

Breeding Centers, Private Ranches, and Genomics for Creating Sustainable Wildlife Populations

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Human-induced changes to environments are causing species declines. Beyond preserving habitat (in situ), insurance (ex situ) populations are essential to prevent species extinctions. The Conservation Centers for Species Survival (C2S2) is leveraging space of breeding centers and private ranches to produce “source populations”—genetically diverse reservoirs that also support research and reintroductions. The initial focus is on four African antelopes. C2S2 has developed a program, the Source Population Alliance, that emphasizes animals living in spacious, naturalistic conditions in greater numbers than can be accommodated by urban zoos. Simulation modeling demonstrates how herds can rapidly increase population abundance and retain genetic diversity. Advances in genomics and resulting DNA data allow monitoring of genetic diversity and parentage as well as refined decision-making. This approach, neither pure in situ nor ex situ, but rather “sorta situ”, is an innovative way of linking public and private sector resources to ensure that endangered species survive.

Keywords: conservation, species, endangered, herds, sustainability

Like the resource it seeks to protect, wildlife conservation must be dynamic, changing as conditions change, seeking always to become more effective.

Rachel Carson (<http://www.thoughtco.com>;
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The International Union for Conservation of Nature (IUCN) indicates that ~25% of vertebrate species are at risk of extinction (http://www.iucnredlist.org/about/summary-statistics#How_many_threatened) from human overpopulation, habitat loss, exploitation, pollution, disease, alien species, and climate change. Among the most concerning threats are global greenhouse emissions predicted to cause the eventual disappearance of at least 50% of animal species in certain locales (www.worldwildlife.org/publications/wildlife-in-a-warming-world-the-effects-of-climate-change-on-biodiversity). Although all species are susceptible to environmental disruptions, larger animals requiring more space and complex ecosystems are most vulnerable. Ripple et al. (2015) have reported the collapse of the world’s 74 wild herbivore species ≥100 kg comprising 11 families (Elephantidae, Rhinocerotidae, Hippopotamidae, Giraffae, Bovidae, Camelidae, Tapiridae, Equidae, Cervidae, Suidae,

and Hominidae). Approximately 60% of these species are threatened due to killing for bush meat/body parts, land-use change, and resource competition by livestock. The result is demographically impoverished populations, lost gene diversity, fewer large carnivores and scavengers, and altered ecosystem services (Ripple et al. 2015).

Historically, preserving biodiversity has focused on saving habitat and, by default, protecting all species living in that native environment (*in situ*). Although always the priority, this goal is outpaced by reality. Few wilderness areas are unaffected by human influence (Watson et al. 2018), and more and more wildlife is confined behind fences (Minter 2018), sometimes with military-level security. Although a conservation success story, there is a global tendency for protected areas to be <10,125 hectares, too small for sustainable herbivore populations (Cantú-Salazar and Gaston 2010). Besides competing demands for always too few resources (Watson et al. 2014), there is also concern about enough safeguarded wild space to assure viability. One analysis of ~4000 threatened mammals, birds, and amphibians revealed that 17% of species are absent in protected areas, and 85% are of insufficient population abundance to ensure survival (Venter et al. 2014).

Therefore, there is a growing loss of confidence that wild populations can continue existing in relevant numbers in

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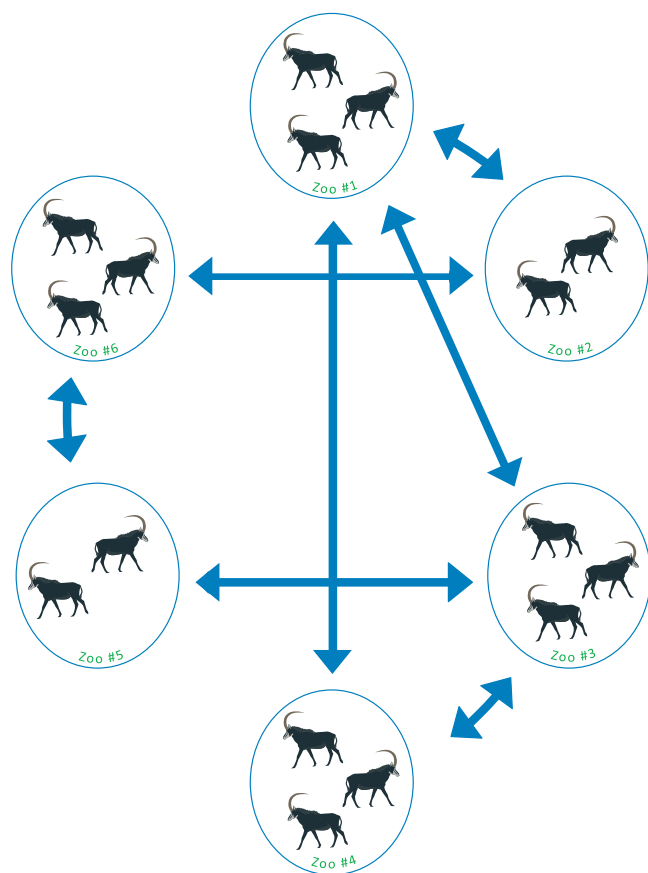


Figure 1. Typical intensive management scenario for zoos, requiring transfer of animals between institutions (arrows) for matings to retain gene diversity.

native ranges (Conway 2010). This is our concern, especially for large vertebrates. In the absence of assurance of survival in the wild, there is an increasing need for threatened species to be sustained under some form of human care. This *ex situ* management is recognized by the IUCN as a legitimate, feasible conservation tool (McGowan et al. 2016). Besides serving as insurance in safe havens, such a resource allows (1) learning about basic species biology (studies challenging to do in elusive wild counterparts), (2) raising public awareness and inspiring financial support of field conservation, and (3) recovering species from the edge of extinction. There are iconic examples of *ex situ* breeding and then successful reintroductions to the wild, including the black-footed ferret (*Mustela nigripes*), California condor (*Gymnogyps californianus*), golden lion tamarin (*Leontopithecus rosalia*), Mexican gray wolf (*Canis lupus baileyi*), Iberian lynx (*Lynx pardinus*), Przewalski's horse (*Equus ferus przewalskii*), and scimitar-horned oryx (*Oryx dammah*) (Soorae 2008; Wildt et al. 2009, 2010; World Association of Zoos and Aquariums 2005; Traylor-Holzer et al. 2018).

Ex situ programs and zoos

Most *ex situ* programs require a long-term commitment—perhaps in perpetuity—to maintain and propagate target

species sustainably. For a carefully managed program with adequate founders, population abundance increases over time without the need for removing more animals from the wild. The population also retains a high level of genetic diversity to avoid inbreeding depression while remaining adaptable and resilient to environmental change (Frankham et al. 2017).

The idea for creating sustainable insurance populations for rare species was pioneered nearly 40 years ago by zoos (Conway 1980). In this “ark” paradigm, certain species are intensively managed by cooperating institutions that share individuals (figure 1), or occasionally germplasm (Santymire et al. 2018), in a “metapopulation” (Long et al. 2011). A pedigree is maintained and relatedness among animals (mean kinship) used to determine best matings to retain gene diversity (Ballou and Lacy 1995). Individual animals are identifiable (via ear tag, transponder, tattoo) and then moved between institutions to avoid inbreeding that can lead to infertility, disease susceptibility, morphological defects, and mortalities (Frankham et al. 2017). Mostly, the goal is to retain 90% of existing genetic diversity for 100 to 200 years (Soulé et al. 1986), a level predicted to preserve species integrity and evolutionary potential (Lacy 2013).

An effective population size (N_e) describes a genetically idealized population that displays the same rate of loss of genetic variation and increase in inbreeding as a natural wild population. Frankham et al. (2017) proposed that N_e for a typical wildlife population should be at least 500 individuals to minimize loss of genetic variation while also retaining long-term adaptability to continued environmental change. Because N_e is usually only a small proportion of the total census population size, a genetically viable *ex situ* population may require thousands of individuals (Ballou and Traylor-Holzer 2011). Although these specific recommended abundances remain open to scrutiny (Jamieson and Allendorf 2012), it is important to recognize that large *ex situ* populations of endangered species are necessary to ensure long-term viability.

There have been significant lessons learned from zoo breeding programs, especially new information on natural history, animal husbandry, welfare, record keeping, and mating recommendations (Lacy 2013). There are a few species, such as the African penguins (*Spheniscus* spp.), giraffe (*Giraffa* spp.), and Western lowland gorilla (*Gorilla gorilla*) where demographic and genetic stability are being maintained (Lacy 2013). But despite good intentions, accredited zoos hold only ~15% of the world's threatened terrestrial vertebrates and in small-sized populations (Conde et al. 2013). The Association of Zoos and Aquariums (AZA), which accredits North American zoos, reports that only 44 of 622 managed species programs are self-sustaining (<https://www.aza.org/animal-program-sustainability-designations>). Of 428 species with studbooks, the median population is only 66 individuals (Long et al. 2011). Approximately 39% of all mammal, bird, reptile, and amphibian zoo populations are comprised of 50 or fewer individuals, and only 25% of these

are successful breeders. Results from the European zoo community are similar. Of 31 carnivore, 37 primate, 12 ungulate, and 7 rodent species, 48% of populations have bred to replacement, and only 55% are retaining gene diversity at or above the 90% retention value (Lees and Wilcken 2009).

Zoos are challenged in providing safe havens for more species in larger numbers due to insufficient resources (Monfort and Christen 2018; Powell 2018). Most significant is a lack of space. Zoos are complex, expensive operations, often existing on prime real estate in bustling cities. A dominant mission is attracting the public to share stories on hundreds of species. There is growing concern to promote welfare, which has led to elaborate exhibits that accommodate fewer animals, which may be one cause for the 45% size decline in zoo mammal populations (Long et al. 2011). We assessed AZA data available to members and ascertained that the 158 accredited urban institutions averaged only 27.3 hectares each. This translates into a modest 4306 total “zoo hectares” in all of North America to meet the needs of thousands of wildlife species for breeding, exhibition, education, merchandizing, and other zoo-related functions. Therefore, sustaining rare species in secure populations—to prevent extinction, generate new knowledge, and as a source for reintroductions—requires many times more animals than can be produced by typical zoo programs (Conway 2010; Lacy 2013). William Conway, pioneer in conservation breeding, noted 40 years ago that, because city zoos are “land poor,” “rural breeding farms and ranches will be needed” (Conway 1980).

Species conservation using land resources of breeding centers and private citizens

The Conservation Centers for Species Survival. As a complementary tactic, we created the Conservation Centers for Species Survival (C2S2; www.conservationcenters.org), a consortium of many of the world’s top endangered species facilities. This non-profit entity is dedicated to cooperatively applying its collective space to conserve species that require large areas, natural group sizes, minimal public disturbance, and scientific research. The full and affiliate C2S2 members in the USA, Canada, and Australia collectively manage >17,000 hectares for species propagation, study, recovery, and reintroduction. C2S2 also pools its expertise, specialized facilities, and network to implement new ways to build populations on a scale ensuring demographic and genetic security.

C2S2 embraces a “*sorta situ*” philosophy (Wolfe et al. 2012) where wildlife populations are grown in large, protected spaces under conditions reminiscent of the wild, and managed less intensively than zoos. A priority is managing wildlife in simple, spacious, and naturalistic areas (figure 2) with less emphasis on the individual animal and more value on the collective group. Because C2S2 institutions maintain more individuals per species (table 1), animals generally live in normal social groupings, interacting with conspecifics of

diverse ages and both sexes, often with limited exposure to the public.

Ungulates and the Source Population Alliance

C2S2 and wild ungulates. C2S2 uses a programmatic approach for various taxa, from carnivores to passerine songbirds. Its focus on ungulates, specifically African antelopes, is driven by three factors. First, many of the world’s wild herbivore populations are in severe decline (Ripple et al. 2015). Forty-four of 74 (59.4%) of the largest species are threatened with extinction (12 are classified as “Critically Endangered” <http://www.iucnredlist.org/about/summary-statistics>). Primary threats are hunting, livestock competition, and habitat loss from cultivation, deforestation, and forces associated with climate change (Payne and Bro-Jorgensen 2016). Second, zoos are not providing sustainable insurance populations or expanding exhibit space. On the contrary, only two of 89 ungulate species managed in AZA institutions meet sustainability goals, and 42% are in decline (AZA 2009; <https://www.aza.org/animal-program-sustainability-designations>).

The third reason for C2S2’s interest in ungulates is member capacity in breeding and studying these species for decades. The Smithsonian Conservation Biology Institute (SCBI; Virginia) is comprised of barns constructed in the early 1900s to produce horses and mules for the US military. Now modernized, these facilities are used for conservation breeding of scimitar-horned oryx (*Oryx dammah*) and dama gazelle (*Nanger dama ruficollis*). The Fossil Rim Wildlife Center (Texas), with landscapes and climate similar to African savannahs, has produced prodigious numbers of scimitar-horned oryx as well as addax (*Addax nasomaculatus*) and sable antelope (*Hippotragus niger*). The Wilds (Ohio), set on vast reclaimed mining lands, reproduces these antelopes as well as southern white rhinoceroses (*Ceratotherium simum simum*), the latter through four successive generations. White Oak Conservation (Florida) has a similar success with antelopes, rhinoceroses, giraffe as well as the okapi (*Okapia johnstoni*). Among the successes for African Lion Safari (Ontario, Canada) is the Asian elephant (*Elephas maximus*), including a multi-generational herd with semi-free-ranging opportunities. Austin Savanna (Texas) manages its wildlife in combination with its waste management and recycling business, an innovative way of linking conservation and industry. These institutions also facilitate research by having (1) chutes and restraint devices for safe animal handling and sample collection (figure 3), and (2) significant animal numbers to permit robust research, ranging from understanding a species’ natural history (Koester et al. 2015) to facilitating recovery through assisted breeding (Schook et al. 2013).

Private ranchers and wild ungulates

Animal resources in C2S2 breeding centers pale compared to those in the private sector. Texas, New Mexico, Oklahoma, Arizona, and Florida, among other states, have ranches with



Figure 2. *Scimitar-horned oryx living in a naturalistic herd structure at The Wilds, Ohio, USA (Photograph: Budhan Pukazhenth).*

significant non-native wildlife populations (figure 4). Texas alone has more than 5000 such ranches (www.texaslandconservancy.org/about-tic) where wild ungulates thrive in climates and terrains often analogous to range countries. It is common that these operations exceed 2000–4000 hectares each (table 1), a vastness where animals can go unseen for weeks, which contributes to truly wild behaviors (Mungall 2018a).

Such ranches exist for personal and/or professional use, from hobbies, to ecotourism, to hunting. As with commercial livestock, prime, genetically under-represented individuals are retained for breeding and herd improvement. Animals with many descendants are hunted/culled, sold, or traded. Revenue generation is important because generally there are no gate fees, government subsidies, or philanthropic donations (Mungall 2018a). Proceeds are re-purposed to reimburse operational costs, make capital improvements, purchase unrelated stock, and/or expand to other species. Remaining costs often are offset by the owner's private business and/or investments. Generally, wildlife ranch operators manage for full production, do not mark animals for identification, and occasionally rotate bulls to maintain herd heterozygosity (Mungall and Sheffield 1994). Ranchers are independent, generally operating with little or no connectivity to traditional conservation or research communities.

Value proposition of a Source Population Alliance

Given the under-appreciated contributions and potential of the private wildlife sector, C2S2 established a program called the Source Population Alliance (SPA; www.sourcepopulation.org). Participants with significant land and animal resources collaborate with an aim of producing sustainable populations of rare species. We define a source population as a dependable reservoir for *ex situ* or *in situ* conservation and utilization, including insurance, research, awareness, exhibition, raising funds for conservation, trade, and reintroductions into the wild. Although most SPA participants are ranches or C2S2 breeding centers, zoos are encouraged to join. Our goals are to (1) recruit qualified alliance participants to establish demographically sound metapopulations, (2) model the predicted impact of herd type (smaller versus larger) and number of herds to achieve ideal population growth, and (3) demonstrate how advances in genomics can be used practically for management.

Species targets

We identified the scimitar-horned oryx, dama gazelle, addax, and sable antelope for initial study, all having high conservation value (figure 5). Named for its long, backward sweeping, blade-like horns, the scimitar-horned oryx

Table 1. General modes of operations for zoos, breeding centers, and private ranches involved in conservation breeding of rare wildlife species.

	Urban-Based Zoos	C2S2 Breeding Centers	Private Ranches
Purpose	Public awareness, research, entertainment	Animal production, research, some awareness	Hobby, pleasure, ecotourism, hunting
Infrastructure/size	Elaborate, simulated habitat, limited space	Simple, semi-naturalistic, expansive	Simple, near natural, large to vast
Visitor numbers	Millions	Usually modest or few	Few, none
Species/animals	Many/few	Few/more	Least/more
Management/estimated cost	Intensive, expensive	Less intensive, less expensive	Least intensive, least expensive
Perception of animals	Focus on individual	Less emphasis on individual, more on group	Least emphasis on individual, most on group
Research	Yes, with limited animals	Yes, with many animals	No, with excellent potential



Figure 3. Restraint device for safe, hands-on sample and data collection from wild ungulates. Photograph: John Newby/Environment Agency-Abu Dhabi/Sahara Conservation Fund.

(figure 5a) is the largest mammal to disappear from the wild in the last 35 years. The tall, elegant dama gazelle (figure 5b) once inhabited 13 North African countries (Jebali 2018), but now is restricted to three tiny fragments of <300 individuals in Niger and Chad (Mungall 2018a). Likewise, perhaps only

300 addax (figure 5c) remain in vestigial pockets, mostly within Niger (Wacher et al. 2008). Each of these desert species has been hunted relentlessly, and relict populations have been pushed into marginal habitat with scarce grasses and shade critical to survival. Our fourth species is the sable antelope (figure 5d), endemic to southern Africa. Although designated by the IUCN as “Least Concern” the sable antelope is adversely impacted by human population growth that has increased poaching and caused significant grassland and savannah losses (e.g., Butynski et al. 2015).

What is unknown to the general public, and even some conservation experts, is that numbers of scimitar-horned oryx, dama gazelle, and addax in the private sector far exceed numbers in the wild (figure 6). Stuningly, there are >5000 scimitar-horned oryx and >2800 addax in Texas alone (Mungall 2018b), most on private lands. All four target species are candidates for reintroduction. Captive born scimitar-horned oryx, dama gazelle, and addax have been returned to Tunisia, Senegal, and Morocco with mixed success (Iyengar et al. 2007; IUCN 2009; Mungall 2018a). Since 2016, there have been serial reintroductions of scimitar-horned oryx into the Ouadi-Rimé-Ouadi Achim Wildlife Reserve of Chad, a cooperative venture of the Chadian government, the Environment Agency-Abu Dhabi, and the Sahara Conservation Fund (Catherine Mertes, personal communication). This program, initiated in 2016, has included the release of more than 150 oryx – with some originating from Texas ranches. In turn, many of these animals have mated and produced calves.

SPA principles and participant demographics

The SPA emerged from a C2S2 leaders meeting with credible representatives from the private sector. An Executive Committee produced guidelines, describing expectations for highest quality animal care, mutual cooperation, and, if interested, becoming involved in research. The SPA’s emphasis on simplicity has incentivized private landowner involvement. A key tenet is that each participant retains ownership and control of their animals, husbandry protocols, and all terms of transactions. The SPA encourages animal exchange to ensure gene diversity retention, but each owner



Figure 4. Addax living in a naturalistic herd structure on a private ranch in Texas (Photograph: Ten Triple X Ranch).

determines the preferred partner(s) for stock acquisition or dispersal. Informed decision-making to protect heterozygosity and species integrity is encouraged. There are three mandates for formal SPA participation: (1) manage animals in suitable enclosures that prevent escape, meet biological needs, encourage natural behaviors, and protect against injury and ill health; (2) complete an annual survey of total numbers of owned animals; and (3) abide by all laws, including those regulating animal welfare, animal transactions, and transportation. Candidates for inclusion in SPA undergo a nomination and rigorous evaluation. All programmatic activities are overseen by an SPA manager. Currently, there are 37 participants, 60% being private sector facilities, 20% C2S2 breeding centers, and 20% public zoos. Collectively, these institutions have >32 000 hectares and maintain more than 1500 animals of the four target species (figure 7).

Simulation modeling to demonstrate value of herd management

Most wild ungulates live in polygamous, multi-generational herds where one male mates with multiple females. Offspring develop with age-matched cousins, a survival adaptation conferring social, behavioral, and reproductive benefits to

the young (Walther 1984; Estes 1991). Compared to zoos, our *sorta situ* herds model offers more opportunities for normal behaviors related to development, courtship, mating, and parturition. Under herd management, adult males typically are rotated from the population every 2 to 3 years to avoid inbreeding. By contrast, AZA managed breeding programs emphasize the use of mean kinship to identify individuals with the fewest relatives in the population (Ballou and Lacy 1995). The concept of increasing contributions from the most genetically under-represented individuals is sound, but complicated by the need to translocate individuals between zoos, often long distances. Resulting pairs can be sexually incompatible and, even when pairing occurs, offspring are never guaranteed. For example, only 50% of female addax exposed to a male in zoos conceive, and calf mortality is 16% to 20% by 1 year (Houston et al. 2017).

We examined the potential demographic and genetic benefits from managing wild ungulates using an SPA herd approach compared to a traditional zoo program. We used the software package Vortex (Lacy and Pollak 2017) to model population dynamics across two alternative scenarios featuring population-specific input parameters (Table 2). We assumed that a population managed under a typical zoo

a) Scimitar-horned oryx
(*Oryx dammah*)



IUCN Red List: 'Extinct in the Wild'

Habitat: Sahelian grasslands, sparse acacia woodlands

Threats: unregulated hunting, civil war, drought, expansion of pastoralism

b) Dama gazelle
(*Nanger dama*)



IUCN Red List: 'Critically Endangered'

Habitat: Sahelian grasslands, sub-desert steppes

Threats: unregulated hunting, civil war, habitat loss, drought, expansion of pastoralism

c) Addax
(*Addax nasomaculatus*)



IUCN Red List: 'Critically Endangered'

Habitat: desert

Threats: unregulated hunting, habitat loss, drought

d) Sable antelope
(*Hippotragus niger*)



IUCN Red List: 'Conservation Dependent/ Least Concern'

Habitat: wooded savannah

Threats: habitat loss and degradation, drought, disease

Figure 5. Four antelope species comprising the Source Population Alliance and associated IUCN status, habitat preference, and species threats (Photographs: Gavin Livingston).

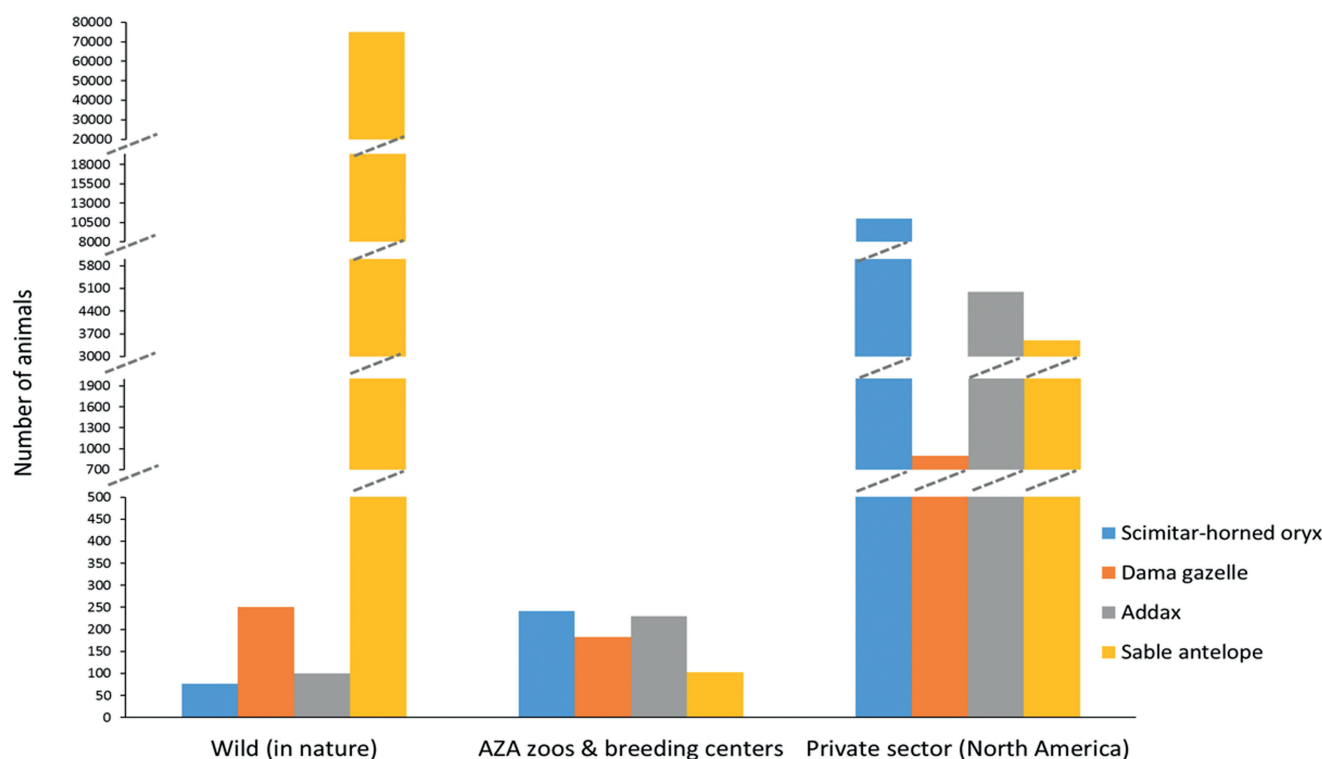


Figure 6. Estimated numbers of the four target antelope species in the wild in Africa (nature), in AZA-accredited zoos and breeding centers, or in the North American private sector. Number estimates are derived from the IUCN/SSC Antelope Specialist Group (2016a, b, c; 2017) or the Exotic Wildlife Association (Mungall 2018a).

approach would have: (a) A smaller, long-term, maximal abundance (i.e., carrying capacity) due to less space. (b) More intensive reproductive management whereby available breeding males and females are chosen for pairing based on mean kinship values to reduce average relatedness among individuals to avoid high inbreeding. (c) Lower rates of reproductive success due to a higher frequency of institutions unable to comply with mating recommendations. (d) Lower calf mortality because of more thorough post-natal care. By contrast, the simulated SPA population would have: (a) A larger long-term carrying capacity due to more space. (b) Breeding management via periodic bull rotations or as guided by genomic assessments. (c) Enhanced reproductive success because animals would be living in a more natural environment that would promote normal herd behaviors. (d) Modest increases in calf mortality due to less intensive oversight post-birth.

We discovered that the simulated urban zoo population grew ~5.5% per year for the first decade of model projections, but this increase quickly faded as the population filled available space (figure 8). After reaching maximal abundance within 25 years, population abundance began to decline because of the (1) negative impact of random variation in reproductive success and survival across years, and (2) gradual accumulation in inbreeding that occurs in persistently small populations. Genetic impacts can occur

even in zoo populations that are properly managed by mean kinship-based metrics (e.g., Santymire et al. 2018). In contrast, the SPA population continued to grow ~6% annually for almost 40 years before slowing (figure 8).

Our analysis also revealed improved gene diversity retention for the SPA compared to the zoo-based program. After 100 years, the larger SPA population retained ~94% of the variation at simulation onset compared to ~88% for the mean-kinship approach (figure 8). Importantly, the zoo population showed a slightly enhanced retention of gene diversity early in the simulation, largely because of more intensive management and selection of under-represented individuals for breeding. After ~35 years, however, the fourfold larger SPA population was losing gene diversity at a slower rate, largely because of less genetic drift (Lacy 2000). Similar models could be structured to examine other SPA scenarios, including: (1) threshold size of component populations required to maintain demographic and genetic viability; (2) the ideal rate and magnitude of demographic connectivity (typically through bull rotation); and (3) levels of tolerable inbreeding before population stability is compromised.

Genomics for understanding ungulate herd genetics

One priority for improving SPA's ability to manage herds is a better understanding of population and individual animal genetics. Levels of heterozygosity, ancestry, and population

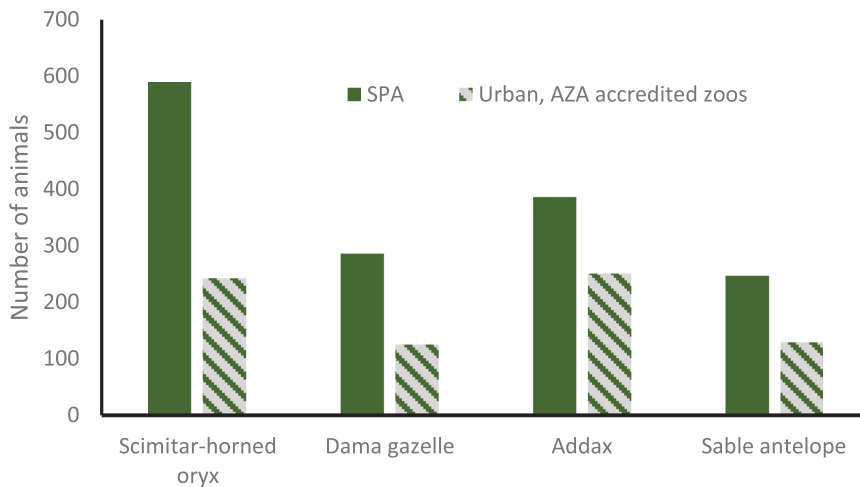


Figure 7. Animal numbers from each of the four African antelope species within the Source Population Alliance (SPA) compared to those living in North American urban zoos.

structure are almost completely unknown in ranch herds due to lack of pedigrees, presence of multiple sires, and inconsistent re-stocking schedules. We predict the genetic status of these less intensively managed populations can be resolved by applying advanced genomic tools.

Estimates of genetic diversity for most endangered species have been limited to a few putatively neutral (i.e., microsatellites) or adaptive (e.g., the major histocompatibility complex) loci (Ouborg et al. 2010). Next-generation sequencing allows determining the quantity and distribution of variation across the genome as well as relatedness and inbreeding (Allendorf et al. 2010; Kardos et al. 2016). Practical applications are increasingly impressive, including for personalized human health care (Snyder 2016) and improved livestock production and food quality (e.g., Hayes et al. 2013). Genomic data may also revolutionize how endangered species are managed under human care. In the case of the SPA, genomic evaluations will be invaluable for herds with unknown pedigrees. In the presence of multiple males and perhaps even mate selection, it is essential to determine paternity to select appropriate new breeding stock to ensure long-term heterozygosity and adaptive potential.

There are two broad categories for characterizing genetic variation across the genome, one being a whole genome approach and the other by reduced representation (Fuentes-Pardo and Ruzzante 2017). The former includes sequencing the whole genome of multiple conspecifics and then comparing results to a reference genome. By contrast, reduced representation allows high-throughput characterization of variation in only a subset of loci that may be restricted to specific genomic components containing protein-coding genes, ultraconserved elements, or on restriction sites. A major advantage of whole genome sequencing is the ability to design a customized, species-specific array to capture single nucleotide polymorphisms (or SNPs) through targeted enrichment (Fuentes-Pardo and Ruzzante 2017).

This array can then be used to collect genotypes across thousands of loci from hundreds of individuals simultaneously using next-generation sequencing methods (Jones and Good 2016).

Genomics utility in the SPA approach

Applying genomics to the SPA model offers opportunities to produce sustainable populations by estimating genetic diversity, inbreeding status, lineage integrity, ancestry, and kinship. Computer simulations and empirical evidence demonstrate that evaluations based on a large sampling of genomic markers provide more precise measures of inbreeding and relatedness than pedigrees (Kardos et al. 2015; Kardos et al. 2018). Genomic assessments offer enormous information

useful for decision-making by wildlife managers. Of particular relevance is the utility of this tool to ranchers who have little knowledge about their animals' genetic health or relatedness within their own herds or to the larger conservation breeding community.

To date, we have generated reference genomes and additional whole genome resources for the sable antelope (Koepfli et al. 2019), dama gazelle, and scimitar-horned oryx. Briefly, this is accomplished by sequencing and assembling a reference genome from a single individual that is then annotated to characterize the gene and repeat DNA content. Genomes of additional individuals are re-sequenced and mapped to the reference to identify millions of SNPs. A subset is then used to design a species-specific SNP array (figure 9).

In a recent extensive study of the sable antelope, we demonstrated the power of genomics for generating high-resolution, conservation-relevant information. A sable antelope-specific in-solution capture array containing 5000 SNPs was used to genotype 40 individuals from two C2S2 breeding centers (Fossil Rim Wildlife Center, Texas and The Wilds, Ohio; $n = 21$ and 9 animals, respectively) and from two other SPA participants, both Texas ranches ($n = 10$ animals). Estimates revealed heterozygosity values of <0.3 to 0.45, indicating that genetic diversity fell within a narrow margin within this mixed source population (figure 9, lower left panel).

Most interesting was the analyses of genetic structure and ancestry. Nine sable antelope from C2S2 member The Wilds formed a distinctive genetic cluster according to principal component analyses (figure 9, lower middle panel) and assessment of genetic ancestry using the program ADMIXTURE (Alexander et al. 2009; figure 9, lower right panel). It was clear that animals in Ohio bunched separately from the Texas cohort. A closer analysis revealed that The Wilds' herd had been isolated for multiple generations, which stimulated acquiring an unrelated sable antelope sire

Table 2. Summary of demographic model input parameters used in simulation models of alternative population management approaches.

Model Input Parameter	Urban-Based Zoo Population	Breeding Center/Ranch (SPA) Population
Initial abundance	50	50
Carrying capacity	100	500
Age of first breeding (years)	2	2
Adult females reproducing annually (%)	50	60
Adult males in the breeding pool (%)	20	20
Annual calf mortality (%)	20	25
Annual adult mortality (%)	8	8
Severity of inbreeding depression ^a	4.5	4.5
Mean initial inbreeding coefficient	0.1	0.1
Genetic management protocol	MK; $F < 0.25^b$	$F < 0.25$
Demographic management protocol ^c	Breeding constrained to maintain population at K^c	Breeding constrained to maintain population at K

^aNumber of lethal equivalents (Ralls et al. 1988).

^bMK, choose breeding pairs to reduce mean kinship (average relatedness) in the population; $F < 0.25$, restrict pair selection to an inbreeding coefficient (F) among offspring of <0.25 (as occurs with full-sibling or parent-offspring pairings).

^c K , population carrying capacity.

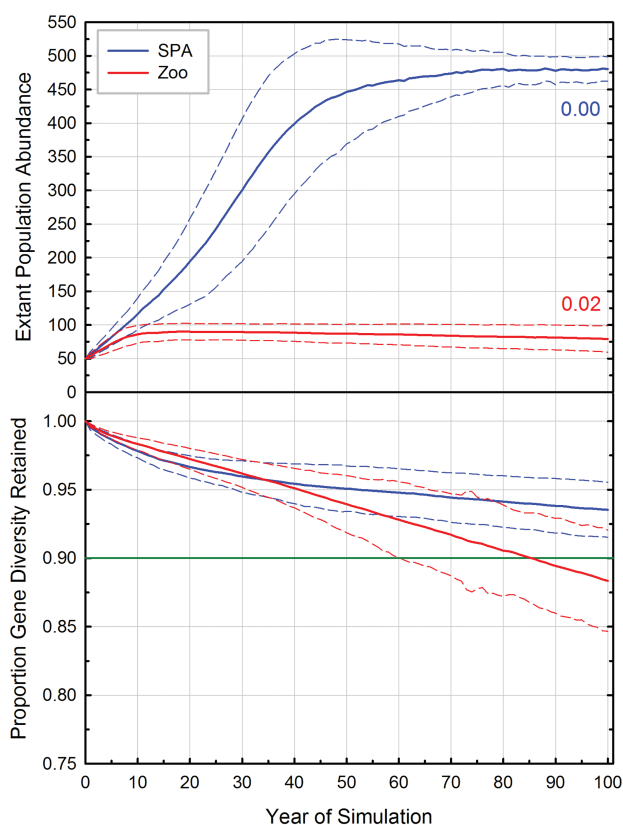


Figure 8. Simulation modeling results depicting future dynamics of a typical wild ungulate population managed according to a traditional urban zoo (mean kinship) versus the Source Population Alliance (SPA herd) approach. Top panel: Mean population abundance trajectories (± 1 standard deviation [SD]) with extinction probabilities over 100 years for the two alternatives. Bottom panel: Proportional gene diversity retained (± 1 SD) for each alternative. Green horizontal line represents gene diversity retention typically targeted in conservation breeding programs for endangered species (e.g., Lees and Wilcken 2009).

from the Fossil Rim Wildlife Center to infuse new genetic diversity.

None of the sable antelope in AZA-accredited urban zoos has been genetically analyzed, and only 27% of the pedigree is known (Piltz et al. 2016). These obscurities can be eliminated via genomic assessment with a high likelihood of identifying valuable and under-represented individuals in both the public and private sectors. Such discoveries can be integrated into modeling (as demonstrated above using Vortex) to better inform breeding male selection and animal exchanges in all directions (figure 10).

Conclusions and perspectives for the future

C2S2 and its SPA program connects breeding centers, the private sector, and zoos to fill a gap not addressed by the purely *in situ* or *ex situ* communities. Although the preference always is to maintain wild species in wild places, accelerated human population growth, habitat loss, and climate change require more options. The intensive management practiced in urban zoos for large-sized species cannot meet well-established demographic and genetic goals. Although the infrastructure and expertise in breeding centers and zoos are important, that capacity also is inadequate when thousands of animals of many species are required to achieve sustainability. That is the reason for adding credible private landowners to the mix, a novel way that brings diversity, resources, and new approaches for the greater good of species conservation.

There now are several areas for priority attention. Our simple, yet realistic modeling exercise demonstrated clear demographic and genetic advantages of the SPA herd approach over a traditional zoo breeding program. There also are likely to be financial benefits due to operational scale and the use of cheaper, rural land that includes spacious pastures requiring less supplemental feeding and a smaller labor-force. As more data are collected, such factors can be incorporated into more complex models to identify

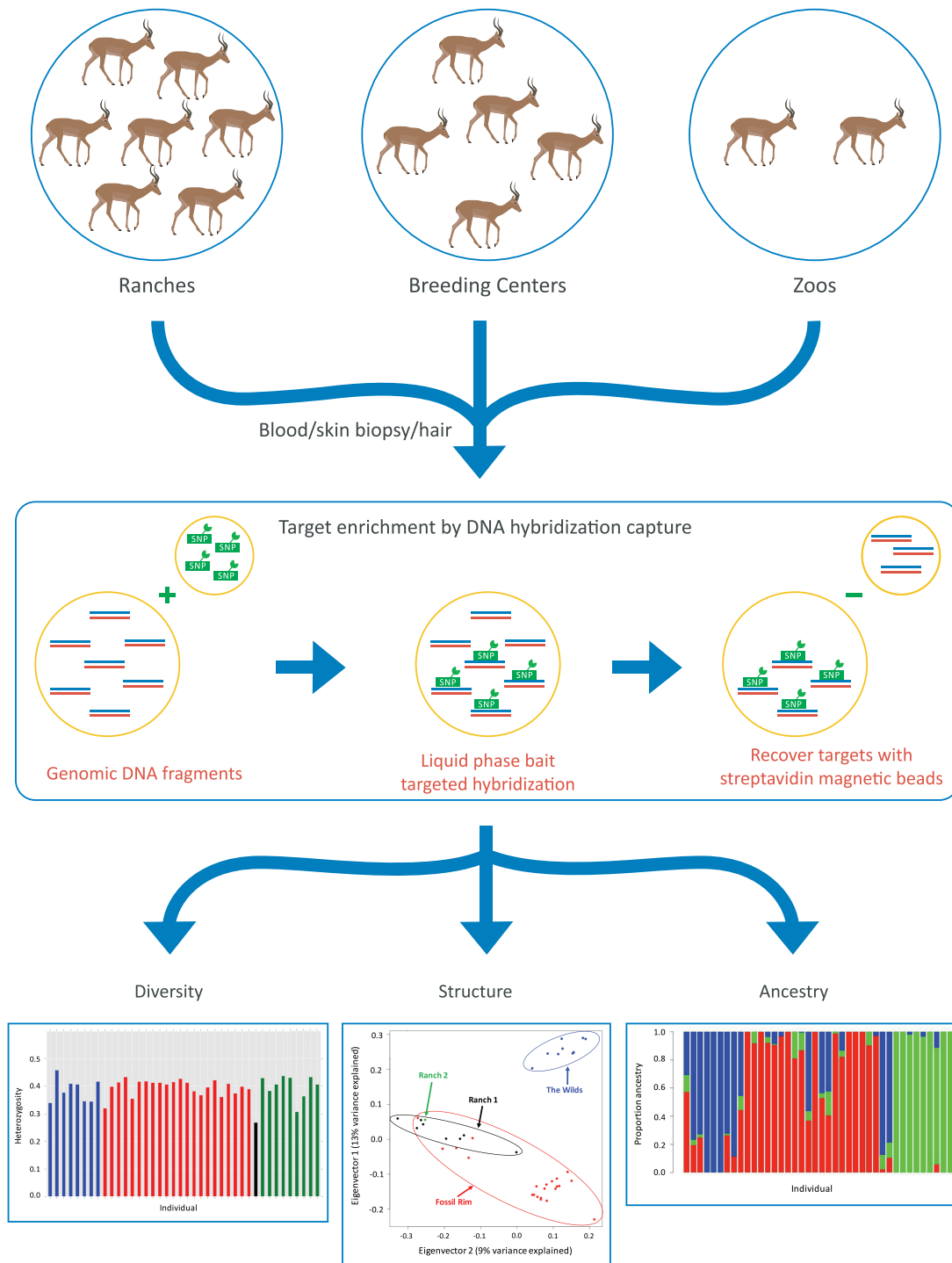
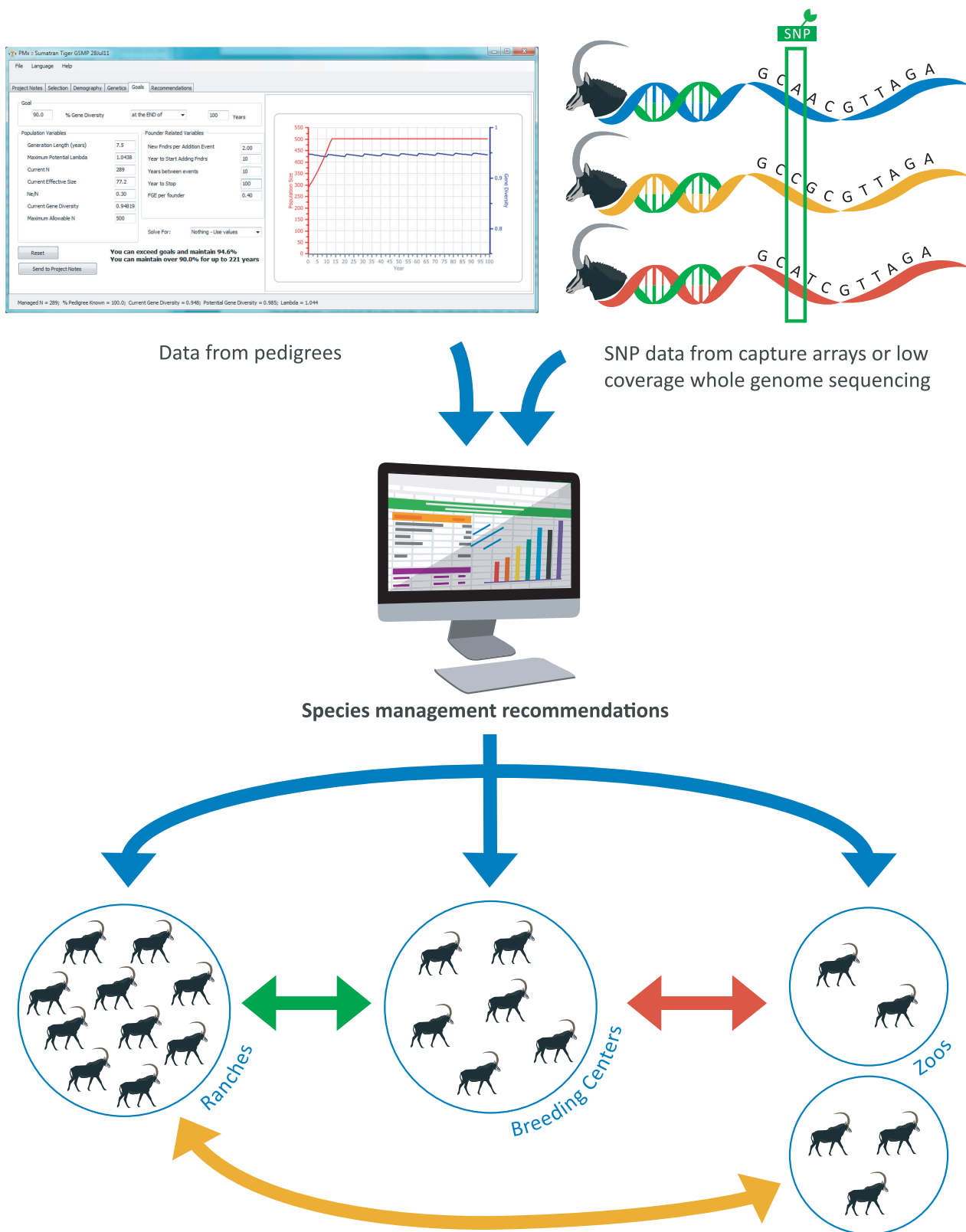


Figure 9. Illustrations of value of genomic data for identifying differences or similarities among wild ungulates in genetic diversity, population structure, or admixture/ancestry to make more informed management decisions. Top: Blood, skin biopsy, and/or hairs are collected from animals managed on ranches, breeding centers, or zoos from which genomic DNA is isolated. Middle: The DNA of each individual is fragmented and prepared into a genomic library to which in-solution biotinylated probes complementary to specific single nucleotide polymorphisms (SNPs) are bound to allow target enrichment of these parts of the genome. Bound fragments are recovered with magnetic beads, and the enrichment is prepared for next-generation sequencing. This process can be applied to 100 or more individuals simultaneously. Bottom: Sampled individuals are genotyped at thousands of SNPs from across the genome. Resulting data can be used to estimate individual or population-level heterozygosity (left panel), genetic structure (middle panel), and genetic ancestry (right). Each point or bar represents a single sable antelope genotyped at 5000 SNPs.



Data from pedigrees

SNP data from capture arrays or low coverage whole genome sequencing

Species management recommendations

Ranches

Breeding Centers

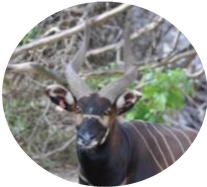
Zoos

Figure 10. Conventional information gleaned from Vortex modeling will be enhanced by supplementing with genomic data to further guide species management across the metapopulation, especially animal translocations in all directions to achieve demographic and genetic security. Arrows at the bottom of the figure represent recommended animal translocations among ranches, breeding centers, and zoos based on empirically derived results from combined demographic modeling and genomic data.

Antelope



Arabian oryx (*Oryx leucoryx*)
Endangered



Bongo (*Tragelaphus eurycerus*)
Critically Endangered



Roan antelope (*Hippotragus equinus*)
Least Concern

Asian cattle



Anoa (*Bubalus depressicornis*)
Endangered



Banteng (*Bos javanicus*)
Endangered

Equid



Grevy's zebra (*Equus grevyi*)
Endangered

Caprids



Nubian ibex (*Capra nubiana*)
Vulnerable



Transcaspien ural (*Ovis orientalis*)
Vulnerable

Rhinoceros



Southern black rhinoceros (*Diceros bicornis minor*)
Critically Endangered

Figure 11. Species (or subspecies) recently added to the Source Population Alliance for public-private sector conservation breeding (Photographs: Gavin Livingston).

other potential advantages and improvements to herd management. There also is a need for definitive evidence that calves developing in herds in naturalistic, expansive areas express social behaviors comparable to their wild counterparts. This is essential for individuals and populations to thrive, not only in a *sorta situ* environment, but also for successful reintroductions. Indeed, it would be challenging to prepare large-sized animals to withstand the rigors of wild habitats when raised with only a few conspecifics in an urban zoo. Furthermore, these long-held captive populations generally are not exposed to predation, forage limitations, interspecific competitions, and other elements that no doubt influence adaptability to surviving in nature. We would argue, however, that specimens managed under *sorta situ* conditions may be more adaptive to change than zoo counterparts. There already is early evidence in that

scimitar-horned oryx produced in extensive, semi-wild conditions with little or no supplemental feeding and watering appear to perform better when returned to nature compared to those reared under more confined conditions (Catherine Mertes, personal communication). Therefore, we expect that the SPA model can influence not only efficiency of production and genetic health, but also retaining behavioral integrity, all translating into more robust, adaptable animals. These risks can be mitigated through the use of genomic data to ensure that diverse genetic lineages have equal representation in captive populations and to monitor reintroduced populations to assess how founders are contributing to overall genetic diversity across successive generations.

Finally, there is a need to determine if DNA analytical costs can be sufficiently low to ensure widespread utilization

by the wildlife managers. Genomic assessments are likely to become more economical based on experiences from human and livestock applications. However, there are far fewer wild animal specimens to assess, even from combined *ex situ*, *sorta situ*, and *in situ* populations. Therefore, it may be necessary to expect a higher evaluative cost for this service, which is essential given that maintaining gene diversity and minimizing deleterious variation are core principles of species conservation. Regardless, as biosamples have been solicited for this project, we have experienced enthusiasm from private and public sector owners, all of whom realize that a confirmed pedigree increases the conservation (and financial) value of these resources. C2S2 is considering developing a DNA service that includes guidance on practical use of data for SPA participants.

The SPA recently has expanded its portfolio to include more ungulates from the IUCN Red List, including more antelopes, an equid, and two caprids (figure 11). C2S2 also has combined forces with the International Rhino Foundation (IRF) to develop a security population of the southern black rhinoceros (*Diceros bicornis minor*), no longer in an AZA managed program due to lack of space. The struggle to keep rhinos secure within their range in South Africa (Harper et al. 2018) is incentive for establishing insurance populations in other countries where climate, terrain, and natural browse are available. C2S2 and IRF are cooperating with breeding centers, private ranchers, and zoos keen to acquire and establish breeding pairs where this black rhino subspecies is most likely to thrive, especially Texas, Florida, and New South Wales, Australia.

There is no one solution for ensuring species persistence. Rather, preventing extinction must be viewed across a continuum, ranging from protecting large landscapes with a wealth of biodiversity to zoos exhibiting amazing species to inspire awareness and financial contributions for conservation. We as authors leave to others how to protect enough intact ecosystems to sustain viable populations *in situ*, especially given the >10 billion humans expected on the planet by century's end. This alone mandates the investment of more people in these initiatives beyond traditional, professional conservationists. Zoos formulated a terrific idea in the 1980s—organized conservation breeding programs for endangered species. The concept is sound, but the resources for achieving the sustainability goal for large species is wanting. This is where C2S2 and SPA lie on the conservation spectrum—to recruit, coordinate, and implement significant new resources and opportunities. Of course, the charitable environmental organization, The Nature Conservancy (www.nature.org) has long recognized the value of private landowners for promoting local biodiversity. In a way, the SPA program of C2S2 is thinking similarly, but through linking private landholders to conservationists and scientists to ensure survival of the world's rarest wild ungulates. Lastly, we are confident that this concept can be scaled to other taxa, including carnivores and birds, especially those

requiring significant space and expertise to produce sustainable populations.

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