Sustaining the Ark: the challenges faced by zoos in maintaining viable populations

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In the World Zoo and Aquarium Conservation Strategy, the world’s leading zoos commit to focusing their efforts on conserving wildlife. Such a commitment is made as human activities are driving many species of wildlife towards extinction. The world’s leading zoos aim to act as a counterbalance to activities that undermine the sustainability of wild populations of threatened species. However, to date, this same group of zoos has largely failed to manage its own populations of wildlife sustainably despite distinguished calls to action over the past 25 years, significant scientific input and much organizational effort. This paper explores the efforts of the global zoo community to bring sustainability and conservation value to its animal populations. It looks at where we have come from, where we are now and where we need to go from here.

Key-words: Australasian zoos; captive programmes; global programmes; professional coordination; small populations; sustainability; target population size; zoo collaboration; zoo programme success.

INTRODUCTION

In the World Zoo and Aquarium Conservation Strategy, the world’s leading zoos commit to focusing their efforts on conserving wildlife (WAZA, 2005). Such a commitment is made as human activities are driving many species of wildlife towards extinction (Magin et al., 1994; IUCN, 2007).

However, to date, this same group of zoos has largely failed to manage its own populations of wildlife sustainably (Magin et al., 1994; Earnhardt et al., 2001; Baker, 2007) despite distinguished calls to action over the past 25 years (e.g. Conway, 1980; Seal, 1986; Soulé et al., 1986), significant scientific input (e.g. Mace, 1986; Lacy, 1987; Foose & Ballou, 1988; Frankham et al., 2002) and much organizational effort (e.g. de Boer, 1993; Wiese & Willis, 1996; Lees & Wilcken, 2002).

The need for sustainability

The number of vertebrate taxa regarded as threatened by the World Conservation Monitoring Centre more than doubled between 1996 and 2007 (IUCN, 2007). In addition, some 15–37% of species are predicted to be ‘committed to extinction’ in the future as a result of climate change (Thomas et al., 2004). Habitat loss and unsustainable use remain significant threats to wildlife (Pimm, 2001; Wilson, 2002; Smith, 2003). Such threats arise primarily as a result of the increasing demands of a growing human population and are unlikely to abate globally until human populations have stabilized – perhaps in 100–200 years from now (United Nations, 2004). Under such circumstances, conservation solutions are necessarily long term.

Zoos now operate an extensive portfolio of conservation activities to help combat these threats (Hutchins & Conway, 1995; Baker, 2007). Zoos design and deliver environmental education programmes, support wildlife research, provide funds, manpower and expertise in intensive management to support...
conservation efforts, and reintroduce captive animals into the wild. This last component, reintroduction, may be used to re-establish lost wild populations, to support struggling ones or as part of an interactive, meta-population approach to the management of wild and captive stocks (Seal, 1991; Magin et al., 1994). These activities rely on the presence of living animal collections in zoos. To fulfil the full suite of conservation roles required of them, these animal collections must be demographically robust, genetically representative of wild counterparts and able to sustain these characteristics for the foreseeable future.

**What is a sustainable population?**

We define a sustainable population here as one that is able to persist, indefinitely, with the resources available to it. Sustainable populations fall into two categories.

The first contains those populations with sufficient internal resources to persist without supplementation; that is, they are able to withstand or avoid the potential population hazards of fluctuating birth and death rates, sex-ratio skews, inbreeding and low gene diversity (Frankham et al., 2002). This subset of sustainable populations is considered ‘self-sustaining’ and populations in this category are necessarily very large.

The second category contains populations that, usually because of their smaller size, do not have sufficient internal resources for sustainability, but are sustained by external supplementation. For the sustainability test to be satisfied, this supplementation must be from source populations able to sustain the required harvest themselves without depletion. A population of any size can be sustainable, provided that the supplementing source population can accommodate the required harvest. The larger and better managed the population, the lower the rate of supplementation needed (Willis & Wiese, 1993).

**Collaboration for sustainability**

Overwhelmingly, the population sizes and/or supplementation rates required for sustain-ability are beyond the reach of an individual zoo. It has long been recognized that cooperation between institutions is the only realistic route for sustaining most species held in zoos (Seal, 1986; Baker & George, 1988; Foose & Ballou, 1988).

In a landmark paper, Soulé et al. (1986) proposed a rationale and framework for maximizing the number of sustainable populations held in the world’s zoos through global cooperation. The paper *The millenium ark: how long a voyage, how many staterooms, how many passengers?* carved out a scheme for optimal allocation of global zoo space coupled to the application of (then) emerging science. Their proposal is perhaps the most elegant presented to date in terms of making efficient, sustainable and conservation-relevant use of zoo space.

**The Ark paradigm**

The Ark paradigm as described by Soulé et al. (1986) responds to the then predicted ‘demographic winter’ of 500–1500 years after which the current trend of environmental degradation would be expected to stabilize, allowing for the re-establishment of wild areas. The authors propose a role for zoos in sustaining a subset of species through this period.

To retain their value as a genetic reservoir, a target of retaining 90% of wild source gene diversity in these populations was proposed, offering an intuitive threshold between the need to retain genetic diversity and the constraints of available space.

Further, recognizing the large size of captive populations needed to meet this target over 500–1500 years, they instead proposed a 200 year target, arguing that within 200 years technological developments will allow much less space-intensive means of preserving populations through cryopreservation of gametes and assisted reproduction. [Coincidentally, this accords well with the more recent 100–200 year estimates for the time frame for achieving a stable human population size (United Nations, 2004).]
In short, the authors were proposing that zoos around the world collaborate to establish a modern-day Noah’s Ark.

So powerful was this vision that it drove considerable global activity for the next decade. The world’s zoos embarked on unprecedented levels of cooperation. Regional Taxon Advisory Groups (TAGs) in the United Kingdom, Europe, North America and Australasia were charged with measuring the quantity and quality of zoo space and with prioritizing species to occupy that space (Hopkins & Stroud, 1995; Hutchins et al., 1995; Mallinson, 1995). This in turn fuelled the rapid expansion of regional cooperative zoo programmes, such as the Australasian Species Management Programs of Australasia (Lees & Wilcken, 2002), the European Endangered Species Programmes of Europe (de Boer, 1993) and the Species Survival Plans of North America (AZA, 2007), and many of these regional cooperative species programmes adopted standard targets of retaining 90% of wild source gene diversity for 200 years. Similarly, at the global level, the IUCN (International Union for Conservation of Nature) Species Survival Commission’s Conservation Breeding Specialist Group organized a series of planning workshops to identify global species priorities for the Ark and to massage regional priorities into a coherent global framework (Global Captive Action Plans: GCAPs) (Seal et al., 1994).

Further, global plans (Global Animal Survival Plans: GASPs) were written for high-profile species, such as tigers Panthera spp and rhinoceros (e.g. Tilson et al., 1993; Foose, 1995). These calculated the population sizes needed to achieve programme goals and divided up responsibility for providing the necessary space and resources among the participating regions.

For a while it looked as though the world’s zoos could indeed mould themselves into a modern-day Ark.

Over the last decade, though, Ark-related activity has declined as zoos have diversified their conservation activities, re-directing efforts into other areas, such as conservation education, research, fund-raising and other support for in situ projects (Hutchins & Conway, 1995; Baker, 2007).

GCAPs and GASPs are no longer produced, none are in current use and no equivalent processes have replaced them. In the face of available regional resources, the 200 year target for individual species programmes has been almost universally revised down to 100 years or even lower.

What impact has this had on zoo populations? What state is the Ark in?

The state of the Ark

Because of the small volume of zoo space in Australasia, most programmes there are sustained through periodic importation from captivity elsewhere, or by acquisition from the wild. As a result, the status of overseas captive populations and of wild populations within the region are of direct and ongoing relevance to the management of captive stocks. In this context, the Australasian Regional Association of Zoological Parks and Aquaria (ARAZPA) recently assessed the sustainability of 87 predominantly North American and European zoo populations of species featuring on the long-term collection plans of ARAZPA institutions. Data for the analyses were taken from the global pool of zoo data maintained by the International Species Information System (ISIS) (ISIS, 2005a; ISIS/WAZA, 2005). The results, for 31 carnivore, 37 primate, 12 ungulate and seven rodent populations, showed that only 48% are breeding to replacement and only 55% currently retain levels of gene diversity at or above the recommended threshold (GD ≥ 90%).

This study echoes the findings of others over the years (e.g. Magin et al., 1994; Earnhardt et al., 2001; Baker, 2007); that is, that zoo populations are in poor shape and are not achieving the conditions for sustainability. The Ark, it seems, is sinking.

What went wrong?

The science underpinning the management of small populations has been well tested and validated by computer simulation (Ballou &
Lacy, 1995) and in trials with living animals (Montgomery et al., 1997; Margan et al., 1998). We assume here, then, that the scientific basis for captive population management is sound. Therefore, if programmes are failing, it is likely to be either because the science is not being appropriately translated into management recommendations or because those recommendations are not being implemented within institutions.

Translating the science into management recommendations

The aim of captive management is to take a representative ‘snapshot’ of the species’ genetic diversity and preserve it in captivity, unchanged, for future use. The science dictates that to achieve this, we need to capture a good sample of genetic diversity from the wild in the form of unrelated founder animals; we need to grow that group of founders, as quickly as possible, to the population size required; we need to sustain the population at that size; we need to keep the genetic contributions of founders as even as possible and we need to maintain inbreeding below damaging levels (Foose & Ballou, 1988; Ballou & Lacy, 1995).

Founders

The number of founders needed for a programme depends to some extent on its length and purpose, but 20–50 is generally considered to be a reasonable sample (Foose & Ballou, 1988; Frankham et al., 2002). In the ARAZPA study, 59% of all populations outside Australasia were based on fewer than 20 founders. A substantial number of programmes, then, may not meet their long-term gene diversity targets because of a lack of founders. This should be addressed wherever possible.

Growth rates

The faster a population grows to the target size and the larger that size is, the slower the loss of genetic variation. The ARAZPA study did not assess historical population growth rates, but it did assess current breeding rates. Fifty-two per cent of all populations were not breeding to replacement rate and are therefore declining. Birth rates need to be higher to sustain population size in many populations.

Target size

Further, 67% of the populations studied fell below the 200 size threshold used by Baker (2007) as an indicator of viability. Similarly, of 961 managed populations registered by ISIS in 2005 (ISIS/WAZA, 2005) 78.6% fell below this threshold. In North America, based on a study of 63 AZA populations, Earnhardt et al. (2001) concluded that target sizes are not sufficiently informed by the science. Programmes will fail where the target size is too small.

Existing population size targets are usually based on maintaining gene diversity for a finite period – often 200 years (Soulé et al., 1986) or 100 years (Foose & Seal, 1992).

Both time frames were predicated on the eventual widespread use of gene banking to provide less space-intensive means of storing species. However, 20 years on, gene banks have not grown up alongside captive populations as envisaged and nowhere are they routinely used to sustain gene diversity in captive populations of wild animals. We suggest that targets for captive programmes should factor in the benefits of gene banking only where an appropriate gene bank is established and, further, that targets should not be based on finite periods unless a plan for the end of that period (e.g. reintroduction) is in place.

Adopting the definition of a sustainable population presented in the introduction – that is, one that is able to persist indefinitely, with the resources available to it – we suggest a different approach to setting population size, one more directly linked to wild status.

We first need to determine which populations need to be self-sustaining and which can be sustained through supplementation. We suggest that all taxa for which the captive population constitutes a significant part of the species’ genome, or for which further
collection from the wild is considered impossible, be managed as self-sustaining captive populations. Included would be all species categorized by the IUCN as Extinct in the Wild (EW) or Critically Endangered (CR), and some of those categorized as Endangered (EN) or Vulnerable (VU). The only exception to this may be those captive programmes that are explicitly short term. For example, those managed for immediate release into the wild over a defined period.

Those species for which further collection from the wild is still considered possible should be sustained by periodic, minimal and scientifically calculated rates of supplementation from the wild.

As for any scheme, population size targets must be calculated and periodically revised for each individual population based on its characteristics and management. However, indicative ranges of population sizes can be suggested for each of these categories of sustainability.

**Targets for self-sustainability**

For self-sustainability, populations need to encounter no net loss of genetic diversity; genetic diversity is the raw material for evolution and as it declines so does a population’s adaptive potential (Frankham et al., 2002). Genetic diversity is lost through chance processes (drift) and gained by mutation. The smallest population size for which drift is balanced by mutation is thought to be about $N_e = 500$ (Franklin, 1980; Lande & Barrowclough, 1987; Frankham et al., 2002) where $N_e$ is the effective population size and genetic diversity is measured through heterozygosity and additive genetic variance.

‘Effective population size’ ($N_e$) is a measure of that proportion of the census population that is contributing to the next generation (Wright, 1931; Crow & Kimura, 1970). The ratio of effective to actual population size is the greatest where the number of animals that reproduce is high, the sex ratio of breeding animals is equal and the life-time family sizes of reproducing animals are also equal, with the latter having the most influence in zoo populations (Seal, 1986). Wild populations differ significantly from these ideal characteristics and may achieve $N_e/N$ ratios of around $0.1$ (Frankham et al., 2002). That is, they may require $c. 5000$ animals to achieve a sustainable effective population size of 500. Through management, captive populations can be brought closer to these ideal characteristics. A study of 17 captive populations indicated an average $N_e/N$ of $0.26$ (Frankham et al., 2002), but ratios as high as $0.7$ have been reported (Willis & Wiese, 1993).

For well-founded captive populations to be self-sustaining, they will need an $N_e$ of at least 500 or an actual population size of 700–1900 animals. Where sufficient gene diversity has been captured at the founding and growth stages, such a population size will allow this level of gene diversity to be retained without any further loss. Although this is an ambitious target, it is not an impossible one. Of the populations registered in international studbooks (ISIS/WAZA, 2005), 9% fall within this range, including Przewalski’s horse *Equus przewalskii* (EW), Scimitar-horned oryx *Oryx dammah* (EW) and Siberian tiger *Panthera tigris altaica* (CR).

**Targets for supplemented sustainability**

Models suggest that it is also possible to achieve a similar equilibrium in smaller populations through the periodic addition of new founders (Lacy, 1987; Willis & Wiese, 1993). At low population sizes (50–100), the supplementation rates required are too high to be contemplated (Willis & Wiese, 1993) and demographic factors pose a real risk (Ballou, 1992). However, Lacy (1987) calculated that, once a population had reached an $N_e$ of 120 (while retaining 95% of wild gene diversity), it was possible to prevent any further loss of gene diversity indefinitely through the addition of five new founders in each generation. In zoos, $N_e = 120$ would equate to between 170 and 460 animals depending on the effectiveness of management. Of the populations registered in international studbooks (ISIS/
WAZA, 2005), 57.3% fall at least within this range.

The extent to which new wild founders may be responsibly available will depend on political and community sensitivities, and logistical and biological constraints. Any such initiatives should be based on an appropriate assessment of wild population viability. In reality, this may prove an option for fewer species than at first imagined. Certainly, current recruitment to priority populations is less than the figure suggested [generation time for species sampled ranged 6–20 years; mean number of founders added per programme in the last 35 years = 2.3 \( n = 87 \)]. Where recruitment cannot be sustained, a higher \( N_e \) will be needed.

### Resourcing priority populations

These assessments suggest a framework for applying zoo resources to priority populations (Fig. 1). Where species are common, resources should focus on securing supplementation and the net movement of animals is likely to be from the wild to captivity; as species experience greater risk, resources should be redirected towards growing captive space and net movements would necessarily be captive to wild. Tasmanian devils *Sarcophilus harrisii* are an example of this application in Australasia. Devils, which occur only on the island of Tasmania, are currently under acute threat from a new and universally fatal devil facial tumour disease (Loh *et al*., 2006; DPIW, 2008). In line with the current prognosis of possible extinction in 25–30 years, ARAZPA’s pre-disease target population size of 94 (Johnson *et al*., 2005), which was supplemented by regular recruits from Tasmania, has been revised upwards to a global target of \( N_e = 500 \) (DPIW/ARAZPA, 2007). A species that has come full circle is the Greater stick-nest rat *Leporillus conditor*. Once considered Endangered, it was bred in captivity and re-established at five new sites. It now numbers in excess of 5000 animals (Copley *et al*., 2007). To make way for other species, the captive population is now reduced to a small core for education purposes, supplemented periodically from wild sites.

Coupling captive targets to changing wild status in this way should lead to a more direct and dynamic relationship between wild and captive populations, taking us closer, for a greater number of species, to the symbiotic models of interactive management proposed by various authors (Conway, 1995; Stanley Price & Fa, 2007). It will also allow for a more focused allocation of a scarce resource: space in zoos.

### Professional programme coordination

There are computerized tools that can help with setting target population sizes, for example, PM2000 (Pollak *et al*., 2007) and VORTEX (Lacy, 2007). Using them appropriately requires an understanding of the underlying science and of the management consequences of experimenting with values such as effective population size, supplementation rates, generation time and growth rate.
In Australasia, as in other parts of the world, programme coordination is mostly carried out by professional animal keepers and curators supported by a very small number of population-biology practitioners. In 2006, a survey by ARAZPA showed that 75 zoos and aquariums in Australasia, holding c. 1000 vertebrate and 1000 invertebrate taxa (Johnson et al., 2007), employed over 70 veterinarians, 50 marketing specialists, 90 specialist educators and 35 full-time records officers, but fewer than three population biologists. Sound programme management requires sufficient investment in professional species managers. Clearly, any move towards this is not keeping pace with the development of other areas of zoo activity. (Since 2006, the Australasian region has employed a further two population-biology practitioners to work solely on the coordination of species programmes, although it is estimated that intensive management of the region’s 150–200 priority taxa would take 15–20 full-time professional coordinators.)

Translating small population-biology science into sound management recommendations requires accurate genetic and demographic data about the population (Foose, 1980; Flesness & Mace, 1988; Lacy et al., 1995). In the 87 populations studied by ARAZPA, 71 of which are the focus of regional and/or global studbooks, pedigree records were substantially incomplete (mean pedigree known: 56.7%). Population management relies on sound animal records keeping. This problem is well recognized by the global zoo community and is being addressed through the ISIS Zoological Information Management System project and the associated data clean-up campaign (ISIS, 2005b).

Implementing recommendations within institutions

No matter how closely programme recommendations adhere to the science, programmes will not achieve their goals unless those recommendations are actually implemented in zoos. A study in Australasia (van Doorn, unpubl.) followed the progress of 735 programme recommendations generated over a 5 year period, aiming to identify the factors most limiting the effectiveness of programmes.

The study found that Australasian zoos attempted to follow around four out of every five (83%) recommendations made but were only successful in implementing 68% of them. The largest category of failures was within-institution communication/inaction (64%). Problems with managing the biology of breeding programmes, including pair incompatibility and unexpected deaths, represented the next most significant category of failure (32%), with regulatory obstacles contributing to 4% of the problems.

In Australasia, all recommendations are reviewed and, after appropriate modification, formally endorsed by each participating zoo before finalization. Given the inclusive nature of this process, the figure for failure as a result of within-institution communication problems or inaction was unexpectedly high. To raise the profile of population management within zoos, ‘Compliance Officers’ are now appointed by each institution to track, report on and improve annual implementation rates. Importantly, these rates are now considered part of ARAZPA Accreditation assessments. Since these appointments, average ‘compliance rates’ have risen from 83 to 91% (R. Wilkins, pers. comm.). These results may be useful to other regions experiencing similar difficulties.

The second largest area of programme failure is the inability to manage biological factors effectively. The more closely populations can be managed towards the optimal conditions for retention of genetic diversity (see effective size discussions above), the smaller the population needed for sustainability (Frankham et al., 2002).

Few species currently allow close direction of these parameters. Many species live in polygamous groups with strict hierarchies and/or skewed sex ratios, resulting in large differences in the relative breeding success of individuals. Many of the species that live in pairs are highly selective in their choice of mate and may pair-bond permanently.
(Wedekind, 2002). For many species, behavioural cues for breeding are not well understood and pairing success is significantly below 100% (Lindburg & Fitch-Snyder, 1994). These issues frustrate the success of demographic and genetic management towards sustainability. They need to be addressed by innovative husbandry and appropriate technology.

For example, behavioural and chemical cues can be used to predict and respond to reproductive opportunities (Lindburg & Fitch-Snyder, 1994). Innovative enclosure design and behavioural management can enhance opportunities for lower-ranking animals to share breeding opportunities in group situations (Lees, 1993; Blount, 1998). Male rotation, animal conditioning, selective contraception, artificial insemination and embryo transfer are all techniques that can assist with ensuring that breeding is genetically optimal (Foose & Ballou, 1988; Wildt & Roth, 1997; Santiago & Caballero, 2000). There remains huge scope for strategic collaboration between population management and husbandry experts in the area of programme design. We need to foster this potential urgently.

A philosophy of sustainability

Institutional planning Perhaps more than anything, there is a need to foster a philosophy of sustainability with regard to zoo animal collections. This requires a move away from opportunistic acquisition and dispersal of stocks and towards strategic, sustainable ‘life-cycle’ planning for every exhibit in the collection. For example, it should be possible to identify how each species will be sustained in the collection over time: where will new, unrelated animals come from? How many will be needed, how often and can the available sources sustain this? How many offspring must be bred each year to sustain preferred holdings? What are the options for dispersal and are these options sustainable? Answering these questions requires population-level analysis, consideration of circumstances well beyond the exhibit and the institution. Within-institution planning at every level needs to be informed by wider sustainability considerations. Where populations are managed cooperatively for sustainability, institutions can plan the management of their animal collections confidently into the future.

Regional planning Space in the Ark is limited, and attempts have been made to craft suitable criteria with which to select species for it (e.g. Soulé et al., 1986; Balmford et al., 1995). Although these have informed considerable efforts by TAGs to re-shape regional animal collections over the past 10–15 years, the result is only a modest re-configuration of regional collections (studies by AZA and ARAZPA indicate that c. 60% of species have moved in the direction of TAG recommendations) (Allard et al., in press). Meanwhile, the resident global animal collection, as evidenced by the studies described here, is deteriorating.

There is no clear way of knowing which species may need reintroduction support in future; the local impact of climate change is currently unpredictable and the impact of new diseases can be random. Therefore, all species that have the potential to operate as useful genetic reservoirs should be managed as such, regardless of current threat status. Coordinated management should not wait until a species becomes threatened in the wild. By then, gene diversity in the captive population may be low, inbreeding high, the pedigree obscured and acquisition of new founders more difficult. Using captive populations of low quality to re-stock wild areas may be predisposed to failure (Jiménez et al., 1994) or even harmful (Ryman et al., 1995). Similarly, management resources should not be expended on permanently small populations that have no future. Rather they should be re-directed to taxa held in sufficiently large numbers: at least 170 if supplementation from the wild is still possible, or 700 if self-sustainability is required.

Finally, to ensure that populations reach their full potential, there needs to be a return to global planning.
Global versus regional management

Early proponents of the Ark thought globally rather than regionally about captive populations (Seal, 1986; Soule et al., 1986; Foose & Ballou, 1988) yet global management remains the exception and regional management the norm. The reasons for this are easily identified. Within-region transfers are logistically simpler and often less expensive; permitting and quarantine requirements are less onerous; and the necessary administrative structures and lines of communication are (usually) better established and more effective. Indeed, the zoo region is often the most sensible unit for cooperation, particularly for local species, which are the focus of short-term breed-for-release initiatives. However, as described above, many regional populations are not reaching viable sizes. Populations tracked across multiple regions reach necessarily larger sizes. Inter-regional or global management, although difficult to implement successfully, offers not only the advantage of scale but also of strategic overview. For example:

- For small, widely dispersed populations, global management provides an opportunity to link up a number of isolated, unsustainable units, improving demographic stability and managing inbreeding and gene diversity more effectively.
- Research (Margan et al., 1998) demonstrates that the genetic diversity of large global populations may benefit from strategic population sub-division and restricted but carefully managed migration between these sub-populations. Regional populations offer convenient sub-populations for use in this context.
- For expanding populations that are primarily held in one region but sought after in others, global management may be a useful mechanism for distributing important founder lines so that overall genetic diversity is maximized. In the absence of such management, over-represented lines are often continually exported from the source region to found new populations. This can reduce the genetic potential and therefore the conservation value of those populations and of overall global stocks.

Under certain circumstances, global management offers greater potential for extending the life of zoo populations and improving their value to conservation. For the Global Ark to reach its potential, global management needs to be a more accessible option. The new WAZA framework for inter-regional or global management (Wilcken, 2007) provides this access, drawing on the successful attributes of long-standing global programmes, such as those for Golden lion tamarins Leontopithecus rosalia (Smithsonian, 2008) and Red pandas Ailurus fulgens (Prince & Glatston, 1992), and its use should be encouraged. Using data from the ISIS/WAZA (2005) CD-ROM, we estimate that by linking up regionally managed populations, the average population size for vertebrate taxa can be increased from 120 to 170, placing many taxa within the range for supplemented sustainability.

CONCLUSIONS

If zoo populations are not sustainable, neither are zoos themselves. Too few populations are currently satisfying the conditions for sustainability. There is scope for revitalizing the Ark, but it requires renewed commitment and new investment. The following six-point plan summarizes steps that could be taken to set the Ark back on course.

**Step 1. Global audit**

A complete audit of populations held in WAZA-affiliated institutions, similar to the pilot study by ARAZPA, to provide a useful snapshot of the Ark’s remaining potential, for use in planning.

**Step 2. Global planning**

An inclusive process, based on the audit, to identify a list of priority species for the Ark based on population potential as well as threat.
Step 3. Global targets

Calculation of global target population sizes for each species, based on appropriate science and a rationale of sustainability.

- All taxa categorized by the IUCN as Extinct in the Wild or Critically Endangered should be assigned a target $N_e$ of 500 – (700 < $N$ < 1900).
- All other taxa for which recruitment from the wild is considered inappropriate or impossible should also be assigned a target $N_e$ = 500.
- For taxa where new founders can be recruited from wild populations, smaller target population sizes should be set. These should follow a documented assessment of species biology, the capacity of the wild population to sustain harvest and the political and logistical constraints limiting supplementation. It is unlikely that the resulting target population sizes will be less than an $N_e$ of 120 (170 < $N$ < 460), in conjunction with the input of around five new founders each generation.
- Exceptions to this could be: taxa being deliberately phased out; taxa present for short-term research or breed-for-release programmes; and taxa for which there are established gene banks that allow gene diversity targets to be met at lower numbers (noting that demographic considerations should dictate the minimum number in such cases).

Step 4. Global investment

Appropriate investment in professional species managers, in husbandry innovation and in supporting technology will help ensure that science-based targets are set and that programmes are designed and managed to meet those targets at achievable population sizes.

Step 5. Global commitment

Long-term programmes require long-term commitment. Mechanisms for securing this commitment from participating zoos should be factored into industry bench-marking and accreditation programmes.

Reintroduction from captivity, although difficult and expensive, remains the only option where other measures have failed. By responsible, sustainable management of their core asset – the animal collection – zoos are able to keep this option open for a large number of species. No other network of agencies can or will. However, for the Ark to stay afloat, there needs to be a greater understanding within the zoo community that many more zoo populations than we might imagine are irreplaceable conservation resources. We need to manage them as such; every year we delay, the potential returns diminish.

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Supporting Information

Table S1. Summary table of data and data sources used to assess the sustainability of zoo populations. Au. Australasia; Eu. Europe; GD. gene diversity; Int. international; m.
month(s); mean MK. average mean kinship; N. America. North America; NK. not known; No. number; S. Africa. South Africa; S. America. South America; SB. studbook; UTC. unable to calculate (too few known data in the studbook); W. Africa. West Africa; y. year(s). Note (1) Gene diversity (GD) is the proportion of genetic variability in the wild source population that is retained in the captive population; average mean kinship (mean MK) is a measure of the average relatedness of animals in the population: the higher the average mean kinship value, the more interrelated the population. Note (2) Dates in ‘Current to’ column follow the British date system of day/month/year, where 12/07/2006 is 12 July 2006.

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