COMMENTARY

Achieving True Sustainability of Zoo Populations

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For the last 30 years, cooperative management of irreplaceable animal populations in zoos and aquariums has focused primarily on the goal of minimizing genetic decay within defined time frames, and large advances have been made in technologies to optimize genetic management of closed populations. However, recent analyses have shown that most zoo programs are not projected to meet their stated goals. This has been described as a lack of achieving "sustainability" of the populations, yet by definition a goal of managed decay is not a plan for sustainability. True sustainability requires management of the resource in manner that does not deplete its value for the future. Achieving such sustainability for many managed populations may require changing from managing isolated populations to managing populations that are part of a broader metapopulation, with carefully considered exchange between populations across a spectrum of ex situ to in situ. Managing zoo populations as components of comprehensive conservation strategies for the species will require research on determinants of various kinds of genetic, physiological, behavioral, and morphological variation and their roles in population viability, development of an array of management techniques and tools, training of population managers in metapopulation management and integrated conservation planning, and projections of impacts of management strategies on the viability of the captive populations and all populations that are interactively managed or affected. Such a shift in goals and methods would result in zoo population management being an ongoing part of species conservation rather than short-term or isolated from species conservation. Zoo Biol. 32:19–26, 2013.

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INTRODUCTION

There has recently been much discussion about achieving sustainability of our zoo populations (e.g., papers in Gusset and Dick [2011]). This attention is appropriate given that without such sustainability both zoos and some species will not have a future. Analyses of population management programs of the regional zoo associations, as described in Baker [2007], Lees and Wilcken [2009, 2011], Leus et al. [2011], and Long et al. [2011] and in talks presented in the recent annual meetings of World Association of Zoos and Aquariums, Association of Zoos and Aquariums, European Association of Zoos and Aquariums, and Zoo and Aquarium Association have all documented that many of our most valued and often irreplaceable breeding programs are not projected to meet demographic and genetic goals designed to ensure that the populations persist and that the animals within them remain as healthy, genetic representatives of the wild populations. In every region, most of the cooperatively managed breeding programs have too few animals, too few animals in appropriate situations for breeding, too few successful breeders, too few founders, too many animals with undocumented ancestries, and/or too little cooperation with scientifically designated breeding recommendations. These deficiencies are resulting in declining populations or declining gene diversity or both. Conway [2011] noted that too little attention and resources are devoted to ensuring that even endangered species are managed in zoos in ways that will ensure a future for the populations and species: He quotes the rhetorical devil as saying "How is it, that zoos spend so much effort on exhibits of animals vanishing in nature but so little to assure that they don't vanish—even in the zoo?".

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The zoo profession has made huge strides since the start of cooperative management programs to develop the record-keeping, scientific methods, and program management that are necessary to achieve protection of the demographic growth and stability and genetic variation within our breeding programs [e.g., Ballou et al., 1995, 2010; Foose and Ballou, 1988; Hedrick and Miller, 1992; Ivy and Lacy, 2012; Lacy, 1987, 1989, 1994, 2009; Lacy et al., 2012; Leus et al., 2011; Oliehoek, 2009; Willis and Willis 2010]. Retrospective analyses have shown that rigorously managed programs can provide the population growth and reliability of numbers that are desired [Lacy 2000]. However, as noted above, in spite of the technical advances, many managed populations are in decline. Much can be done to improve the situation (e.g., see the recommendations in Lees and Wilcken [2009, 2011]), but it may also be time to rethink our goals for "sustainability" for many of the species for which the zoo-based breeding programs are intended to serve as a safeguard against extinction and a resource for future recovery efforts. Zoos were once reliant on harvest from the wild to populate their exhibits; in the past few decades zoos proudly and appropriately shifted away from reliance on continued wild collection to breeding of closed populations; perhaps we need now to move to a third era of thinking about the best way to care for species assurance populations.

What Is "Sustainability"?

"Sustainability" is defined as "a method of using a resource so that the resource is not depleted or permanently damaged" [Merriam-Webster, 2008], or a little less strictly as resource use "that meets the needs of the present without compromising the ability of future generations to meet their own needs" [World Commission on Environmental and Development, 1987]. A sustainably managed wildlife population is one that keeps its full value for the defined purposes of conservation, education, research, or entertainment. With very few exceptions, such sustainability is not what is being achieved with zoo breeding populations, and (as explained below) our measures of "sustainability" aremeasuring success toward goals that are actually counter to true sustainability.

Our current paradigm for managing essential populations is to minimize the rate of genetic decay [Lacy, 1994, 2009], slow adaptation to the captive environment [Frankham, 2008; Williams and Hoffman, 2009], and retain as many species-typical behaviors as is practical [McPhee and Carlstead, 2010]. However, for each of these goals, we can slow the negative trends in closed captive populations, but we cannot halt them altogether. It is widely accepted that the more generations a population spends in captive breeding, the less suitable it is for attempted restorations of wild populations [Earnhardt, 2010; Williams and Hoffman, 2009]. Thus, our population management is designed to not deplete too quickly the resource obtained from the founders. We are mining often-irreplaceable resources rather than sustainably managing them as renewable resources.

When Is 100 Years Up? What Then?

Our very criteria for "sustainability" belie the mistaken notion that we have accepted a mandate for the truly sustainable use of wildlife populations, and reveal instead that we are aiming, at best, for minimizing the rate of depletion so that populations would not become too badly damaged within a designated time frame. A common goal for our population management programs is to retain at least 90% of the gene diversity that was once present in the source wild population, for a time period of 100 years—although often zoo programs accept goals or outcomes of lesser retained representation and for fewer years. Moreover, this simple goal ignores that in many other aspects—such as behavioral variation, reproductive patterns, mate choice behaviors, and parental care, disease resistance, and physiological responsiveness to environmental cues—our populations might be changing in captivity much faster than is the neutral genetic variation that is modeled in our pedigree calculations of gene diversity. We put untested faith in the expectation that if genetic diversity is not badly depleted, then all the other characteristics of the conserved populations will also be protected adequately.

The 90%/100-year goal is in some ways arbitrary, in the sense that different species [Ralls et al., 1988] and even populations of the same species [Lacy et al., 1996] differ in how severely they are affected by inbreeding, and there is not a threshold level of genetic diversity that sharply demarcates for any species the transition from genetically healthy to imperiled populations. Moreover, the 100-year goal is not appropriate for all purposes. However, the goal (first set at 200 years) was not without scientific basis, but instead arose from consensus by zoo managers, conservationists, and evolutionary geneticists that it represented "the zone between a potentially damaging and tolerable loss of heterozygosity" [Soulé et al., 1986]. It is well documented that declining genetic diversity (concordant with increased accumulated inbreeding) causes poorer reproduction, individual health, and longevity, and increased probability of population extirpation [Lacy, 1997; Ryan et al., 2002; Frankham et al., 2009; Reed, 2010]. A huge number of animal breeding studies have shown that significant increase in genetic problems and decrease in productivity typically become apparent in sexually reproducing animals as inbreeding rises above about 10% [Falconer and Mackay, 1996]. Thus, decisions to aim for lower genetic goals, because it seems difficult to retain gene diversity at levels that can more predictably preserve individual animal health (rather than because it has been demonstrated that the species has more diversity than it needs), are arbitrary and dangerous, and abrogate our conservation responsibilities. Moreover, the rate of adaptation of a population to changed environments and new selective pressures is proportional to the current genetic diversity [Fisher, 1958], and we know that the global environment is changing at an accelerating rate. Therefore, most species will need more, not less, adaptability in the future, and populations being managed as reservoirs for species conservation will often have to be the source of that restored variation.

Although the 90% of initial gene diversity has justification as a goal for retaining reasonable individual health and population adaptability and has been used in other conservation contexts as an appropriate measure of population viability, the 100-year time frame is not compatible with true sustainability, which by definition requires that the resource not be depleted to lesser value for future generations. The 100-year goal was set with the expectation that within that time we will have better ways to protect species than to keep them in zoos, so that the current zoo populations will no longer be needed as conservation resources. For example, there may be frozen gamete or tissue banks from which genetic diversity can later be restored, or perhaps there will be other modes of population management not yet envisioned [Holt et al., 2003; Wildt et al., 1997]. The goal may also be justified by a trust that the human population will have restrained our use of resources and created adequate nature reserves for the species within that time frame, so that we do not need to care sustainably for our captive populations. It may be disconcerting to some in the zoo profession that our most ambitious goals were based on an assumption that zoo-breeding programs will become irrelevant to species conservation. Given that association-led cooperative management programs started 30 years ago, we are seemingly aiming for a collapse or replacement of our most valued living populations about 70 years from now.

Alternatively, it may be that the current paradigm is that zoos will not sustain our current populations indefinitely, but will instead become the temporary caretakers of a progressively changing array of species, as different species become imperiled by threats that cannot be adequately managed in the wild at that time. Thus, the zoo of the future may not have any rhinoceroses, tigers, lions, great apes, condors, Bali mynas, Aruba island rattlesnakes, Puerto Rican crested toads, or Lake Victoria cichlids, but will instead be maintaining large populations of perhaps plethodontid salamanders, corals, fresh-water mussels, insectivorous bats, Amazon beetles, Hawaiian drosophilid flies, Galápagos finches, and polar bears—all rescued from destroyed habitats or other uncontrolled threats—until those captive populations fade (or are released back to the wild) and are replaced by the latest crisis species. This is not a view of the future zoo that is often explained as a consequence of our current population goals, but related ideas have received some consideration from the perspective of maximizing the conservation contribution of zoo populations [Balmford, 2000; Balmford et al., 1996; Leader-Williams, et al., 2007].

Achieving True Sustainability

Even if this concept of zoos serving only as temporary homes for the species of current fashion or conservation need is not appealing, it may provide insight into a new paradigm for population management for species that we do wish to keep indefinitely for conservation, display, education, and research—a paradigm of true sustainability through constant refreshing of populations. The goal for populations under such a paradigm could be to sustain indefinitely at least 90% gene diversity (although at least 95% gene diversity, representing 10 rather than five founder genomes [Lacy, 1989], might be a more appropriate goal when we accept responsibility for the future of a species). Moreover, because the value of the resource is in more than its variation at hypothetical genetic loci that are not under selection, sustaining those populations would require attention also to other values, such as variation in genes under selection, disease resistance, reproductive patterns, behavioral variation, and morphological variation. It has not been clear if the common understanding and application of the 90/100 goal is to aim for finite length programs (as was indicated in the original formulation of the concept [Soulé, et al. 1986]), or instead the intent is to manage species such that they always are positioned to be able to sustain 90% of gene diversity for the next 100 years. To the extent that it is the latter, indefinite goal, then use of the 90/100 goals might closely resemble the new paradigm described above—but, again, in most cases we are not on track to meet such a goal. For humans with life spans typically less than 100 years, and for zoo directors and curators, with job tenures much less than 100 years, 100 years might be seen as the functional equivalent of forever. Given the rapid and accelerating rate of global change, it might be argued that even 25–50 years is a very long time and that managing for more distant goals is not practical. While that may be true of strategic planning, it misses (or perhaps even reinforces) the point that achieving true sustainability is not a matter of extending the planning horizon, but instead actively and continually managing in such a way so that the resource is not depleted—so that there is no end point to the projections against which we are measuring our progress.

Any closed population will lose genetic diversity, fast or slowly depending on its effective population size. In a very large population (much larger than almost any zoo population) those lost variants might be countered by new mutations appearing at a comparable rate, although replacement of prior adaptive variation with random new mutations is not the kind of sustainability that we desire in conservation. Adaptive genetic sustainability of an evolving population is the result of balance between random loss of alleles, generation of new mutation, selection filtering that variation to maintain adaptations and respond to new challenges, and exchange among local populations that have experienced different chance events and been exposed to different selective forces [Frankham et al., 2009; Lacy, 1987; Lande and Barrowclough, 1987]. Maintaining ecologically viable and resilient populations buffeted by such forces requires populations many times greater and under more diverse selective pressures than could typically be achieved in zoo breeding programs [Belovsky, 1987; Franklin and Frankham, 1998; Lande and Barrowclough, 1987]. Thus, for zoo populations to be truly sustainable, they cannot be maintained indefinitely as static, closed populations, but must instead by managed as a dynamic component of a metapopulation that includes wild populations and perhaps also less intensively managed populations in semi-wild environments.

Similar proposals have been made before, for example, the metapopulation management concepts promoted by Seal, Foose, and colleagues in the IUCN SSC Conservation Breeding Specialist Group [Seal et al., 1993; Foose et al., 1995]. Conway [1995] made a call for interactive management of zoo and wild populations, with thinking typically ahead of his time, but the strategy has not yet replaced the currently dominant thinking that we should almost always be aiming for sustainable [sic] closed zoo populations. Conway's suggestion of "extractive reserves" or "zoo reserves" relies on well-managed wild populations to provide the genetic and demographic renewal to counter decay in captive populations [Conway, 1999, 2007]. If the reserve populations are very large or openly exchanging individuals within a large wild metapopulation, then such a strategy could be said to be sustainable. However, for many species, the wild populations from which we might draw reinforcements are far from ecologically healthy and resilient; hence, Conway's recent call for better management of larger captive populations of endangered species [Conway, 2011]. However, if extractive reserves become interactive reserves, with animals moving in both directions, then the stability and sustainability of the overall system could be enhanced [Conway, 1995]. The golden lion tamarin program [Ballou et al., 2002] has partially used this strategy, in that the captive population has been used to help reinforce the smaller wild populations (and animals have been moved between sites in the wild), thereby restoring some of the genetic variation that had been lost. Lees and Wilcken [2009, 2011] proposed that zoo populations could be allocated into either self-sustaining populations of endangered species (aiming for traditional management goals) or supplemented populations of less endangered species (supported from extractive reserves or other responsibly managed wild sources). This would be a significant advance over the current situation that they document of most zoo populations—both those threatened and those of less conservation concern—dwindling due to inadequate resources being devoted to the programs. However, to achieve real sustainability may require that this separation not be made, as very rarely will zoo populations be self-sustaining except in a purely demographic sense for short-term programs. Perhaps every program (captive and wild) should be evaluated for how well and for how long it can be protected in isolation, how often and from what sources it will need reinforcing, and when and how best it can serve as a source for reinforcing other populations.

Interactive management of captive and wild populations will not be the right paradigm for all species held by zoos. First, for a small number of species, sufficient interest and commitment may exist in zoos to sustain such large populations, at least on a global level, that decay is so slow as to allow for a viable population to be maintained for such a long time as to be close enough to "sustainability" to assuage any concerns about its future. African penguins, gorillas, and giraffes might be examples—or at least have the potential to be nearly sustainable if rigorous cooperative management is applied at the international level. Second, for some species, the wild population no longer exists (e.g., Pere David's deer, Kihansi spray toad, a number of *Partula* snail species), or was only recently reestablished from the captive stock (e.g., California condor, black-footed ferret, Przewalski's horses, Arabian oryx), or is so small and fragile that it provides no reassurance for the captive stock and may need ongoing supplementation (e.g., Iberian lynx, Puerto Rican parrot, Puerto Rican crested toad). For such species we cannot assure true sustainability of our captive populations, and the best that we can do is to preserve as much as we can of what once comprised the species. Third, for many species there is no conservation need for an intensively managed captive population, because the species can be adequately protected in its natural habitats. Many such species might continue to be maintained in zoos for purposes other than providing assurance populations for the species—such as for education, research, and ambassador roles that might be equally important to overall wildlife conservation. For such species it might not be as much of a concern if the original diversity and wildness of the captive population diminishes over time, and if the current captive population were to collapse then the role might be filled with a new representative species. Finally, in some parts of the world and for some species, a past history of zoos as exploiters of wildlife rather than partners in sustainable conservation has resulted in zoos not yet being trusted by governmental agencies and field conservation organizations as credible partners in conservation initiatives that will require joint planning and implementation. If zoos are to be accepted by the conservation community as responsible and valued partners in sustaining wildlife [Baker et al., 2011], zoos will need to practice and demonstrate diligence in using every animal in their care in ways that meet the best interests of the species.

Implications for Population Management

Sustainable management of zoo populations via integration with populations outside of zoos will change population management goals. Instead of aiming for not too much genetic decline by the end of a time frame, the goal would be to stay above a healthy, resilient level of diversity—continually. The PMx software has a modeling tool to guide planning for such goals [Ballou et al., 2011; Lacy et al., 2012], although it seems that tool is not yet being used to manage toward such a goal of true sustainability. As a consequence of open population management, the populations within zoos could be smaller. Closed populations of vertebrates typically require 250–1000 animals to meet the 90/100 goal [Earnhardt et al., 2001; Soulé et al., 1986]. If exchanges of animals were part of the management plan, the required numbers of breeders could be reduced [Lacy, 1987; Willis and Wiese, 1993], although probably not as low as the typical current program size of about 50 [Conde et al., 2011; Long et al., 2011]. At the same time, genetic goals for how well the species is represented in captivity can probably be set higher than they are now. It is embarrassing that the standard current goal is so minimal as to accept as a species conservation "success" any program that retains only the amount of variation present in five wild individuals (90% gene diversity = five founder genome equivalents). Perhaps the most significant shift in population management goals would be that no longer would conservation programs be predicated on the assumption that within 100 years (often starting from the 1980s) intensive population management would no longer be needed, or that in any case zoos would no longer be part of the conservation plan for the species.

Implementation of plans for truly sustainable captive animal populations will require changes to the practices of population management by zoos. Management plans would need to include not just recommended transfers and breeding of the existing stock, but also equally careful and scientifically rigorous planning for acquisition of new founders as needed and exchanges of animals among populations, captive and wild and everything in between. Consideration needs to be given to the integrated use of gamete banks. There should also be active consideration of the role of the physical and social environments as drivers of natural selection, with management of the use of multiple environments to diversify selection occurring in the breeding program.

Monitoring of programs for sustainability will require more than studbook-derived statistics on demographic trends and pedigree estimates of genetic variation. Instead of trusting that all forms of adaptive variation will be maintained along with the modeled neutral genetic variation, we will need to monitor morphological, behavioral, and physiological variation. Instead of hoping that the managed population will be able to readapt to a wild environment if reintroductions are ever needed, we should periodically be testing the adaptability of our populations to more natural or even novel environments.

The requirements for successful programs of truly sustainable population management make clear that ending the mandate for closed populations and including exchange with wild populations is not a recipe or excuse for more relaxed population management. Instead, the requirements for program management, monitoring, research, and integration with in situ conservation will be substantially greater than has been typical zoo community practice to date. The difficulties in achieving true sustainability of populations that depend on our care include also changing expectations (or at least our perceptions of expectations) of visitors, increasing funding for ex situ conservation programs, changing restrictive legislation that blocks animal transfers with little regard for the conservation value, training zoo employees in new approaches to animal management, bringing more conservation scientists onto zoo staffs, and making the activities necessary for conservation and management of populations a core part of the operations of every zoo. These shifts will not be easy or quick, but they have little chance of occurring unless we first change our strategic goals for the populations under our care.

Research Needs

Fortunately, many of the advances in zoo biology and conservation science that are required to enable a new paradigm are already well underway. For example, guidance has been provided on the incorporation of new founders into breeding programs [Odum, 1994; Willis and Willis, 2010], pedigree management with partial parentage information [Lacy, 2012; Willis, 1993, 2001], use of gamete banks as adjuncts to breeding programs [Johnston and Lacy, 1995; Harnall et al., 2002], use of DNA data to improve management when pedigrees are incomplete [Jones et al., 2002; Jones and Wang, 2009; Ivy and Lacy, 2010], metapopulation management [CBSG, 2005; Lacy, 1987; McCullough et al., 1996], use of a spectrum of intensity of management [Princée, 1995], population management of reintroductions [Earnhardt, 1999, 2010; Jamieson and Lacy, 2011], the use of PVA to assess captive population viability [Bustamante, 1996; CBSG, 2005; Earnhardt et al., 2008], and management of species maintained in groups [Wang, 2004]. These efforts, however, have been mostly focused on management of gene diversity, with less work to date on integrating other population viability and sustainability goals into management. (See papers in Ganslosser, et al. [1995] and Kleiman et al. [2010] for some notable exceptions.) There remain significant challenges to the field of zoo biology before truly sustainable population management can be achieved. Some questions that will need to be answered by research and implemented by new methodologies include (with citations to a few of the papers that have provided insights into how such questions can be addressed):

- How can we integrate the management of quantitative variation, molecular variation, and behavioral variation into our well-established methods for kinship-based pedigree management?
- How much variation—of each kind—is needed for individual, population, and species health and adaptability? [Lande, 1995]
- How best can we maintain and share records on the diverse kinds of variation that we wish to protect?
- How fast do populations adapt to captivity and in what ways? How reversible are the changes? [Arnold, 1995; Frankham, 2008]
- How important is environmental variation in creating the diversifying selection that can sustain adaptive variation? To what extent do husbandry standards inadvertently become powerful forces of selection? [Carroll and Watters, 2008]
- What are the most effective ways to move animals or just genetic material among populations, including between captivity and the wild?
- What are the disease risks of moving animals periodically among captive and wild populations, and how best can those risks be managed? [Wolff and Seal, 1993, and many articles in that special issue; Armstrong et al., 2003]
- What are the sociological and organizational considerations that will need to be addressed to implement effective joint management of ex situ and in situ populations? [Dickie et al., 2007; Field and Dickie, 2007]

The above partial list is a very big agenda. Tackling these issues will make clear that zoo biology is an essential part of conservation biology, rather than a specialized field focused on the care of isolated wildlife populations within zoos.

Implications for Species Conservation

The opening of our breeding programs to manage active exchanges with wild populations will force zoo population management to be integrated within broader species conservation strategies, such as the Species Conservation Strategies being developed by the IUCN SSC [IUCN/SSC, 2008]. Decisions about which species need ex situ care as a component of conservation efforts will become the purview of field biologists, governmental wildlife authorities, and conservation NGOs, as well as the zoo professionals and zoo associations that generally now try to make those prioritization decisions on their own. Balmford [2000], Balmford et al. [1996], and Leader-Williams et al. [2007] suggest that zoos should preferentially maintain species that can easily and soon be returned to the wild, but that the species maintained in zoos currently usually are not those. The Amphibian Ark has been developing protocols for collaborative species prioritization [Amphibian Ark, 2009].

Planning for the future of the captive populations that are dependent on exchanges with the wild will require careful analysis (probably using PVA modeling tools) of the positive and negative impacts of removals from the wild and releases to the wild. For wild populations that might be or become dependent on reinforcement from viable captive stock, the trajectory and stability of the captive population should be tested regularly with PVA models that incorporate uncertainty in parameters and inherent stochasticity. For integrated assessment and management, it will be necessary also to monitor not only the numbers, trajectory, and health of the captive populations but also of the wild populations. The habitats available to the wild populations will also need to be watched, so that we can know when habitat restoration, additional adaptive variation, translocations, or restored connectivity is needed. Finally, the roles that zoos fill in species conservation may need to be portrayed both internally in the zoo profession and externally to the many audiences in very different language than had become standard. It may not be easy to explain to various audiences why the often-lauded paradigm of making zoo populations self-sufficient may not be achievable and will not serve species conservation goals. Managing ex situ populations alone is not species conservation [Lacy, 2011]. The zoos of the future will be justified by how well they contribute positively to overall species conservation efforts, not by how well they can minimize harm to wildlife populations.

The shift to pursuing real sustainability for zoo populations will involve a change from isolating zoo populations in order to minimize damage to the wild, while managing decay and loss in captivity to delay failure of the ex situ population, to a strategy of managing for ongoing population health, viability, resilience, and adaptability as part of overall species conservation programs. Rather than seeing zoo populations as last resort insurance to prevent species loss when all else fails in the field, zoo populations would be managed as an integral component of ongoing conservation success [Baker et al., 2011; Dickie et al., 2007].

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REFERENCES

Amphibian Ark. 2009. AArk amphibian conservation planning process. Available online at: http://www.amphibianark.org/pdf/Aark%20material/AArk_Conservation_Needs_ Assessment_ tool.pdf. Accessed 22 December 2011.

Armstrong D, Jakob-Hoff R, Seal US, editors. 2003. Animal movements and disease risk: a workbook. 5th edition. Apple Valley, MN: IUCN/SSC Conservation Breeding Specialist Group.

Arnold SJ. 1995. Monitoring quantitative genetic variation and evolution in captive populations. In: Ballou JD, Gilpin M, Foose TJ, editors. Population management for survival & recovery. Analytical methods and strategies in small population conservation. New York: Columbia University Press. p 295–317.

Baker A. 2007. Animal ambassadors: an analysis of the effectiveness and conservation impact of ex situ breeding efforts. In: Zimmerman A, Hatchwell M, Dickie LA, West C, editors. Zoos in the 21st century: catalysts for conservation? Cambridge: Cambridge University Press. p 139–154.

Baker AM, Lacy RC, Leus K, Traylor-Holzer K. 2011. Intensive management of populations for conservation. WAZA Mag 12:40–43.

Ballou JD, Gilpin M, Foose TJ, editors. 1995. Population management for survival & recovery. Analytical methods and strategies in small population conservation. New York: Columbia University Press.

Ballou JD, Kleiman DG, Mallinson JJC, Rylands AB, Valladares-Padua C, Leus K. 2002. History, management and conservation role of the captive lion tamarin populations. In: Kleiman DG, Rylands AB, editors. Lion tamarins: biology and conservation. Washington: Smithsonian Institution Press. p 95–114.

Ballou JD, Lees C, Faust LJ, Long S, Lynch C, Bingaman Lackey L, Foose TJ. 2010. Demographic and genetic management of captive populations. In: Kleiman DG, Thompson KV, Baer CK, editors. Wild mammals in captivity: principles and techniques for zoo management, 2nd ed. Chicago: University of Chicago Press. p 219–252.

Ballou JD, Lacy RC, Pollak JP. 2011. PMx: software for demographic and genetic analysis and management of pedigreed populations. Version 1.0. Brookfield, IL: Chicago Zoological Society.

Balmford A. 2000. Priorities for captive breeding—which mammals should board the ark? In: Entwistle A, Dunstone N, editors. Priorities for the conservation of mammalian diversity. Cambridge: Cambridge University Press. p 291–307.

Balmford A, Mace GM, Leader-Williams N. 1996. Designing the ark: setting priorities for captive breeding. Conserv Biol 10:719–727.

Belovsky GE. 1987. Extinction models and mammalian persistence. In: Soulé ME, editor. Viable populations for conservation. Cambridge: Cambridge University Press. p 35–57.

Bustamante, J. 1996. Population viability analysis of captive and released bearded vulture populations. Conserv Biol 10:822–831.

Caballero A, Rodríguez-Ramilo ST, Ávila V, Fernández J. 2010. Management of genetic diversity of subdivided populations in conservation programmes. Conserv Genet 11:409–419.

Carroll SP, Watters JV. 2008. Managing phenotypic variability with genetic and environmental heterogeneity: Contemporary evolution as a first principal of conservation biology. In: Carroll S, Fox C, editors. Conservation biology—evolution in action. Oxford: Oxford University Press. p 181–198.

CBSG. 2005. Population and habitat viability analysis for the Puerto Rican crested toad final report. Apple Valley, MN: IUCN/SSC Conservation Breeding Specialist Group.

Conde DA, Flesness N, Colchero F, Jones OR, Scheuerlein A. 2011. An emerging role of zoos to conserve biodiversity. Science 331:1390–1391.

Conde DA, Flesness N, Colchero F, Jones OR, Scheuerlein A. 2011. Zoos can lead the way with *ex situ* conservation. WAZA Mag 12:26–33.

Conway WG. 1995. Wild and zoo animal interactive management and habitat conservation. Biodivers Conserv 4:573–594.

Conway WG. 1999. Linking zoo and field, and keeping promises to dodos. In: Roth TL, Swanson WF, Blattman LK, editors. Proceedings seventh world conference on breeding endangered species: linking zoo and field research to advance conservation. Cincinnati, OH: Cincinnati Zoo and Botanical Garden. p 5–11.

Conway WG. 2007. Entering the 21st century. In: Zimmerman A, Hatchwell M, Dickie LA, West C, editors. Zoos in the 21st century: catalysts for conservation? Cambridge: Cambridge University Press. p 12–21.

Conway WG. 2011. Buying time for wild animals with zoos. Zoo Biol 30:1–8.

Dickie L, Bonner JP, West C. 2007. In situ and ex situ conservation: blurring the boundaries between zoos and the wild. In: Zimmerman A, Hatchwell M, Dickie LA, West C, editors. Zoos in the 21st century: catalysts for conservation? Cambridge: Cambridge University Press. p 220–235.

Earnhardt JM. 1999. Reintroduction programmes: genetic trade-offs for populations. Anim Conserv 2:279–286.

Earnhardt, JM. 2010. The role of captive populations in reintroduction programs. In: Kleiman DG, Thompson KV, Baer CK, editors. Wild mammals in captivity: principles and techniques for zoo management. 2nd edition. Chicago: University of Chicago Press. p 268–280.

Earnhardt J, Thompson ST, Marhevsky E. 2001. Interactions of target population size, population parameters, and program management on viability of captive populations. Zoo Biol 20:169–183.

Earnhardt JM, Bergstrom YM, Lin A, Faust LJ, Schloss CA, Thompson SD. 2008. Zoo risk: a risk assessment tool. Version 3.8. Chicago, IL: Lincoln Park Zoo.

Falconer DS, Mackay TFC. 1996. Introduction to quantitative genetics. 4th edition. Harlow, England: Longman.

Field DA, Dickie LA. 2007. Zoo coalitions for conservation. In: Zimmerman A, Hatchwell M, Dickie LA, West C, editors. Zoos in the 21st century: catalysts for conservation? Cambridge: Cambridge University Press. p 287–302.

Fisher RA. 1958. The genetical theory of natural selection. 2nd edition. New York: Dover.

Foose TJ, Ballou JD. 1988. Population management: theory and practice. Int Zoo Yearbook 27:26–41.

Foose TJ, deBoer L, Seal US, Lande R. 1995. Conservation management strategies based on viable populations. In: Ballou JD, Gilpin M, Foose TJ, editors. Population management for survival & recovery. Analytical methods and strategies in small population conservation. New York: Columbia University Press. p 273–294.

Frankham R. 2008. Genetic adaptation to captivity in species conservation programs. Mol Ecol 12:131–140.

Frankham R, Ballou JD, Briscoe DA. 2009. Introduction to conservation genetics. 2nd edition. Cambridge: Cambridge University Press.

Franklin IR, Frankham R. 1998. How large must populations be to retain evolutionary potential? Anim Conserv 1:69–70.

Ganslosser U, Hodges JK, Kaumanns W, editors. 1995. Research and captive propagation. Fürth, Germany: Filander Verlag.

Gusset M, Dick G, editors. 2011. Issue on “Towards sustainable population management.” WAZA Mag 12:1–44.

Harnal VK, Wildt DE, Bird DM, Monfort SL, Ballou JD. 2002. Computer simulations to determine the efficacy of different genome resource banking strategies for maintaining genetic diversity. Cryobiology 44:122–131.

Hedrick PW, Miller P. 1992. Conservation genetics: theory and management of captive populations. In: Sandlund OT, Hindar K, Brown AHD, editors. Conservation of biodiversity for sustainable development. Oslo: Scandinavian University Press. p 70–87.

Hibbard C, Hogg CJ, Ford C, Embury A. 2011. Maintaining the status of species management in a changing operating environment: outcomes over outputs. WAZA Mag 12:6–10.

Holt WV, Pickard AR, Rodger JC, Wildt DE, editors. 2003. Reproductive science and integrated conservation. Cambridge: Cambridge University Press.

Ivy JA, Lacy RC. 2010. Using molecular methods to improve the genetic management of captive breeding programs for threatened species. In: DeWoody JA, Bickham JW, Michler CH, Nicols KM, Rhodes OE, Woeste KE, editors. Molecular approaches in natural resource conservation and management. Cambridge, UK: Cambridge University Press. p 267–295.

IUCN/SSC. 2008. Strategic planning for species conservation: a handbook. Gland, Switzerland: IUCN Species Survival Commission.

Ivy JA, Lacy RC. 2012. Acomparison of strategies for selecting breeding pairs to preserve maximal genetic diversity in breeding programs. J Hered 2012:186–196.

Jamieson IG, Lacy RC. 2011. Managing genetic issues in reintroduction biology. In: Ewen JG, Armstrong DP, Parker KA, Seddon PJ, editors. Reintroduction biology: integrating science and management. Oxford, UK: Wiley-Blackwell. p 448–482.

Johnston LA, Lacy, RC. 1995. Genome resource banking for species conservation: selection of sperm donors. Cryobiology 32:68–77.

Jones KL, Glenn TC, Lacy RC, Pierce JR, Unruh N, Mirande CM, Chavez-Ramirez F. 2002. Refining the whooping crane studbook by incorporating microsatellite DNA and leg banding analyses. Conserv Biol 16: 789–799.

Jones O, Wang J. 2009. Molecular marker-based pedigrees for animal conservation biologists. Anim Conserv 13:26–34.
Kleiman DG, Thompson KV, Baer CK, editors. 2010. Wild mammals in captivity: principles and techniques for zoo management. 2nd edition. Chicago: University of Chicago Press.
Lacy RC. 1987. Loss of genetic diversity from managed populations: interacting effects of drift, mutation, immigration, selection, and population subdivision. Conserv Biol 1:143–158.
Lacy RC. 1989. Analysis of founder representation in pedigrees: founder equivalents and founder genome equivalents. Zoo Biol 8:111–124.
Lacy RC. 1994. Managing genetic diversity in captive populations of animals. In: Bowles ML, Whelan CJ, editors. Restoration and recovery of endangered plants and animals. Cambridge: Cambridge University Press. p 63–89.
Lacy RC. 1997. Importance of genetic variation to the viability of mammalian populations. J Mammal 78:320–335.
Lacy RC. 2000. Management of limited animal populations. In: Duffield D, Robeck T, editors. Bottlenose dolphin reproduction workshop. Report. Silver Spring, MD: AZA Marine Mammal Taxon Advisory Group. p 75–93.
Lacy RC. 2011. Re-thinking *ex situ* vs. *in situ* species conservation. In: Dick G, editor. Biodiversity is life. Proceedings of the 65th Annual Conference of the World Association of Zoos and Aquariums. Gland, Switzerland: WAZA. p 25–29.
Lacy RC. 2009. Stopping evolution: genetic management of captive populations. In: Amato G, DeSalle R, Ryder OA, Rosenbaum HC, editors. Conservation genetics in the age of genomics. New York: Columbia University Press. p 58–81.
Lacy RC. 2012. Extending pedigree analysis for uncertain parentage and diverse breeding systems. J Hered 2012:197–205.
Lacy RC, Alaks G, Walsh A. 1996. Hierarchical analysis of inbreeding depression in *Peromyscus polionotus*. Evolution 50:2187–2200.
Lacy RC, Ballou JD, Pollak JP. 2012. PMx: software package for demographic and genetic analysis and management of pedigreed populations. Methods Ecol Evol 3:433–437.
Lande R, Barrowclough GF. 1987. Effective population size, genetic variation, and their use in population management. In Soulé ME, editor. Viable populations for conservation. Cambridge: Cambridge University Press. p 87–123.
Lande R. 1995. Breeding plans for small populations based on the dynamics of quantitative genetic variance. In: Ballou JD, Gilpin M, Foose TJ, editors. Population management for survival & recovery. Analytical methods and strategies in small population conservation. New York: Columbia University Press. p 318–340.
Leader-Williams N, Balmford A, Linkie M, Mace GM, Smith RJ, Stevenson M, Walter O, West C, Zimmermann A. 2007. Beyond the ark: conservation biologists' views of the achievements of zoos in conservation. In: Zimmerman A, Hatchwell M, Dickie LA, West C, editors. Zoos in the 21st century: catalysts for conservation? Cambridge: Cambridge University Press. p 236–254.
Lees CM, Wilcken J. 2009. Sustaining the Ark: the challenges faced by zoos in maintaining viable populations. Int Zoo Yearbook 43:6–18.
Lees, CM, Wilcken J. 2011. Global programmes for sustainability. WAZA Mag 12:2–10.
Leus K, Traylor-Holzer K, Lacy RC. 2011. Genetic and demographic population management in zoos and aquariums: recent developments, future challenges and opportunities for scientific research. Int Zoo Yearbook 45:213–225.
Leus K, Bingaman Lackey L, van Lint W, de Man D, Riewald S, Veldkam A, Wijmans J. 2011. Sustainability of European Association of Zoos and Aquaria bird and mammal populations. WAZA Mag 12:11–14.
Long S, Dorsey C, Boyle P. 2011. Status of association of zoos and aquariums cooperatively managed programs. WAZA Mag 12:15–18.
McCullough DR, Fischer JK, Ballou JD. 1996. From bottleneck to metapopulation: recovery of the Tule Elk in California. In: McCullough DR, editor. Metapopulations and wildlife conservation. Washington: Island Press. p 375–403.
McPhee ME, Carlstead K. 2010. The importance of maintaining natural behaviors in captive mammals. In: Kleiman DG, Thompson KV, Baer CK, editors. Wild mammals in captivity: principles and techniques for zoo management. 2nd edition. Chicago: University of Chicago Press. p 303–313.
Merriam-Webster. 2008. Merriam-Webster's collegiate dictionary. 11th edition. Springfield, MA: Merriam-Webster.
Odum RA. 1994. Assimilation of new founders into existing captive populations. Zoo Biol 13:187–190.
Oliehoek P. 2009. Genetic conservation of endangered animal populations [PhD thesis]. Wageningen, The Netherlands: Wageningen University.
Princée, FPG. 1995. Overcoming the constraints of social structure and incomplete pedigree data through low-intensity genetic management. In: Ballou JD, Gilpin M, Foose TJ, editors. Population management for survival & recovery. Analytical methods and strategies in small population conservation. New York: Columbia University Press. p 124–154.
Ralls K, Ballou JD, Templeton A. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. Conserv Biol 2:185–193.
Reed DH. 2010. Albatrosses, eagles and newts, Oh My!: exceptions to the prevailing paradigm concerning genetic diversity and population viability? Anim Conserv 13:448–457.
Ryan KK, Lacy RC, Margulis SW. 2002. Impacts of inbreeding on components of reproductive success. In: Holt WV, Pickard AR, Rodger JC, Wildt DE, editors. Reproductive science and integrated conservation. Cambridge: Cambridge University Press. p 82–96.
Seal US, Foose TJ, Ellis S. 1993. Conservation assessment and management plans (CAMPs) and global captive action plans (CAPs). In: Olney PJS, Mace GM, Feistner ATC, editors. Creative conservation: interactive management of wild and captive animals. London: Chapman & Hall. p 312–325.
Soulé M, Giplin M, Conway W, Foose T. 1986. The millennium ark: how long a voyage, how many staterooms, how many passengers? Zoo Biol 5:111–114.
Wang J. 2004. Monitoring and managing genetic variation in group breeding populations without individual pedigrees. Conserv Genet 5: 813–825.
Wildt DE, Rall WF, Critser JK, Monfort SL, Seal US. 1997. Genome resource banks: living collections for biodiversity conservation. Bioscience 47:689–698.
Williams SE, Hoffman EA. 2009. Minimizing genetic adaptation in captive breeding programs: a review. Biol Conserv 142:2388–2400.
Willis K. 1993. Use of animals with unknown ancestries in scientifically managed breeding programs. Zoo Biol 12:161–172.
Willis K. 2001. Unpedigreed populations and worst-case scenarios. Zoo Biol 20:305–314.
Willis K, Wiese RJ. 1993. Effect of new founders on retention of gene diversity in captive populations: a formalization of the nucleus population concept. Zoo Biol 12:535–548.
Willis K, Willis, RE. 2010. How many founders, how large a population? Zoo Biol 29:638–646.
Wolff PL, Seal US. 1993. Implications of infectious disease for captive propagation and reintroduction of threatened species. J Zoo Wildlife Med 24:229–230.
World Commission on Environment and Development. 1987. Our commonfuture. Oxford: Oxford University Press.