Genetic and demographic population management in zoos and aquariums: recent developments, future challenges and opportunities for scientific research

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Over the last 40 years or so the zoo and aquarium world has made significant progress in its cooperative management of *ex situ* populations. Our community's strategy for the future is no less ambitious. However, it is becoming clear that we must do even better and even more, and for a much wider range of species. Additional needs for population management are increasingly being expressed that cannot be met by our current methods and tools. This paper aims to highlight some of the recent developments, scientific and technical challenges, and needs for scientific research in three broad areas that represent important fields for the future: the management of group-living organisms, the minimization of adaptation to captivity and the management of metapopulations. It is our intention for this paper to function as a brief description of the status quo in these fields of population management for *ex situ* breeding programmes for conservation, particularly those run by zoo and aquarium associations, and for it to function as a source of inspiration for researchers working in and with zoos and aquariums.

Key-words: analysis tools; group management; metapopulation management; population fragmentation; record keeping.

INTRODUCTION

Although conservation of genetic diversity has often been overlooked in international conservation policy implementation (Laikre, 2010), for the setting of population viability targets (Traill *et al.*, 2010) and in more commercially orientated captive-breeding operations [e.g. stock enhancement programmes for fish (Taniguchi, 2003; Kitadi *et al.*, 2009)], zoological gardens have implemented genetic and demographic management in their cooperative programmes for decades

(Flesness, 1977; Foose *et al.*, 1986; Soulé *et al.*, 1986; Foose & Ballou, 1988; Lacy *et al.*, 1995; Ballou & Foose, 1996; Princée, 1998; Frankham *et al.*, 2010). Over the last 40 years or so the zoo and aquarium world has made significant progress in its cooperative management of *ex situ* populations, and our community's strategy for the future is no less ambitious (WAZA, 2005; Penning *et al.*, 2009). However, it is becoming clear that we must do even better and even more, and for a much wider range of taxa, some with very different life-history patterns than the higher vertebrate taxa on which, until recently, attention has largely been focused. There is also a growing awareness that a substantial proportion of our existing programmes are not able to reach the genetic and demographic goals formulated for them (Baker, 2007; Lees & Wilcken, 2008; Dickie, 2009). Solving this problem of population sustainability will require a combination of radical paradigm shifts in the zoo and aquarium world, and the development of novel scientific and practical population-management strategies, methods and tools (CBSG, 2010; Conway, 2010). Additional needs for population management are increasingly being expressed that cannot be met by our current methods and tools (CBSG, 2009). This paper aims to highlight some of the recent developments, scientific and technical challenges, and needs for scientific research in three broad areas that represent important fields for the future: the management of group-living

organisms, the minimization of adaptation to captivity and the management of metapopulations. It is our intention for this paper to function as a brief description of the status quo in these fields of population management for *ex situ* breeding programmes for conservation, particularly those run by zoo and aquarium associations, and for it to function as a source of inspiration for researchers working in and with zoos and aquariums.

POPULATION MANAGEMENT OF GROUPS

The majority of breeding programmes currently run by zoo and aquarium associations base the genetic management of these populations on the analysis of individual pedigrees in order to determine the kinship between individuals and to base pairing recommendations for individuals on the principle of minimizing kinship – currently the best strategy to maximize retention of the wild genetic diversity in a captive population (Ballou & Lacy, 1995; Montgomery *et al*., 1997; Frankham *et al*., 2010). This approach is best suited to species in which individuals can be recognized and marked, that allow some level of control over who mates with whom, for which parentage of the offspring can be determined relatively easily, that have fairly small litter or clutch sizes, and that exhibit sexual reproduction whereby an offspring inherits 50% of the genetic material from each parent. The software packages for data registration and data analysis most commonly used for the management of cooperative-breeding programmes of zoo and aquarium associations [i.e. Animal Records Keeping System (ARKS: ISIS, 2010), Single Population Analysis and Records Keeping System (SPARKS: ISIS, 2004), Population Management 2000 (PM2000: Pollak *et al*., 2007), PopLink (Faust *et al*., 2009) and ZooRisk (Earnhardt *et al*., 2008)] are also best suited for these types of organisms.

Needless to say there are numerous species/taxa that do not possess these characteristics, such as all organisms that are managed in groups or colonies, ranging from individually recognizable penguins or primates living in groups, to schools of fish, clouds of brine shrimp or coral colonies (Mace *et al*., 1998). For the majority of these species the current methods and tools are inconvenient at best, and inappropriate at worst. However, the conservation status for these taxa is equally worrying (e.g. Stuart *et al*., 2004; Wilkinson, 2008; Darwall *et al*., 2009; Vié *et al*., 2009) and the need for *ex situ* breeding programmes for these species/taxa is growing (e.g. Gascon *et al*., 2007; Reid & Zippel, 2008: http://www.amphibianark.org).

In order to allow genetic and demographic management of group-living organisms in captivity, four components simultaneously need to be present: (1) the scientific knowledge and mathematical algorithms allowing data analysis and management to optimize the demographic health and the retention of the genetic diversity of the wild population in the captive population for the duration of the programme; (2) computerized record-keeping systems that allow the compilation and sharing (within and among institutions) of detailed records for all kinds of group-living organisms, that can then be exported to; (3) computer software programs for genetic and demographic analysis of records for group-living organisms, with the aim of guiding management towards optimization of the retention of genetic diversity; (4) training in new population-management methods and software tools, and improved training in existing methods and tools. The first three of these components will be dealt with in detail below.

Strategies for population management of groups

Different methods have been proposed for the genetic management of groups of organisms and are described below.

Maximum avoidance of inbreeding (MAI) schemes (Wright, 1921; Princée, 1998) MAI schemes have as their main objective to avoid inbreeding for as long as possible, or to slow down the process of inbreeding when avoidance is no longer possible (Princée, 1995), thus delaying effects of inbreeding depression. MAI

is less effective in maximizing the retention of gene diversity of the wild population than the 'minimization of kinship' method, but performs better than random breeding (Ballou & Lacy, 1995; Montgomery *et al.*, 1997). Variations on MAI schemes involve systematically transferring individuals among groups in a 'round robin' manner; for example, transferring a certain number of individuals per generation, transferring all juveniles to new next-generation groups before they breed themselves, or transferring all animals of one sex to the next group (Princée, 1995; Schad, 2008). MAI schemes are most effective in avoiding/slowing inbreeding when the number of groups equals a 'power of 2' and when the exchange of individuals or the formation of new groups is based on strict rules (Princée, 1995). It remains to be established how effectively inbreeding is delayed when a more relaxed 'round robin' movement of individuals between groups is applied and/or when the number of starting groups is not a 'power of 2', or when some groups do not breed or go extinct.

Maintaining a high and constant effective population size in all generations (including the founder generation) This method is widely recommended for the management of populations of fish in hatcheries, particularly for those populations that will be used for restocking/supplementing wild populations for reintroductions (Tave, 1993; Taniguchi, 2003). The effective size of a population is the size of an idealized population that would lose genetic diversity at the same rate as the real population (Frankham *et al.*, 2010). The effective size of a population (N_e) is generally much smaller than its true size (N), and the ratio of N_e/N reflects how 'effective' the true population size can be in terms of preserving the genetic diversity of the taxon. The N_e of a population can be maximized by maximizing the number of breeding animals, equalizing the sex ratio of breeding animals, equalizing family sizes, avoiding fluctuations in population size and avoiding overlapping generations (Frankham *et al.*, 2010). For this reason fish managers are often recommended, for example, to spawn fish over the entire spawning season, spawn fish of all sizes, spawn as many fish as possible (and if necessary in terms of space limitations, only keep a fraction of each spawn), and aim for an equal sex ratio among the breeders (Tave, 1993).

Population fragmentation This strategy involves splitting the founder population into a series of smaller groups and allowing the individuals in each to interbreed (and perhaps inbreed). Individuals from different groups are not bred together, unless monitoring demonstrates severe signs of inbreeding depression, upon which transfers between groups can be organized to alleviate this (Schad, 2008). Although each subpopulation is likely to lose genetic diversity fast (and accumulate inbreeding), random genetic drift likely results in different alleles being preserved in different subpopulations, resulting in a genetically diverse metapopulation. The effectiveness of this method for the retention of gene diversity is sensitive to, among other factors, the extinction of subpopulations (e.g. through inbreeding depression or demographic stochasticity) (see also section on 'Adaptation to captivity and metapopulation management').

Minimization of kinship Pedigree analysis techniques based on the minimization of kinship used for individually managed diploid species make use of the calculation of the matrix of all pairwise kinship coefficients to determine the genetic diversity retained, the levels of inbreeding and the most genetically valuable breeding combinations. Managing the breeding on the basis of the mean kinship values of the individuals in a captive population has proven to be an effective and relatively easy method to ensure the retention of both expected heterozygosity and allelic diversity (Ballou & Lacy, 1995). The genetic importance of an individual is determined by its mean kinship value, being the average of the kinship coefficients of that individual with every individual in the population, including itself. Individuals with few relatives in the population will therefore have a low mean kinship value and carry alleles that are relatively rare in the population, and

vice versa. In order to maximize the retention of gene diversity in the population, breeding priority is given to individuals with low mean kinships, and pairings are formed between individuals with similar mean kinship values (to avoid valuable genes to be combined with less valuable genes, which often happens if avoidance of inbreeding is given priority). Only secondary consideration needs to be given to avoiding or limiting inbreeding, as slowing the accumulation of inbreeding across generations will be an automatic result of minimizing mean kinships (Lacy, 1994; Ballou & Lacy, 1995).

The concept of 'kinship', the probability that two entities share alleles because of a shared ancestry, is applicable to propagating units beyond just individual organisms. Thus, the techniques for calculating kinships and related measures, and using them in population management, can be adapted and extended to allow genetic management of any entity (individual organisms, social groups, breeding colonies, sets of potential parents, clones, gametes), for any breeding system and inheritance type [although see Frankham (2010) for challenges regarding consequences of different breeding systems], for overlapping generations and for entities with partially unknown or uncertain ancestry (Ballou & Lacy, 1995; Lacy, 1998; Wang, 2004). For example, Wang (2004) provides the algorithms for a group-living monoecious diploid species with discrete non-overlapping generations, random mating (including selfing), a binomial distribution of the number of offspring per parent, migration occurring at preadult age before breeding and migrants with the same fitness as residents. These algorithms can be used to determine the total genetic variation in the metapopulation, the genetic value of a given population, the genetic value of an individual taken at random from a given population, optimal pairing schemes and culling schemes, optimal movement of breeders among populations and long-term predictions of genetic variation in the captive populations. Using information on the demography of the populations in the form of the number of breeding individuals

and the number of animals moving between populations, it is possible to calculate the inbreeding and kinship coefficients required. This method was successfully applied to the management of breeding programmes for Partula snails *Partula* spp (Burlingham-Johnson *et al*., 1994; Pearce-Kelly *et al*., 1995). Wang (2004) considered it difficult, if not impossible, to develop a comprehensive theoretical model that includes all the possible complexities of captive populations of any type of group-bred organism and considered it more feasible to have different aspects of the complexities covered by different models, depending on the natural history of the organism, and the detail and type of the information that can practically and realistically be observed and recorded from the population. Initially this approach had the potential disadvantage that a suite of different recording and analysis models and packages might need to be developed, and for which some level of user support and training would need to be made available. The recent development of the new data-recording software ZIMS (Zoological Information Management System) and the upcoming release of the new analysis software package PMx, into which algorithms for the calculation of mean kinships for individuals and groups have been incorporated, means that a wide array of group management complexities will be able to be handled by the combination of these two programmes (see below for details).

The fact that the genetic-management strategy based on the principle of minimizing kinship that zoos and aquariums are successfully applying to species managed at the individual level can be extended to just about any type of group-living organism seems to be excellent news. We are, however, far from a situation where we have identified and developed the precise scientific strategy to manage genetically any kind of organism we wish to manage. Many challenges, and therefore a whole host of research needs and opportunities, remain. Some of these are listed below.

1. *Assessment of strategy effectiveness*. The strategy of minimization of kinship has proven to be the best strategy to maximize

retention of the wild genetic diversity in captive populations with individual pedigrees (Ballou & Lacy, 1995; Montgomery *et al.*, 1997; Frankham *et al.*, 2010). However, is this also true for populations managed at the group level? Wang (2004) points out that group breeding models rely on several specific model assumptions (which may not hold true in the real-world) and parameters (for which we might not have data and thus have to estimate). While applying group models is likely better at maintaining genetic diversity than imposing no genetic management at all (Wang, 2004), it is uncertain if they are better than other, non-kinship-based models. The performance of different models needs to be compared, and the influence of assumptions and uncertainty in parameters within the same model need to be evaluated. Wang (2004) suggests this could be done through the use of stochastic simulation models, or through the use of DNA analysis to compare the genetic variation in the real-life groups/populations with what is predicted by the model algorithms, or through the application of the group model to a case population with fully known individual pedigrees so that the performance of the group model using population-level information can be compared. This represents a wealth of valuable and urgent research opportunities. Furthermore, the results of such studies would highlight those parameters that are critical for the behaviour of the model and, therefore, need further research to be able to define their values better (Wang, 2004).

2. *Incorporation of DNA data.* In contrast to individuals, entities composed of more than one individual (i.e. groups) lose genetic diversity over time with each generation that passes within the entity (owing to genetic drift, inbreeding, unequal sex ratio, unequal family sizes and related factors) (e.g. Fiumera *et al.*, 2000). Thus, optimal genetic algorithms would need to include (as did those of Wang) both the genetic changes that occur when new groups are formed by sampling from parental groups and those that occur within the lifetime of each group. To account fully for these processes, we most likely would need to keep generations separate (i.e. not allow intergenerational genetic change to occur within the lifetime of what we consider to be one group entity in our records and management), and to conduct regular censuses that track the number of breeding individuals and the number of migrants between groups. This, however, also implies a much higher management intensity, which is linked to the need for more resources. In fact, a general principle might be that the more detailed the level of management employed, the more effective it will be in maintaining genetic diversity, but the more information it will require and the higher the costs will be to obtain that information (Wang, 2004). An alternative to detailed tracking of the demography of groups would be to conduct DNA analysis on (a representative sample of) each generation and to base management decisions for the next generation on these results. For example, Doyle *et al.* (2001) and Sekino *et al.* (2004) conducted microsatellite DNA analysis on parent stock to produce pairwise relatedness coefficients, then calculated the mean relatedness between each fish and all other fish in the tank as an estimator of its mean kinship, and used these values to select the breeders for the next generation of Red seabream *Pagrus major* and Japanese flounder *Paralichthys olivaceus*, respectively. DNA analysis can also be used to determine the N_e, genetic diversity and inbreeding level of the founder population (compared with the wild source population) and of each subsequent generation to inform future management decisions (Fiumera *et al.*, 2000; Perez-Enriquez *et al.*, 2001; Lemay & Boulding, 2009). This approach has the advantage that management decisions are based on factual information derived from DNA analysis rather than on theoretical information derived from models. As Wang (2004) indicates, genetic monitoring with markers is especially important and useful for populations/taxa for which relatively little information is available and, thus, more assumptions and estimations need to be made, especially if this involves long-term conservation

programmes, as prediction errors based on assumptions can then accumulate to a dangerous level. Disadvantages are the intense collaboration needed between a DNA laboratory and the breeding programme and the cost of DNA studies (although the latter is steadily decreasing and the technical possibilities steadily increasing). Research programmes are required to investigate the relative performance of different theoretical models versus a DNA analysis approach (or a combination of the two), both in terms of scientific accuracy and of the different kinds of resources required, so that it becomes clear which approach provides the best balance between scientific ideal and practical feasibility.

3. *Incorporation of reproductive strategies*. Successful implementation of any breeding strategy requires a good understanding of the reproductive strategies, mate-choice strategies, breeding systems and the truly realized contribution of the potential breeders to the next generation. For example, the polygynous mating system of the Lake Victoria cichlid *Prognathochromis perrieri* is thought to have contributed to the low effective population size of the captive-bred populations (Fiumera *et al.*, 2000). Despite the gathering and mixing of gametes from individually spawned brood stock of Northern abalone *Haliotis kamtschatkana*, each hatchery-spawned group still had one very large full-sib family and several much smaller families, suggesting that issues such as sperm motility, age of gametes and sperm competition played an important role in fertilization (Lemay & Boulding, 2009). The importance of mate choice for successful reproduction has so far largely been ignored and yet the most carefully designed pairing schemes based on the genetic value of individuals or groups will miss their full potential without a good understanding of the mate-choice strategies of the species, as well as other factors that influence the reproductive success of designated breeding pairs. For many organisms this kind of information is completely lacking. Research into the basic social, reproductive and fertilization strategies will thus

be required for a large number of taxa in order for creative management solutions to be developed that successfully integrate the natural history of the taxon and any breeding scheme adopted to maximize the retention of genetic variation. Furthermore, common assumptions for species may need to be verified, as is illustrated by the surprising discovery of germ-line chimerism in Wied's marmosets *Callithrix kuhlii* (Ross *et al.*, 2007) or parthenogenesis in Komodo dragons *Varanus komodoensis* (Watts *et al.*, 2006). Common but invalid assumptions regarding which individuals are the only possible parents can have important consequences for the pedigrees and future management of these and other species.

Computerized record-keeping systems

Any type of management scheme to maximize retention of genetic diversity will require the keeping of specific records for analysis. Effective record keeping for group-living organisms presents a number of challenges, especially for lower vertebrates and invertebrates (Mace *et al.*, 1998), such as the recording of: different developmental stages (some of which may be hidden); different reproductive systems (e.g. self-fertilization, parthenogenesis, kleptogenesis, clonal reproduction, outbreeding) (sometimes simultaneously at work in a group); possible sex-change events; potentially huge numbers of offspring; population size changes for 'un-countable' organisms; numbers of births/deaths; parent determination. The software packages currently most commonly used by zoo and aquarium associations for recording animal data [ARKS (ISIS, 2010), SPARKS (ISIS, 2004), PopLink (Faust *et al.*, 2009)] are not sufficiently equipped to deal with all of this complexity. A number of institutions, particularly aquariums, have developed their own recording system [e.g. the software programme TRACKS developed by the National Aquarium (Baltimore, MA, USA), the Denver Zoological Foundation (CO, USA) and Zier Niemann Consulting (CO, USA); http://www.trackssoftware.com]. However, the

use of different systems by different institutions makes it difficult to amalgamate and analyse population-level data on a particular species. Systems that are developed for a particular institution are not necessarily easily 'transportable' to other institutions. Data standards will differ between institutions and systems. Likewise, systems developed for particular taxa and for particular levels of management may not be suitable for taxa that have very different life histories and/or that are managed at different levels of detail and intensity. The International Partulid Species Management System (PSMP) (previously CERCI) (Burlingham-Johnson et al., 1994) was developed to record (and report) demographic and pedigree information specifically required for the demographic and genetic management of Partula snails, but this programme cannot readily be applied to taxa with different life histories and with different needs or opportunities for the type and level of detail of data recorded. Finally, recording systems developed in isolation of analysis systems may cause data import/export problems.

A clear need, therefore, presented itself for a widely used and shared record system that would allow the recording of data, at various levels of demographic and genetic detail, on both individuals and all types of groups, for taxa of all life histories, according to global data standards, with a highly user-friendly interface (because data tend to be recorded by animal managers rather than population biologists) and that allows the exportation of data to various types of analysis software. One of the most important recent developments in the zoo and aquarium world was the release in April 2010 of Phase 1 (basic animal-records functions) of ZIMS, implemented and administered by the International Species Information System (ISIS). ZIMS will be the first online, real-time, shared, global animal database and management tool, and will fulfil all of the needs described above (and many more in the general fields of animal management, health and well-being; more information on ZIMS can be found at http://www.isis.org). This database will also provide almost limitless opportunities for zoological research, in general, and the furthering of the science of population management for group-living organisms, in particular.

A temporary challenge is that it will take time for ZIMS to be deployed to the currently more than 850 ISIS members in 82 countries (ISIS, pers. comm.). However, imminent extinctions will not wait; for example, many amphibians and freshwater fishes urgently need scientifically managed captive-breeding programmes. Ad interim, the need remains for the rapid development of small, very simple taxon- or life-history-type specific databases (preferably making use of mainstream spreadsheet and database packages), with user-friendly interfaces, that collect demographic and pedigree information at the level required for the breeding programme in question. It is essential that such developments take place in close consultation with ISIS and any teams working on the development of relevant population-analysis software packages.

Computer software programs for genetic and demographic analysis of groups

Currently the most commonly used software package for demographic and genetic analysis of cooperative-breeding programmes of zoo and aquarium associations, PM2000 (Pollak et al., 2007), is not equipped to deal with data for group-managed species. As was the case for the data recording software, the analysis tool developed for Partula snails cannot readily be used for programmes with different characteristics. An important new development, therefore, is the production of the software package PMx (Ballou et al., 2010), recently released in test version to population managers in the European Association of Zoos and Aquaria (EAZA, Amsterdam, the Netherlands) and the Association of Zoos and Aquariums (AZA, Silver Spring, MD, USA). PMx replaces PM2000 and was developed by J. D. Ballou, R. C. Lacy and J. P. Pollak with funding from the Institute of Museum and Library Services (Washington, DC, USA), AZA, the Chicago Zoological Society (Brookfield, IL, USA) and the National Zoo (Washington, DC, USA), and in collaboration with ISIS/

ZIMS, the AZA Population Management Center (Chicago, IL, USA), the International Union for Conservation of Nature (IUCN)/Species Survival Commission (SSC) Conservation Breeding Specialist Group (CBSG; Apple Valley, MN, USA) and many individuals worldwide. PMx will be able to import data from ZIMS, SPARKS, PopLink, Excel and other sources. In terms of group management, PMx is able to deal with entities consisting of more than one genetic individual, multiple possible sires or dams (uncertainty of parents), multiple sires and dams (group sex), different inheritance methods, the weighted use of animals with some unknown ancestry and the integration of DNA estimates of kinship. For its calculation of mean kinships for groups, PMx assumes that the genetic characteristics of a group do not change, whereas in reality a group will (without new imports) lose genetic diversity every time it passes through another generation of its constituent individuals. Therefore, the more detailed and intensive the day-to-day observation, management, care and housing of the groups, the more detailed demographic and pedigree data can be recorded in ZIMS, allowing for more accurate estimation of mean-kinship values calculated for groups in PMx.

ADAPTATION TO CAPTIVITY AND METAPOPULATION MANAGEMENT

While much emphasis is currently placed on management strategies aimed at the retention of genetic diversity in *ex situ* conservation-breeding programmes, comparatively less attention has been paid to methods specifically aimed at reducing adaptation to captivity. Nevertheless this is important, because individuals that are well adapted to the circumstances in captivity may be less well adapted to the circumstances in the wild and may show lower fitness upon reintroduction (Woodworth *et al.*, 2002; Frankham, 2008; Williams & Hoffman, 2009). Genetic adaptation to captivity has been documented across a broad range of taxa, including mammals, fish and insects, and is a serious concern for long-term *ex situ* management programmes for which the potential or future goal is reintroduction (Frankham, 2008). Strategies used to reduce adaptation to captivity include minimizing selection (through breeding strategies and by creating captive conditions similar to those in the wild), minimizing the number of generations in captivity and fragmentation of populations, of which the latter two are considered to be most effective (Margan *et al.*, 1998; Woodworth *et al.*, 2002; Frankham, 2008; Williams & Hoffman, 2009). Important current challenges in the field of reducing adaptation to captivity are considered to be the study of interactive effects of multiple strategies being implemented simultaneously (Williams & Hoffman, 2009), and testing of the applicability and effectiveness of procedures recommended on the basis of simulation results and laboratory experiments to practical, real-life management situations (Frankham, 2010).

Further exploration is needed into the possible beneficial effects of population fragmentation in cooperative *ex situ* breeding programmes. Fragmentation offers benefits and drawbacks – although genetic adaptation to captivity tends to happen more quickly in larger *vs* smaller populations (Woodworth *et al.*, 2002), smaller populations experience more genetic drift and accumulate inbreeding faster (Frankham *et al.*, 2010). However, because genetic drift is random, different subpopulations are likely to retain different elements of its genetic composition so that the metapopulation as a whole retains more genetic diversity than one large single population of the same size. For these reasons, it has been suggested that in captive settings it may be best to manage smaller subpopulations with occasional transfer of animals among subpopulations to avoid deleteriously high levels of inbreeding (and thus loss of genetic diversity) within each subpopulation (Margan *et al.*, 1998; Woodworth *et al.*, 2002; Frankham, 2008). This would reduce adaptation to captivity (because each subpopulation is small) and improve (or at least not compromise) the retention of genetic diversity. Metapopulation management strategies have been applied to wild populations (in the form of controlled translocations) (Semlitsch,

2002; Madsen *et al*., 2004; Tallmon *et al*., 2004; Bouzat *et al*., 2009; Davies-Mostert *et al*., 2009; Lindsey *et al*., 2009); and were shown to be an effective tool to reduce the effects of inbreeding depression and restore genetic variation in small isolated populations of Prairie chickens *Tympanuchus cupido pinnatus* (Bouzat *et al*., 2009). However, population fragmentation is only beneficial (and not detrimental) to the retention of gene diversity if three important conditions are met.

1. No subpopulation should go extinct (although smaller populations have a higher risk of extinction owing to genetic and demographic stochasticity, these risks can be partially mitigated through population monitoring, adaptive population management and periodic planned exchanges with other subpopulations).

2. The rate of exchange of animals among subpopulations should not be too frequent, as moderate levels of movement, on the scale of two or more animals per generation, will cancel out the genetic benefits of fragmentation while still incurring higher inbreeding levels within subpopulations (Lacy, 1987).

3. For the effect to be significant in practical terms, the subpopulations must remain at fixed effective population size (N_e) (Lacy, 1987; Frankham *et al*., 2010). However, in non-laboratory situations population subdivision can be expected to lead to increased demographic variation in the subpopulations, in turn leading to decreased N_e of the metapopulation and the subpopulations, which is detrimental to the retention of genetic diversity (Lacy & Lindenmayer, 1994).

Metapopulation management offers a new and relatively unchartered frontier in helping regional *ex situ* management programmes meet long-term viability needs of threatened species. A few attempts at global management were made in the mid-1990s as Global Animal Survival Plans (GASPs) and Global Captive Action Plans (GCAPs) organized by CBSG, but these programmes eventually dissolved potentially owing in part to lack of guidance and changing priorities (Lees & Wilcken, 2008). A few species have been successfully managed on a global level for many years [e.g. lion tamarins *Leontopithecus* spp (Ballou *et al*., 2002), Red panda *Ailurus fulgens* (Glatston & Leus, 2005), Okapi *Okapia johnstoni* (Leus, 2004)]. The recent establishment of the Global Species Management Plan (GSMP) by the World Association of Zoos and Aquariums (WAZA) offers both the opportunity, and the challenge, to develop effective strategies for interregional metapopulation management. For some species, it may be the case that each regional programme (subpopulation) cannot meet long-term genetic goals in isolation but that such goals could be met by a well-managed global programme (metapopulation).

Studies using simulation models could help to test the proposed benefit of a metapopulation structure for the reduction of adaptation to captivity and the maximization of retention of genetic diversity, in the framework of real-life, proactively managed, *ex situ* breeding programmes. Many questions remain to be answered. For example, what are the consequences if the subpopulations are established from a different but overlapping set of genetic founders, as might be typical across regional zoo programmes? How might different subpopulations best serve the long-term viability of the species metapopulation? With the increasing development of cooperative *ex situ* management programmes by regional zoo associations in regions of high biodiversity and high numbers of threatened species, there may be the opportunity for mixed metapopulation strategies, in which, for example, the primary *ex situ* population is managed in the range country (and may experience intermittent influx of new founders from the wild) while other regional programmes act as secondary (backup) subpopulations, with periodic and controlled directional migration among these subpopulations, as has been suggested for the Sumatran tiger *Panthera tigris sumatrae* (Traylor-Holzer, 1999).

With the realization that for many species the space needed to house the total population size required for a self-sustaining captive population often cannot be found within one

geographic region, the number of GSMPs is likely to increase. Guidelines need to be developed for global managers stipulating how the number of animals and the genetic diversity is best spread over different subpopulations, as well as the rate and criteria for the transfer of individuals between regions in order to maximize the retention of genetic diversity across the metapopulation, keep inbreeding in each subpopulation at acceptable levels and minimize adaptation to captivity. While general guidelines can and should be developed, species may benefit from a metapopulation viability analysis that takes species- and regional subpopulation-specific information into account and can explore alternative scenarios of interactive management on long-term metapopulation viability and retention of genetic diversity (Pedrono *et al*., 2004). Such an analysis could be carried out using a stochastic simulation modelling program such as Vortex (Lacy *et al*., 2009). Taken to its ultimate extension, metapopulation management can be the bridge to link *ex situ* and *in situ* populations into a continuum of more or less intensively managed subpopulations of a metapopulation (e.g. Valladares-Padua *et al*., 2002).

SUMMARY

From the above we learn that there is a need to (1) evaluate, through modelling and practical experimentation, the effectiveness and efficiency (from a resource point of view) of different methods to maintain gene diversity in group-managed captive-breeding programmes; (2) develop the necessary additional data-recording and analysis tools to support effective and efficient group management; (3) carry out further modelling and laboratory studies to determine the best strategies for metapopulation management, to test the proposed benefit of a metapopulation structure for the reduction of adaptation to captivity and to test these strategies under 'real life' situations faced by breeding programmes.

However, this highlights only a small subset of the current challenges and opportunities for the intensive management of *ex situ* populations for conservation. During a work-

ing-group discussion at its 2008 Annual Meeting in Adelaide, Australia, the IUCN/ SSC CBSG solicited input from a wide range of individuals with varying perspectives on the complexities, constraints and challenges of population management. The working group generated a long list of issues that could be clumped in three groups: Conceptual Issues, Technical Issues and People Issues (CBSG, 2009: http://www.cbsg.org/ cbsg/content/files/2008_Annual_Meeting_ WG_Reports/ex_situ.pdf). The results from this workshop can and will form the impetus for a wide range of additional future activities and research projects.

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