Traylor-Holzer K, Lacy RC (2011) Genetic and demographic population management in zoos and aquariums: recent developments, future challenges and opportunities for scientific research. Int Zoo Yearbook 45:213–225

Lindsey P, Alexander R, Fran] LG, Romañach SS (2006) Potential of trophy hunting to create incentives for wildlife conservation in Africa where alternative wildlife-based land uses may not be viable. Anim Conserv 9:283–298

Lindsey PA, Romañach SS, Davies-Mostert HT (2009) The impact of conservancies for enhancing the value of game ranch land for large mammal conservation in southern Africa. J Zool 227:99–105

Miller SM, Harper CK, Bloomer P, Hofmeyr J, Funston PJ (2015) Fenced and fragmented: conservation value of managed metapopulations. PLoS One 10:e0144605

National Agricultural Marketing Council, NAMC (2006) Report on the investigation to identify problems for sustainable growth and development in South African wildlife ranching. Pretoria

Naude M (2016) South African Hunters and Game Conservation Association. Press Release: SA hunters concerned about new regulations that allow cross breeding of wildlife. http://www.sahunters.co.za/index.php/hunting-jagsake/item/246-sa-hunters-concerned-about-new-regulations-that-allow-cross-breeding-of-wildlife. Accessed 3 Jan 2018

Nel EJ (2015) South African Hunters and Game Conservation Association. Press Release: Risks and impacts associated with intensive and selective breeding of indigenous game for commercial purposes. http://www.sahunters.co.za/index.php/conservation-bewaring/item/60-sahgca-selective-breeding-policy. Accessed 11 Feb 2016

Nogueira SSC, Nogueira-Filho SLG (2011) Wildlife farming: an alternative to unsustainable hunting and deforestation in Neotropical forests? Biodivers Conserv 20:1385–1397

Oberem P (2015) Wildlife ranching in South Africa. Africa Geographic

Owens B (2017) Behind New Zealand's wild plan to purge all pests. Nature 541:148–150

Perrier C, Baglinière JL, Evanno G (2013) Understanding admixture patterns in supplemented populations: a case study combining molecular analyses and temporally explicit simulations in Atlantic salmon. Evol Appl 6:218–230

Pierson JC, Beissinger SR, Bragg JG, Coates DJ, Oostermeijer JGB, Sunnucks P, Schumaker NH, Trotter MV, Young AG (2015) Incorporating evolutionary processes into population viability models. Conserv Biol 29:755–764

Pitman RT, Fattebert J, Williams ST, Williams KS, Hill RA, Hunter LTB, Slotow R, Blame GA (2016) The conservation costs of game ranching. Conserv Lett. https://doi.org/10.1111/conl.12276

Radloff FGT, Birss C, Cowell C, Peinke D, Dalton D, Kotze A, Kerley GIH, Child M (2015) A conservation assessment of *Damaliscus pygargus* ssp. *pygargus*. In: Child MF, Do Linh San E, Raimondo D, Davies-Mostert H, Roxburgh L (ED) The Red list of mammals of South Africa, Swaziland and Lesotho. SANBI and Endangered Wildlife Trust, South Africa

Rogers RL, Slatkin M (2017) Excess of genomic defects in a woolly mammoth on Wrangel island. PLoS Genet 13(3):e1006601

SA Government Gazette (2016) Notice No. 690, Department of Agriculture, Forestry and Fisheries, Animal Improvement Act, 1998 (ACT No. 62 of 1998): Regulation Amendment. 40058:pp 21–28

Schroder B, Reilly BK (2013) A comparison between tick species collected in a controlled and control free area on a game ranch in South Africa. J S Afr Vet Assoc. https://doi.org/10.4102/jsava.v84i1.907

South African National Biodiversity Institute (2007) South African National Biodiversity Institute (SANBI) Annual Report 2006–2007, SANBI, Claremont

Stowell SM, Pinzone CA, Martin AP (2017) Overcoming barriers to active interventions for genetic diversity. Biodivers Conserv 26:1753–1765

Taylor WA, Lindsey PA, Davies-Mostert H (2016) An assessment of the economic, social and conservation value of the wildlife ranching industry and its potential to support the green economy in South Africa. The Endangered Wildlife Trust, Johannesburg

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

Vilà C, Walker C, Sundqvist A-K, Flagstad Ø, Andersone Z, Casulli A, Kojola I, Valdmann H, Halverson J, Ellegren H (2003) Combined use of maternal, paternal and bi-parental genetic markers for the identification of wolf-dog hybrids. Heredity 90:17–24

Wolf DE, Takebayashi N, Rieseberg LH (2001) Predicting the risk of extinction through hybridisation. Conserv Biol 15:1039–1053

Wright D (2015) The genetic architecture of domestication in animals. Bioinform Biol Insights 9:11–20