

Breeding centers, private ranches, and genomics for creating sustainable wildlife populations

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Breeding centers, private ranches, and genomics for creating sustainable wildlife populations

David Wildt, Philip Miller, Klaus-Peter Koepfli, Budhan Pukazhenth, Katy Palfrey, Gavin Livingston, Dan Beetem, Stephen Shurter, Jimmy Gregory, Michael Takács, and Kelley Snodgrass

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Draft Manuscript

Abstract

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 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

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3 46 *Like the resource it seeks to protect, wildlife conservation must be dynamic, changing as*
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6 47 *conditions change, seeking always to become more effective.*
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8 48 *Rachel Carson*
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11 49
12
13 50 The International Union for Conservation of Nature (IUCN) indicates that ~25% of vertebrate
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15 51 species are at risk of extinction ([http://www.iucnredlist.org/about/summary-](http://www.iucnredlist.org/about/summary-statistics#How_many_threatened)
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17 [statistics#How_many_threatened](http://www.iucnredlist.org/about/summary-statistics#How_many_threatened)) from human overpopulation, habitat loss, exploitation,
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20 53 pollution, disease, alien species, and climate change. Among the most concerning threats are
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23 54 global greenhouse emissions predicted to cause the eventual disappearance of at least 50% of
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25 55 animal species in certain locales ([www.worldwildlife.org/publications/wildlife-in-a-warming-](http://www.worldwildlife.org/publications/wildlife-in-a-warming-world-the-effects-of-climate-change-on-biodiversity)
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27 [world-the-effects-of-climate-change-on-biodiversity](http://www.worldwildlife.org/publications/wildlife-in-a-warming-world-the-effects-of-climate-change-on-biodiversity)). Although all species are susceptible to
28 56
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30 57 environmental disruptions, larger animals requiring more space and complex ecosystems are
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33 58 most vulnerable. Ripple et al. (2015) have reported the collapse of the world's 74 wild
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35 59 herbivore species ≥ 100 kg comprising 11 families (Elephantidae, Rhinocerotidae,
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38 60 Hippopotamidae, Giraffae, Bovidae, Camelidae, Tapiridae, Equidae, Cervidae, Suidae, and
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40 61 Hominidae). Approximately 60% of these species are threatened due to killing for bush
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42 62 meat/body parts, land-use change, and resource competition by livestock. The result is
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45 63 demographically impoverished populations, lost gene diversity, fewer large carnivores and
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47 64 scavengers, and altered ecosystem services (Ripple et al. 2015).
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50 65 Historically, preserving biodiversity has focused on saving habitat and, by default,
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52 66 protecting all species living in that native environment (*in situ*). Although always the priority,
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55 67 this goal is outpaced by reality. Few wilderness areas are unaffected by human influence
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(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 also is concern about enough safeguarded wild space to assure viability. One analysis of ~4,000 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 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 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).

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***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

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3 112 adaptability to continued environmental change. Because N_e is usually only a small proportion
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6 113 of the total census population size, a genetically viable *ex situ* population may require
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8 114 thousands of individuals (Ballou and Traylor-Holzer 2011). Although these specific
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11 115 recommended abundances remain open to scrutiny (Jamieson and Allendorf 2012), it is
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13 116 important to recognize that large *ex situ* populations of endangered species are necessary to
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16 117 ensure long-term viability.

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18 118 There have been significant lessons learned from zoo breeding programs, especially new
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21 119 information on natural history, animal husbandry, welfare, record keeping, and mating
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23 120 recommendations (Lacy 2013). There are a few species, such as the African penguins
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25 121 (*Spheniscus* spp.), giraffe (*Giraffa* spp.), and Western lowland gorilla (*Gorilla gorilla*) where
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28 122 demographic and genetic stability are being maintained (Lacy 2013). But despite good
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30 123 intentions, accredited zoos hold only ~15% of the world's threatened terrestrial vertebrates and
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33 124 in small-sized populations (Conde et al. 2013). The Association of Zoos and Aquariums (AZA),
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35 125 which accredits North American zoos, reports that only 44 of 622 managed species programs
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38 126 are self-sustaining (<https://www.aza.org/animal-program-sustainability-designations>). Of 428
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40 127 species with studbooks, the median population is only 66 individuals (Long et al. 2011).
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42 128 Approximately 39% of all mammal, bird, reptile, and amphibian zoo populations are comprised
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45 129 of **50 or fewer** individuals, and only 25% of these are successful breeders. Results from the
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47 130 European zoo community are similar. Of 31 carnivore, 37 primate, 12 ungulate, and seven
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50 131 rodent species, 48% of populations have bred to replacement, and only 55% are retaining gene
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52 132 diversity at or above the 90% retention value (Lees and Wilcken 2009).
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3 133 Zoos are challenged in providing safe havens for more species in larger numbers due to
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6 134 insufficient resources (Monfort and Christen 2018; Powell 2018). Most significant is a lack of
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8 135 space. Zoos are complex, expensive operations, often existing on prime real estate in bustling
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11 136 cities. A dominant mission is attracting the public to share stories on hundreds of species. There
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13 137 is growing concern to promote welfare, which has led to elaborate exhibits that accommodate
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16 138 fewer animals, which may be one cause for the 45% size decline in zoo mammal populations
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18 139 (Long et al. 2011). We assessed AZA data available to members and ascertained that the 158
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21 140 accredited urban institutions averaged only 27.3 hectares each. This translates into a modest
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23 141 4,306 total ‘zoo hectares’ in all of North America to meet the needs of thousands of wildlife
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25 142 species for breeding, exhibition, education, merchandizing, and other zoo-related functions.
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28 143 Therefore, sustaining rare species in secure populations – to prevent extinction, generate new
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30 144 knowledge, and as a source for reintroductions – requires many times more animals than can
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33 145 be produced by typical zoo programs (Conway 2010; Lacy 2013). William Conway, pioneer in
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35 146 conservation breeding, noted 40 years ago that, because city zoos are “land poor”, “rural
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38 147 breeding farms and ranches will be needed” (Conway 1980).
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42 149 **Species conservation using land resources of breeding centers and private citizens**
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45 150 **The Conservation Centers for Species Survival.** As a complementary tactic, we created the
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47 151 Conservation Centers for Species Survival (C2S2; www.conservationcenters.org), a consortium
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50 152 of the world’s top endangered species facilities. This non-profit entity is dedicated to
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52 153 cooperatively applying its collective space to conserve species that require large areas, natural
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55 154 group sizes, minimal public disturbance, and scientific research. The full and affiliate C2S2
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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 a '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

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3 177 sustainability goals, and 42% are in decline (AZA, 2009; [https://www.aza.org/animal-program-](https://www.aza.org/animal-program-sustainability-designations)
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6 178 [sustainability-designations](https://www.aza.org/animal-program-sustainability-designations)).

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8 179 The third reason for C2S2's interest in ungulates is member capacity in breeding and
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11 180 studying these species for decades. The Smithsonian Conservation Biology Institute (SCBI;
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13 181 Virginia) is comprised of barns constructed in the early 1900s to produce horses and mules for
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16 182 the U.S. military. Now modernized, these facilities are used for conservation breeding of
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18 183 scimitar-horned oryx (*Oryx dammah*) and dama gazelle (*Nanger dama ruficollis*). The Fossil Rim
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21 184 Wildlife Center (Texas), with landscapes and climate similar to African savannahs, has produced
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23 185 prodigious numbers of scimitar-horned oryx as well as addax (*Addax nasomaculatus*) and sable
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25 186 antelope (*Hippotragus niger*). The Wilds (Ohio), set on vast reclaimed mining lands, reproduces
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28 187 these antelopes as well as southern white rhinoceroses (*Ceratotherium simum simum*), the
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30 188 latter through four successive generations. White Oak Conservation (Florida) has a similar
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33 189 success with antelopes, rhinoceroses, giraffe as well as the okapi (*Okapia johnstoni*). Among the
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35 190 successes for African Lion Safari (Ontario, Canada) is the Asian elephant (*Elephas maximus*),
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38 191 including a multi-generational herd with semi-free-ranging opportunities. Austin Savanna
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40 192 (Texas) manages its wildlife in combination with its waste management and recycling business,
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42 193 an innovative way of linking conservation and industry. These institutions also facilitate
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45 194 research by having (1) chutes and restraint devices for safe animal handling and sample
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47 195 collection (Figure 3) and (2) significant animal numbers to permit robust research, ranging from
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50 196 understanding a species' natural history (Koester et al. 2015) to facilitating recovery through
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52 197 assisted breeding (Schook et al. 2013).
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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 significant non-native wildlife populations (Figure 4). Texas alone has more than 5,000 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 2,000 to 4,000 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.

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3 222 We define a source population as a dependable reservoir for *ex situ* or *in situ* conservation and
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6 223 utilization. This means for insurance, research, awareness, exhibition, raising funds for
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8 224 conservation, trade, and reintroductions into the wild. Although most SPA participants are
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11 225 ranches or C2S2 breeding centers, zoos are encouraged to join. Our goals are to (1) recruit
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13 226 qualified alliance participants to establish demographically sound metapopulations, (2) model
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16 227 the predicted impact of herd type (smaller versus larger) and number of herds to achieve ideal
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18 228 population growth, and (3) demonstrate how advances in genomics can be used practically for
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24 231 **Species targets**

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26 232 We identified the scimitar-horned oryx, dama gazelle, addax, and sable antelope for initial
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29 233 study, all having high conservation value (Figure 5). Named for its long, backward sweeping,
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31 234 blade-like horns, the scimitar-horned oryx (Figure 5a) is the largest mammal to disappear from
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34 235 the wild in the last 35 years. The tall, elegant dama gazelle (Figure 5b) once inhabited 13 North
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36 236 African countries (Jebali 2018), but now is restricted to three tiny fragments of <300 individuals
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39 237 in Niger and Chad (Mungall 2018a). Likewise, perhaps only 300 addax (Figure 5c) remain in
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41 238 vestige pockets, mostly within Niger (Wacher et al. 2008). Each of these desert species has been
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44 239 hunted relentlessly, and relict populations have been pushed into marginal habitat with scarce
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46 240 grasses and shade critical to survival. Our fourth species is the sable antelope (Figure 5d),
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49 241 endemic to southern Africa. Although designated by IUCN as ‘Least Concern’, the sable
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51 242 antelope is adversely impacted by human population growth that has increased poaching and
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53 243 caused significant grassland and savannah losses (e.g., Butynski et al. 2015).
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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). Stunningly, there are >5,000 scimitar-horned oryx and >2,800 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 (Mertes et al. in press). Initiated in 2016, including with a few animals from Texas ranches, more than 150 oryx have been released, with breeding and calves produced.

SPA principles and participant demographics

The SPA emerged from 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 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,

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3 267 and protect against injury and ill health; 2) complete an annual survey of total numbers of
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6 268 owned animals; and 3) abide by all laws, including those regulating animal welfare, animal
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8 269 transactions, and transportation. Candidates for inclusion in SPA undergo a nomination and
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11 270 rigorous evaluation. All programmatic activities are overseen by an SPA Manager. Currently,
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13 271 there are 37 participants, 60% being private sector facilities, 20% C2S2 breeding centers, and
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16 272 20% public zoos. Collectively, these institutions have >32,000 hectares and maintain more than
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18 273 1,500 animals of the four target species (Figure 7).
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22 275 **Simulation modeling to demonstrate value of herd management**
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24 276 Most wild ungulates live in polygamous, multi-generational herds where one male mates with
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27 277 multiple females. Offspring develop with age-matched cousins, a survival adaptation conferring
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29 278 social, behavioral, and reproductive benefits to the young (Walther 1984; Estes 1991).
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31 279 Compared to zoos, our *sorta situ* herds model offers more opportunities for normal behaviors
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34 280 related to development, courtship, mating, and parturition. Under herd management, adult
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36 281 males typically are rotated from the population every 2 to 3 years to avoid inbreeding. By
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39 282 contrast, AZA managed breeding programs emphasize the use of mean kinship to identify
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41 283 individuals with the fewest relatives in the population (Ballou and Lacy 1995). The concept of
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44 284 increasing contributions from the most genetically under-represented individuals is sound, but
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46 285 complicated by the need to translocate individuals between zoos, often long distances.
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49 286 Resulting pairs can be sexually incompatible and, even when pairing occurs, offspring are never
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51 287 guaranteed. For example, only 50% of female addax exposed to a male in zoos conceive, and
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53 288 calf mortality is 16 to 20% by 1 year (Houston et al. 2017).
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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 approach would have:

- A smaller, long-term, maximal abundance (i.e., carrying capacity) due to less space;
- 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;
- Lower rates of reproductive success due to a higher frequency of institutions unable to comply with mating recommendations; and
- Lower calf mortality because of more thorough post-natal care.

By contrast, the simulated SPA population would have:

- A larger long-term carrying capacity due to more space;
- Breeding management via periodic bull rotations or as guided by genomic assessments;
- Enhanced reproductive success because animals would be living in a more natural environment that would promote normal herd behaviors;
- 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

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3 311 abundance began to decline because of the (1) negative impact of random variation in
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6 312 reproductive success and survival across years and (2) gradual accumulation in inbreeding that
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8 313 occurs in persistently small populations. Genetic impacts can occur even in zoo populations that
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11 314 are properly managed by mean kinship-based metrics (e.g., Santymire et al. 2018). In contrast,
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13 315 the SPA population continued to grow ~6% annually for almost 40 years before slowing (Figure
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18 317 Our analysis also revealed improved gene diversity retention for the SPA compared to
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20 318 the zoo-based program. After 100 years, the larger SPA population retained ~94% of the
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23 319 variation at simulation onset compared to ~88% for the mean-kinship approach (Figure 8).
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25 320 Importantly, the zoo population showed a slightly enhanced retention of gene diversity early in
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28 321 the simulation, largely because of more intensive management and selection of under-
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30 322 represented individuals for breeding. After ~35 years, however, the four-fold larger SPA
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33 323 population was losing gene diversity at a slower rate, largely because of less genetic drift (Lacy
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35 324 2000). Similar models could be structured to examine other SPA scenarios, including: 1)
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38 325 threshold size of component populations required to maintain demographic and genetic
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40 326 viability; 2) the ideal rate and magnitude of demographic connectivity (typically through bull
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42 327 rotation); and 3) levels of tolerable inbreeding before population stability is compromised.
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47 329 **Genomics for understanding ungulate herd genetics**

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50 330 One priority for improving SPA's ability to manage herds is better understanding population
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52 331 and individual animal genetics. Levels of heterozygosity, ancestry, and population structure are
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55 332 almost completely unknown in ranch herds due to lack of pedigrees, presence of multiple sires,
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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 also may 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 through targeted enrichment to capture single nucleotide polymorphisms, or SNPs (Fuentes-Pardo and Ruzzante

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3 355 2017). This array can then be used to collect genotypes across thousands of loci from hundreds
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6 356 of individuals simultaneously using next generation sequencing methods (Jones and Good
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8 357 2016).

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13 359 **Genomics utility in the SPA approach.** Applying genomics to the SPA model offers
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16 360 opportunities to produce sustainable populations by estimating genetic diversity, inbreeding
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18 361 status, lineage integrity, ancestry, and kinship. Computer simulations and empirical evidence
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20 362 demonstrate that evaluations based on a large sampling of genomic markers provide more
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23 363 precise measures of inbreeding and relatedness than pedigrees (Kardos et al. 2015; Kardos et
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25 364 al. 2018). Genomic assessments offer enormous information useful for decision-making by
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28 365 wildlife managers. Of particular relevance is the utility of this tool to ranchers who have little
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30 366 knowledge about their animals' genetic health or relatedness within their own herds or to the
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33 367 larger conservation breeding community.

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35 368 To date, we have generated reference genomes and additional whole genome resources
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38 369 for the sable antelope (Koepfli et al. 2019), dama gazelle, and scimitar-horned oryx. Briefly, this
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40 370 is accomplished by sequencing and assembling a reference genome from a single individual that
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42 371 is then annotated to characterize the gene and repeat DNA content. Genomes of additional
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45 372 individuals are re-sequenced and mapped to the reference to identify millions of SNPs. A subset
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47 373 then is used to design a species-specific SNP array (Figure 9).

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50 374 In a recent extensive study of the sable antelope, we demonstrated the power of
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52 375 genomics for generating high resolution, conservation relevant information. A sable antelope-
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55 376 specific in-solution capture array containing 5,000 SNPs was used to genotype 40 individuals
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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 9b) and assessment of genetic ancestry using the program ADMIXTURE (Alexander et al. 2009; Figure 9c). 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 from the Fossil Rim Wildlife Center to infuse new genetic diversity.

None of the 103 sable antelope in AZA-accredited 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

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3 399 maintain wild species in wild places, accelerated human population growth, habitat loss, and
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6 400 climate change require more options. The intensive management practiced in urban zoos for
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8 401 large sized species cannot meet well-established demographic and genetic goals. Although the
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11 402 infrastructure and expertise in breeding centers and zoos are important, that capacity also is
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13 403 inadequate when thousands of animals of a many species are required to achieve sustainability.
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16 404 That is the reason for adding credible private landowners to the mix, a novel way that brings
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18 405 diversity, resources, and new approaches for the greater good of species conservation.

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20 406 There now are several areas for priority attention. Our simple, yet realistic modeling
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23 407 exercise demonstrated clear demographic and genetic advantages of the SPA herd approach
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25 408 over a traditional zoo breeding program. There also may be financial benefits due to
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28 409 operational scale and the use of cheaper, rural land that includes spacious pastures requiring
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30 410 less supplemental feeding and a smaller labor-force. As more data are collected, such factors
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33 411 can be incorporated into more complex models to identify other potential advantages and
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35 412 improvements to herd management. There also is a need for definitive evidence that calves
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38 413 developing in herds in naturalistic, expansive areas express social behaviors comparable to their
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40 414 wild counterparts. This is essential for individuals and populations to thrive, not only in a *sorta*
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42 415 *situ* environment, but also for successful reintroductions. Indeed, it would be challenging to
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45 416 prepare large-sized animals to withstand the rigors of wild habitats when raised with only a few
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47 417 conspecifics in an urban zoo. Furthermore, these long-held captive populations generally are
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50 418 not exposed to predation, forage limitations, interspecific competitions and other elements
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52 419 that no doubt influence adaptability to surviving in nature. We would argue, however, that
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55 420 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 (Mertes et al. in press). 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 is a core principle of species conservation. Regardless, as biosamples have been solicited for this project, we have experienced enthusiasm from private or public sector owners, all of whom realize that a confirmed pedigree increases 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

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3 443 combined forces with the International Rhino Foundation (IRF) to develop a security population
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6 444 of the southern black rhinoceros (*Diceros bicornis minor*), no longer in an AZA accredited zoo
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8 445 program due to lack of space. The struggle to keep rhinos secure within their range in South
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11 446 Africa (Harper et al. 2018) is incentive for establishing insurance populations in other countries
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13 447 where climate, terrain, and natural browse are available. C2S2 and IRF are cooperating with
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16 448 breeding centers, private ranchers, and zoos keen to acquire and establish breeding pairs
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18 449 where this black rhino subspecies is most likely to thrive, especially Texas, Florida, and New
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21 450 South Wales, Australia.

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23 451 There is no one solution for ensuring species persistence. Rather, preventing extinction
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25 452 must be viewed across a continuum, ranging from protecting large landscapes with a wealth of
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28 453 biodiversity to zoos exhibiting amazing species to inspire awareness and financial contributions
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30 454 for conservation. We as authors leave to others how to protect enough intact ecosystems to
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33 455 sustain viable populations *in situ*, especially given the >10 billion humans expected on the
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35 456 planet by century's end. This alone mandates the investment of more people in these initiatives
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38 457 beyond traditional, professional conservationists. Zoos formulated a terrific idea in the 1980s –
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40 458 organized conservation breeding programs for endangered species. The concept is sound, but
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42 459 the resources for achieving the sustainability goal for large species is wanting. This is where
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45 460 C2S2 and SPA lie on the conservation spectrum – to recruit, coordinate, and implement
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47 461 significant new resources and opportunities. The Nature Conservancy, for example, has long
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50 462 forged alliances with landowners, largely to promote local biodiversity. The SPA program of
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52 463 C2S2 is pursuing the linkage of private landholders with like-minded conservationists and
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55 464 innovative scientific tools to ensure survival of some 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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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 |

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 | 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 ^b | MK; $F < 0.25$ | $F < 0.25$ |
| Demographic management protocol ^c | Breeding constrained to maintain population at K^c | Breeding constrained to maintain population at K^c |

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

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^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 less than 0.25 (as occurs with full-sibling or parent-offspring pairings).

^cK, population carrying capacity.

Figure legends

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

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

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

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

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

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.

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

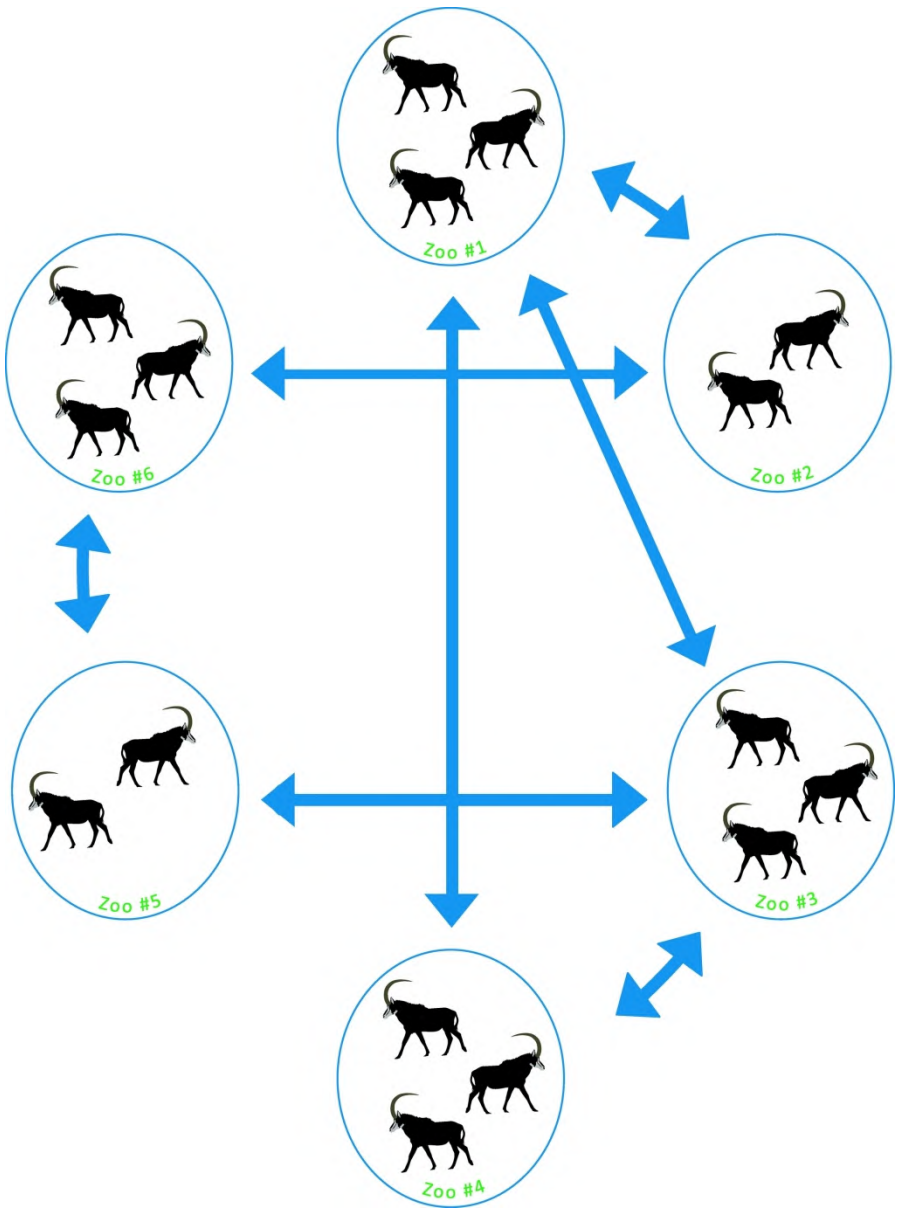
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3 689 Population Alliance (SPA herd) approach. Top panel: Mean population abundance trajectories
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6 690 (± 1 standard deviation [SD]) with extinction probabilities over 100 years for the two
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8 691 alternatives. Bottom panel: Proportional gene diversity retained (± 1 SD) for each alternative.
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11 692 Green horizontal line represents gene diversity retention typically targeted in conservation
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13 693 breeding programs for endangered species (e.g., Lees and Wilcken 2009).
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17 694 **Figure 9.** Illustrations of value of genomic data for identifying differences or similarities among
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19 695 wild ungulates in genetic diversity, population structure, or admixture/ancestry to make more
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21 696 informed management decisions. Top: Blood, skin biopsy, and/or hairs are collected from
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24 697 animals managed on ranches, breeding centers, or zoos from which genomic DNA is isolated.
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26 698 Middle: The DNA of each individual is fragmented and prepared into a genomic library to which
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29 699 in-solution biotinylated probes complementary to specific single nucleotide polymorphisms
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31 700 (SNPs) are bound to allow target enrichment of these parts of the genome. Bound fragments
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34 701 are recovered with magnetic beads, and the enrichment is prepared for next generation
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36 702 sequencing. This process can be applied to 100 or more individuals simultaneously. Bottom:
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39 703 Sampled individuals are genotyped at thousands of SNPs from across the genome. Resulting
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41 704 data can be used to estimate individual or population-level heterozygosity (left panel), genetic
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43 705 structure (middle panel), and genetic ancestry (right). Each point or bar represents a single
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46 706 sable antelope genotyped at 5,000 SNPs.
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49 707 **Figure 10.** Conventional information gleaned from Vortex modeling will be enhanced by
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52 708 supplementing with genomic data to further guide species management across the
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54 709 metapopulation, especially animal translocations in all directions to achieve demographic and
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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.

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



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347x231mm (72 x 72 DPI)





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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

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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

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Addax
(*Addax nasomaculatus*)



IUCN Red List: ‘critically endangered’

Habitat: desert

Threats: unregulated hunting, habitat loss, drought

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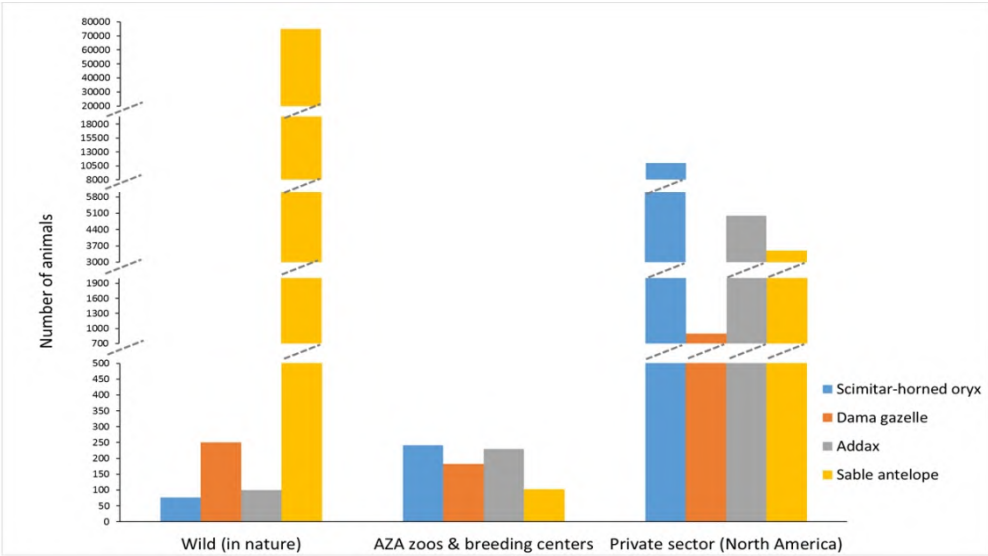
Sable antelope
(*Hippotragus niger*)



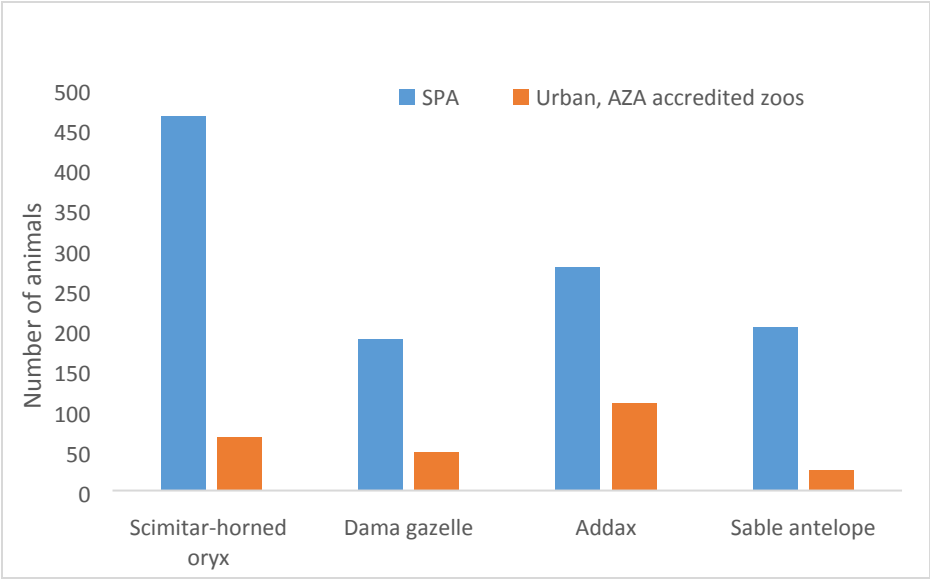
IUCN Red List: ‘conservation dependent/ least concern’

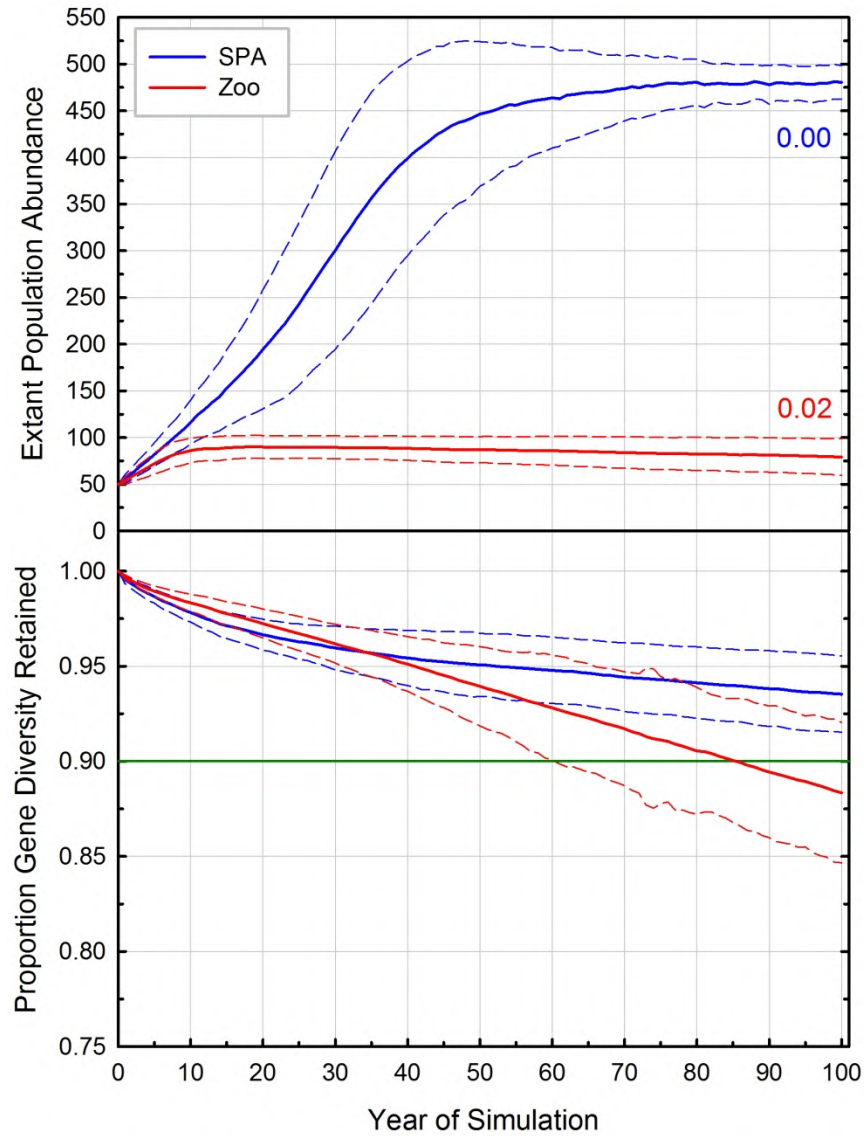
Habitat: wooded savannah

Threats: habitat loss and degradation, drought, disease



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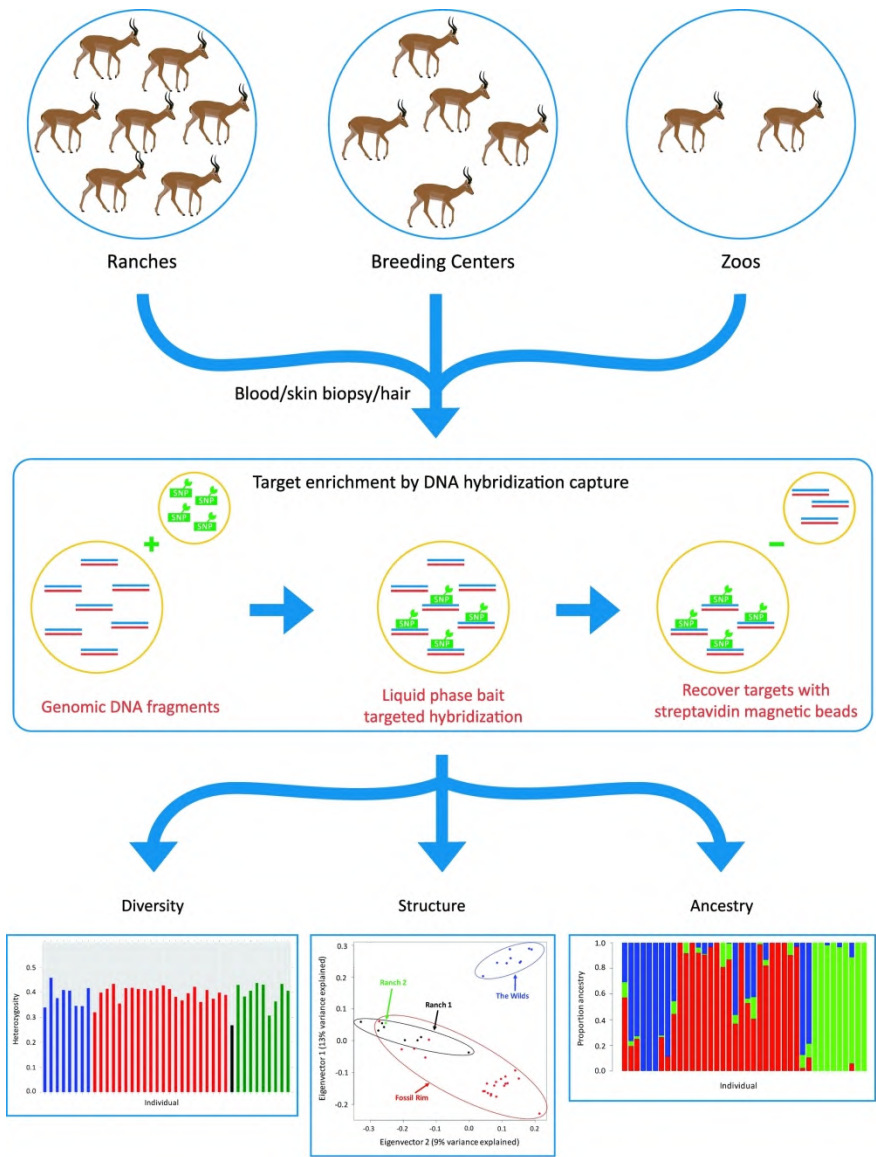


Figure 9

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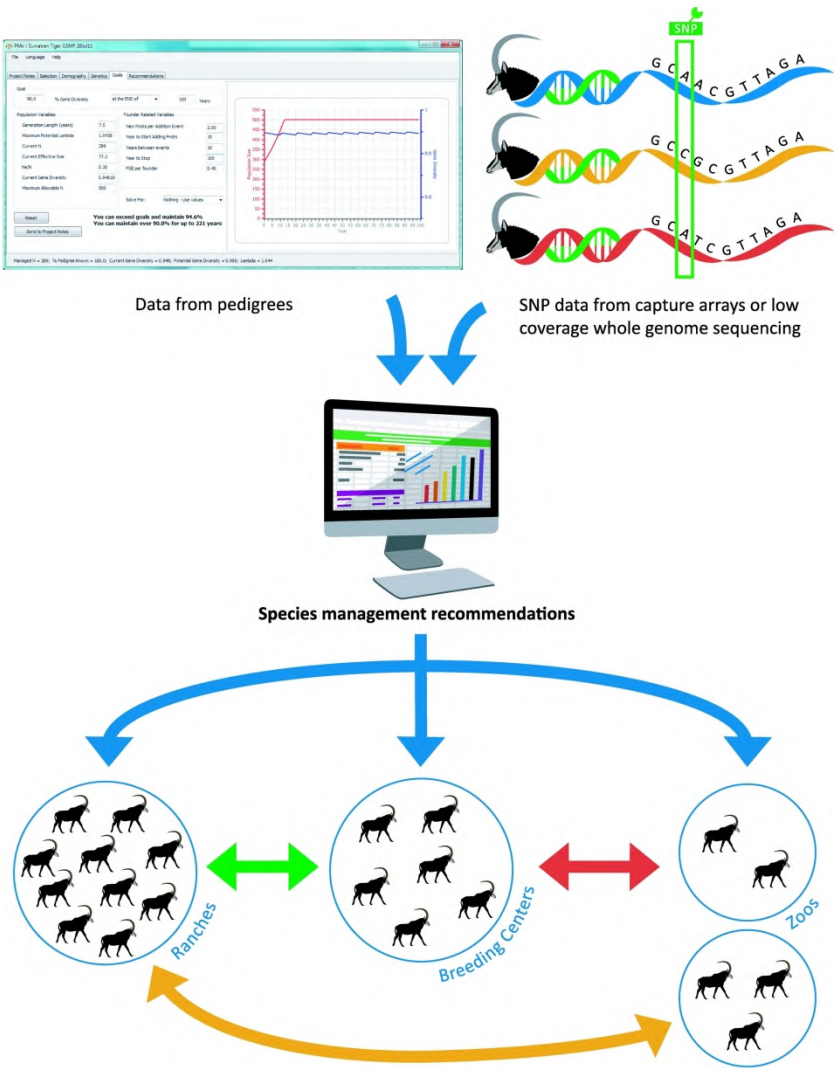
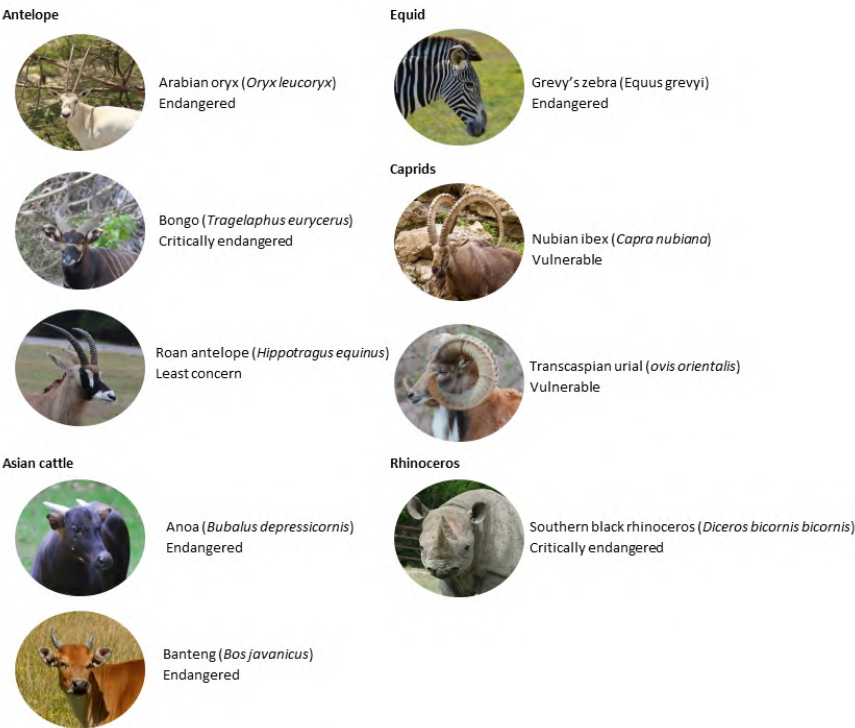


Figure 10

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Breeding centers, private ranches, and genomics for creating sustainable wildlife populations

David Wildt, Philip Miller, Klaus-Peter Koepfli, Budhan Pukazhenth, Katy Palfrey, Gavin Livingston, Dan Beetem, Stephen Shurter, Jimmy Gregory, Michael Takács, and Kelley Snodgrass

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Abstract

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 size and retain genetic diversity. Advances in genomics and resulting DNA data allow monitoring 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

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1046 *Like the resource it seeks to protect, wildlife conservation must be dynamic, changing as*
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1247 *conditions change, seeking always to become more effective.*
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1448 *Rachel Carson*
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1750 The International Union for Conservation of Nature (IUCN) indicates that ~25% of vertebrate
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1951 species are at risk of extinction ([http://www.iucnredlist.org/about/summary-](http://www.iucnredlist.org/about/summary-statistics#How_many_threatened)
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2152 [statistics#How many threatened](http://www.iucnredlist.org/about/summary-statistics#How_many_threatened)) from human overpopulation, habitat loss, exploitation,
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2353 pollution, disease, alien species, and climate change. Among the most concerning threats are
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2554 global greenhouse emissions predicted to cause the eventual disappearance of at least 50% of
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2755 animal species in certain locales ([www.worldwildlife.org/publications/wildlife-in-a-warming-](http://www.worldwildlife.org/publications/wildlife-in-a-warming-world-the-effects-of-climate-change-on-biodiversity)
2856 [world-the-effects-of-climate-change-on-biodiversity](http://www.worldwildlife.org/publications/wildlife-in-a-warming-world-the-effects-of-climate-change-on-biodiversity)). Although all species are susceptible to
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3057 environmental disruptions, larger animals requiring more space and complex ecosystems are
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3258 most vulnerable. Ripple et al. (2015) have reported the collapse of the world's 74 wild
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3459 herbivore species ≥ 100 kg comprising 11 families (Elephantidae, Rhinocerotidae,
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3660 Hippopotamidae, Giraffae, Bovidae, Camelidae, Tapiridae, Equidae, Cervidae, Suidae, and
3761 Hominidae). Approximately 60% of these species are threatened due to killing for bush
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3962 meat/body parts, land-use change, and resource competition by livestock. The result is
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4163 demographically impoverished populations, lost gene diversity, fewer large carnivores and
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4364 scavengers, and altered ecosystem services (Ripple et al. 2015).
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4565 Historically, preserving biodiversity has focused on saving habitat and, by default,
4666 protecting all species living in that native environment (*in situ*). Although always the priority,
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4867 this goal is outpaced by reality. Few wilderness areas are unaffected by human influence
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(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 also is concern about enough safeguarded wild space to assure viability. One analysis of ~4,000 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 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 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).

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10 ***Ex situ* programs and zoos**
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12 Most *ex situ* programs ~~require a long-term commitment – perhaps in perpetuity – to maintain mean~~
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15 species sustainably. For a carefully managed program with adequate founders, population
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17 abundance increases over time without the need for removing more animals from the wild. The
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19 population also retains a high level of genetic diversity to avoid inbreeding depression while
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21 remaining adaptable and resilient to environmental change (Frankham et al. 2017).
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23 The idea for creating sustainable insurance populations for rare species was pioneered
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25 nearly 40 years ago by zoos (Conway 1980). In this ‘ark’ paradigm, certain species are
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27 intensively managed by cooperating institutions that share individuals (Figure 1), or
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29 occasionally germplasm (Santymire et al. 2018), in a ‘metapopulation’ (Long et al. 2011). A
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31 pedigree is maintained and relatedness among animals (mean kinship) used to determine best
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33 matings to retain gene diversity (Ballou and Lacy 1995). Individual animals are identifiable (via
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35 ear tag, transponder, tattoo) and then moved between institutions to avoid inbreeding that can
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37 lead to infertility, disease susceptibility, morphological defects and mortalities (Frankham et al.
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39 2017). Mostly, the goal is to retain 90% of existing genetic diversity for 100 to 200 years (Soulé
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41 et al. 1986), a level predicted to preserve species integrity and evolutionary potential (Lacy
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43 2013).
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45 ~~The~~An effective population size (N_e) describes a genetically idealized population that
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47 displays the same rate of loss of genetic variation and increase in inbreeding as ~~the~~a natural
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49 wild population. ~~population~~ Frankham et al. (2017) proposed that N_e for a typical wildlife
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51 population should be at least 500 individuals to minimize loss of genetic variation while also

Commented [WD1]: DIDN'T UNDERSTAND 'POPULATION IN QUESTION'. DON'T KNOW IF THERE IS A WAY TO REDUCE THE OVERUSE OF 'POPULATION' IN THIS SENTENCE – OR FOR THAT MATTER IN THE ENTIRE PARAGRAPH.

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.

Frankham et al. (2017) proposed that populations should have at least 500 'effective' (or breeding) individuals to minimize overall loss in genetic variation while also retaining long-term adaptability to continued environmental change. This number may be smaller or larger depending on the number of founders originally taken from the wild, the variance in long-term reproductive success, and the species' mean generation length. Because only a small proportion of animals in a typical large mammal population are effective breeders, 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

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1034 in small-sized populations (Conde et al. 2013). The Association of Zoos and Aquariums (AZA),
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1235 which accredits North American zoos, reports that only 44 of 622 managed species programs
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1436 are self-sustaining (<https://www.aza.org/animal-program-sustainability-designations>). Of 428
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1637 species with studbooks, the median population is only 66 individuals (Long et al. 2011).
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1838 Approximately 39% of all mammal, bird, reptile, and amphibian zoo populations are comprised
1939 of **50 or fewer** individuals, and only 25% of these are successful breeders. Results from the
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2140 European zoo community are similar. Of 31 carnivore, 37 primate, 12 ungulate, and seven
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2341 rodent species, 48% of populations have bred to replacement, and only 55% are retaining gene
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2542 diversity at or above the 90% retention value (Lees and Wilcken 2009).
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2743 Zoos are challenged in providing safe havens for more species in larger numbers due to
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2944 insufficient resources (Monfort and Christen 2018; Powell 2018). Most significant is a lack of
3045 space. Zoos are complex, expensive operations, often existing on prime real estate in bustling
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3246 cities. A dominant mission is attracting the public to share stories on hundreds of species. There
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3447 is growing concern to promote welfare, which has led to elaborate exhibits that accommodate
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3648 fewer animals, which may be one cause for the 45% size decline in zoo mammal populations
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3849 (Long et al. 2011). We assessed AZA data available to members and ascertained that the 158
3950 accredited urban institutions averaged only 27.3 hectares each. This translates into a modest
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4151 4,306 total ‘zoo hectares’ in all of North America to meet the needs of thousands of wildlife
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4352 species for breeding, exhibition, education, merchandizing, and other zoo-related functions.
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4553 Therefore, sustaining rare species in secure populations – to prevent extinction, generate new
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4754 knowledge, and as a source for reintroductions – requires many times more animals than can
4855 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 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

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10 **C2S2 and wild ungulates.** C2S2 uses a programmatic approach for various taxa, from carnivores
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12 to passerine songbirds. Its focus on ungulates, specifically African antelopes, is driven by three
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14 factors. First, many of the world’s wild herbivore populations are in severe decline (Ripple et al.
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16 2015). Forty-four of 74 (59.4%) of the largest species are threatened with extinction (12 are
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18 classified a ‘Critically Endangered’; <http://www.iucnredlist.org/about/summary-statistics>).
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20 Primary threats are hunting, livestock competition, and habitat loss from cultivation,
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22 deforestation, and forces associated with climate change (Payne and Bro-Jorgensen 2016).
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24 Second, zoos are not providing sustainable insurance populations or expanding exhibit space.
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26 On the contrary, only two of 89 ungulate species managed in AZA institutions meet
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28 sustainability goals, and 42% are in decline (AZA, 2009; [https://www.aza.org/animal-program-](https://www.aza.org/animal-program-sustainability-designations)
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30 [sustainability-designations](https://www.aza.org/animal-program-sustainability-designations)).
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32 The third reason for C2S2’s interest in ungulates is member capacity in breeding and
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34 studying these species for decades. The Smithsonian Conservation Biology Institute (SCBI;
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36 Virginia) is comprised of barns constructed in the early 1900s to produce horses and mules for
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38 the U.S. military. Now modernized, these facilities are used for conservation breeding of
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40 scimitar-horned oryx (*Oryx dammah*) and dama gazelle (*Nanger dama ruficollis*). The Fossil Rim
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42 Wildlife Center (Texas), with landscapes and climate similar to African savannahs, has produced
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44 prodigious numbers of scimitar-horned oryx as well as addax (*Addax nasomaculatus*) and sable
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46 antelope (*Hippotragus niger*). The Wilds (Ohio), set on vast reclaimed mining lands, reproduces
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48 these antelopes as well as southern white rhinoceroses (*Ceratotherium simum simum*), the
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50 latter through four successive generations. White Oak Conservation (Florida) has a similar
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52 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 significant non-native wildlife populations (Figure 4). Texas alone has more than 5,000 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 2,000 to 4,000 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

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1023 business and/or investments. Generally, wildlife ranch operators manage for full production, do
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1224 not mark animals for identification, and occasionally rotate bulls to maintain herd
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1425 heterozygosity (Mungall and Sheffield 1994). Ranchers are independent, generally operating
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1626 with little or no connectivity to traditional conservation or research communities.
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1928 **Value proposition of a Source Population Alliance.** Given the under-appreciated contributions
2029 and potential of the private wildlife sector, C2S2 established a program called the **Source**
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2230 **Population Alliance** (SPA; www.sourcepopulation.org). Participants with significant land and
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2431 animal resources collaborate with an aim of producing sustainable populations of rare species.
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2632 We define a source population as a dependable reservoir for *ex situ* or *in situ* conservation and
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2833 utilization. This means for insurance, research, awareness, exhibition, raising funds for
2934 conservation, trade, and reintroductions into the wild. Although most SPA participants are
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3135 ranches or C2S2 breeding centers, zoos are encouraged to join. Our goals are to (1) recruit
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3336 qualified alliance participants to establish demographically sound metapopulations, (2) model
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3537 the predicted impact of herd type (smaller versus larger) and number of herds to achieve ideal
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3738 population growth, and (3) demonstrate how advances in genomics can be used practically for
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3939 management.
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4141 **Species targets**
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4342 We identified the scimitar-horned oryx, dama gazelle, addax, and sable antelope for initial
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4543 study, all having high conservation value (Figure 5). Named for its long, backward sweeping,
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4744 blade-like horns, the scimitar-horned oryx (Figure 5a) is the largest mammal to disappear from
4845 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 vestige 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 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). Stunningly, there are >5,000 scimitar-horned oryx and >2,800 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 (Mertes et al. in press). Initiated in 2016, including with a few animals from Texas ranches, more than 150 oryx have been released, with breeding and calves produced.

SPA principles and participant demographics

The SPA emerged from C2S2 leaders meeting with credible representatives from the private sector. An Executive Committee produced guidelines, describing expectations for highest

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1069 quality animal care, mutual cooperation, and, if interested, becoming involved in research. The
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1270 SPA's emphasis on simplicity has incentivized private landowner involvement. A key tenet is
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1471 that each participant retains ownership and control of their animals, husbandry protocols, and
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1572 all terms of transactions. The SPA encourages animal exchange to ensure gene diversity
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1773 retention, but each owner determines the preferred partner(s) for stock acquisition or
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1974 dispersal. Informed decision-making to protect heterozygosity and species integrity is
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2175 encouraged. There are three mandates for formal SPA participation: 1) manage animals in
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2376 suitable enclosures that prevent escape, meet biological needs, encourage natural behaviors,
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2577 and protect against injury and ill health; 2) complete an annual survey of total numbers of
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2778 owned animals; and 3) abide by all laws, including those regulating animal welfare, animal
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2879 transactions, and transportation. Candidates for inclusion in SPA undergo a nomination and
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3080 rigorous evaluation. All programmatic activities are overseen by an SPA Manager. Currently,
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3281 there are 372 participants, 60% being private sector facilities, 20% C2S2 breeding centers, and
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3482 20% public zoos. Collectively, these institutions have >322,000 hectares and maintain more
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3683 than 1,5200 animals of the four target species (Figure 7).

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3985 **Simulation modeling to demonstrate value of herd management**

4086 Most wild ungulates live in polygamous, multi-generational herds where one male mates with
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4287 multiple females. Offspring develop with age-matched cousins, a survival adaptation conferring
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4488 social, behavioral, and reproductive benefits to the young (Walther 1984; Estes 1991).
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4689 Compared to zoos, our *sorta situ* herds model offers more opportunities for normal behaviors
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4890 related to development, courtship, mating, and parturition. Under herd management, adult
4991 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 approach would have:

- A smaller, long-term, maximal abundance (i.e., carrying capacity) due to less space;
- More intensive reproductive management whereby, in which available breeding males and females are chosen for pairing based on mean kinship values to reduce average relatedness among individuals to avoid high inbreeding;
- ~~More intensive reproductive management based on mating by mean kinship to reduce average relatedness among individuals to avoid high inbreeding;~~
- Lower rates of reproductive success due to a higher frequency of institutions unable to comply with mating recommendations; and
- Lower calf mortality because of more thorough post-natal care.

By contrast, the simulated SPA population would have:

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- A larger long-term carrying capacity due to more space;
- Breeding management via periodic bull rotations or as guided by genomic assessments;
- Enhanced reproductive success because animals would be living in a more natural environment that would promote normal herd behaviors;
- 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 size 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 four-fold 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 better understanding population and individual animal genetics. Levels of heterozygosity, ancestry, and population 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 also may 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.

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1058 There are two broad categories for characterizing genetic variation across the genome,
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1259 one being a whole genome approach and the other by reduced representation (Fuentes-Pardo
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1460 and Ruzzante 2017). The former includes sequencing the whole genome of multiple
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1661 conspecifics and then comparing results to a reference genome. By contrast, reduced
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1862 representation allows high-throughput characterization of variation in only a subset of loci that
1963 may be restricted to specific genomic components containing protein-coding genes,
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2164 ultraconserved elements, or on restriction sites. A major advantage of whole genome
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2365 sequencing is the ability to design a customized, species-specific array through targeted
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2566 enrichment to capture single nucleotide polymorphisms, or SNPs (Fuentes-Pardo and Ruzzante
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2767 2017). This array can then be used to collect genotypes across thousands of loci from hundreds
2868 of individuals simultaneously using next generation sequencing methods (Jones and Good
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3069 2016).

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3471 **Genomics utility in the SPA approach.** Applying genomics to the SPA model offers
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3672 opportunities to produce sustainable populations by estimating genetic diversity, inbreeding
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3873 status, lineage integrity, ancestry, and kinship. Computer simulations and empirical evidence
3974 demonstrate that evaluations based on a large sampling of genomic markers provide more
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4175 precise measures of inbreeding and relatedness than pedigrees (Kardos et al. 2015; Kardos et
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4376 al. 2018). Genomic assessments offer enormous information useful for decision-making by
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4577 wildlife managers. Of particular relevance is the utility of this tool to ranchers who have little
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4778 knowledge about their animals’ genetic health or relatedness within their own herds or to the
4879 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 then is 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 5,000 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 9b) and assessment of genetic ancestry using the program ADMIXTURE (Alexander et al. 2009; Figure 9c). 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 from the Fossil Rim Wildlife Center to infuse new genetic diversity.

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1001 None of the 103 sable antelope in AZA-accredited zoos has been genetically analyzed,
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1202 and only 27% of the pedigree is known (Piltz et al. 2016). These obscurities can be eliminated
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1403 via genomic assessment with a high likelihood of identifying valuable and under-represented
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1604 individuals in both the public and private sectors. Such discoveries can be integrated into
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1805 modeling (as demonstrated above using Vortex) to better inform breeding male selection and
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2006 animal exchanges in all directions (Figure 10).

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2308 **Conclusions and perspectives for the future**

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2509 C2S2 and its SPA program connects breeding centers, the private sector, and zoos to fill a gap
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2710 not addressed by the purely *in situ* or *ex situ* communities. Although the preference always is to
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2911 maintain wild species in wild places, accelerated human population growth, habitat loss, and
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3112 climate change require more options. The intensive management practiced in urban zoos for
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3313 large sized species cannot meet well-established demographic and genetic goals. Although the
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3514 infrastructure and expertise in breeding centers and zoos are important, that capacity also is
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3715 inadequate when thousands of animals of a many species are required to achieve sustainability.
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3916 That is the reason for adding credible private landowners to the mix, a novel way that brings
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4117 diversity, resources, and new approaches for the greater good of species conservation.

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4318 There now are several areas for priority attention. Our simple, yet realistic modeling
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4519 exercise demonstrated clear demographic and genetic advantages of the SPA herd approach
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4720 over a traditional zoo breeding program. There also may be financial benefits due to
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4921 operational scale and the use of cheaper, rural land that includes spacious pastures requiring
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5122 less supplemental feeding and a smaller labor-force. As more data are collected, such factors

can be incorporated into more complex models to identify 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 By contrast, 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 (Mertes et al. in press). 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. Nonetheless, we acknowledge that herds zoo-held animals are in general not exposed to predation, forage limitations, interspecific competition etc. which no doubt influences adaptability to living in nature. We can expect that wildlife managed under *sorta situ* conditions also are vulnerable to such captive related conditions but perhaps less so than in zoos, an area rich for research explorations. maintained for many generations in captivity and that are allowed to self-select mating partners, even in spacious enclosures provided by the SPA model, could promote adaptation to

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10 ~~captive conditions that are potentially maladaptive in the wild following reintroduction.~~ These
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12 risks can be mitigated through the use of genomic data to ensure that diverse genetic lineages
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14 have equal representation in captive populations and to monitor reintroduced populations to
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16 assess how founders are contributing to overall genetic diversity across successive generations.
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18 Finally, there is a need to determine if DNA analytical costs can be sufficiently low to
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20 ensure widespread utilization by the wildlife managers. Genomic assessments are likely to
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22 become more economical based on experiences from human and livestock applications.
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24 However, there are far fewer wild animal specimens to assess, even from combined *ex situ*,
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26 *sorta situ*, and *in situ* populations. Therefore, it may be necessary to expect a higher evaluative
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28 cost for this service, which is essential given that maintaining gene diversity is a core principle
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30 of species conservation. Regardless, as biosamples have been solicited for this project, we have
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32 experienced enthusiasm from private or public sector owners, all of whom realize that a
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34 confirmed pedigree increases conservation (and financial) value of these resources. C2S2 is
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36 considering developing a DNA service that includes guidance on practical use of data for SPA
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38 participants.
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40 The SPA recently has expanded its portfolio to include more ungulates from the IUCN
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42 Red List, including more antelopes, an equid, and two caprids (Figure 11). C2S2 also has
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44 combined forces with the International Rhino Foundation (IRF) to develop a security population
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46 of the southern black rhinoceros (*Diceros bicornis minor*), no longer in an AZA accredited zoo
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48 program due to lack of space. The struggle to keep rhinos secure within their range in South
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50 Africa (Harper et al. 2018) is incentive for establishing insurance populations in other countries
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52 where climate, terrain, and natural browse are available. C2S2 and IRF are cooperating with
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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. The Nature Conservancy, for example, has long forged alliances with landowners, largely to promote local biodiversity. The SPA program of C2S2 is pursuing the linkage of private landholders with like-minded conservationists and innovative scientific tools to ensure survival of some 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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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 |

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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 | 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 ^b | MK; F < 0.25 | F < 0.25 |
| Demographic management protocol ^c | Breeding constrained to maintain population at K ^c | Breeding constrained to maintain population at K ^c |

^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 less than 0.25 (as occurs with full-sibling or parent-offspring pairings).

^cK, population carrying capacity.

Figure legends

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

Figure 2. Scimitar-horned oryx living in a naturalistic herd structure at The Wilds, ~~(Ohio, USA~~ (Photo credit: Pukazhenthil)).

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

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

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

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.

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).

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 5,000 SNPs.

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

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1029 genetic security. Arrows at the bottom of the figure represent recommended animal
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1230 translocations among ranches, breeding centers, and zoos based on empirically derived results
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1431 from combined demographic modeling and genomic data.

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1632 **Figure 11.** Species (or subspecies) recently added to the Source Population Alliance for public-
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1833 private sector conservation breeding ([Photo credit: Livingston](#)).

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