

The World Zoo and Aquarium Conservation Strategy -- Chapter 4 Population Management

Summary

This chapter presents a vision of the involvement of zoos and aquariums, as centres of expertise in small population management, in regional or global cooperative breeding programmes. To maximize value to conservation, ex situ populations need to be demographically stable, well-maintained and capable of self-sustaining reproduction. They should be distributed among several institutions and of sufficient size to maintain high levels of genetic diversity. However, many programmes have too few founders and participating institutions, depleted genetic diversity and/or poor breeding success. Strategies to enhance viability include: increasing breeding spaces, expanding from regional to global programmes, increasing the intensity of genetic management, improving husbandry practices through research, and importing founders from the wild or other regions. Population management includes demographic and genetic management, veterinary care and husbandry. The first involves monitoring numbers, and age, social and sex structure. Genetic management involves verifying taxonomic identity, and avoiding deleterious effects of inbreeding and loss of genetic diversity. Management decisions are developed through studbooks. Population data are held on a database system at the International Species Information System (ISIS), supported by registration and analysis software. Other management aspects discussed include confiscated and abandoned animals, ownership, and the impact of regulations on animal transfers. The chapter emphasizes that a primary goal of ex situ programmes is support (including demographic and genetic reservoirs) for in situ conservation. Metapopulation management involves managing a set of interacting populations under a common conservation goal. Its components may include ex situ populations, in-country breeding programmes, wild populations and genome banks. Transfer between populations may involve reintroduction. The chapter ends by stating that many wild populations are like ex situ ones - of small size with limited gene flow between them. The science of small population management developed primarily for managing ex situ populations is thus of direct relevance to field conservation. This expertise is a major contribution that zoos and aquariums can offer conservation.



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Vision

All zoos and aquariums will be primary centres of expertise in small population management and will be involved in global or regional cooperative breeding programmes. All such programmes will be based on sound knowledge using the latest available data on population management, reproductive biology, genetics, behaviour, physiology, nutrition, veterinary care and husbandry.

4.1 Introduction

Zoos and aquariums in the future will be critical for the survival of many species and an integral part of *in situ* conservation programmes for many others. However, animal collections in individual zoos and aquariums are typically too small to be of much value to long-term conservation. How then can these individual collections serve a conservation purpose? The answer will lie in cooperative international or regional *ex situ* breeding programmes to form large, viable populations. These cooperative breeding programmes serve many purposes: providing animals for public educational and/or exhibit opportunities; providing fund-raising material; providing research collections from which to gain basic knowledge of animal biology and husbandry; and, on a larger scale, providing demographic and genetic backup to wild populations. To serve in all of these roles fully, these populations must be viable over the long term. This requires that they be:

- demographically stable;
- healthy, well maintained and capable of self-sustaining reproduction;
- distributed among several institutions to lessen the risks of catastrophic loss;
- of sufficient size to maintain high levels of genetic diversity.

Demographic stability is needed to ensure that an adequate number of animals of breeding age are available to reproduce at the rates needed to increase or maintain the population at its desired size. Healthy populations are

needed to ensure that animals are capable of breeding when needed. Genetic diversity is required for populations to remain healthy and adapt to changing environments (i.e. experience natural selection). *Ex situ* breeding programmes need to preserve this diversity, otherwise the long-term fitness of these populations will be compromised.

4.2 Maintaining viable populations: setting population goals

Conservation biologists have recommended that to be viable, *ex situ* populations should be of sufficient size to retain 90% of the source species' genetic diversity for 100 years. They argue that the sizes needed to achieve this goal will also underlie most other concerns of viability (capacity for reliable reproduction, demographic stability, etc.). The optimum population size depends on the specifics of each population (e.g. species with longer generation lengths or more genetic diversity will require smaller populations) but will typically be in the several hundreds. This clearly illustrates the need for individual institutions to link to global and regional cooperative breeding programmes.

The '90%/100 Year' goal is limiting as it focuses only on genetic criteria for viability. A more comprehensive approach should consider overall population viability. Target population sizes would be set to match a multi-dimensional set of criteria that would include minimizing the probability of extinction, retaining high levels of genetic diversity, maintaining a self-sustaining population and meeting other needs (e.g. exhibit needs, social/behavioural needs of animals, or supply of animals for reintroduction). Future

population planning should consider this approach, and tools need to be developed to conduct these population viability analyses.

Many *ex situ* breeding programmes will not be able to meet general criteria for viability. This is typically due to too few founder animals, already depleted genetic diversity, not enough participating zoos, or a lack of breeding success. Each programme should identify strategies for enhancing the viability of its populations, including:

- increasing breeding spaces allocated to the species, perhaps in off-exhibit facilities;
- expanding a regional to an international programme;
- increasing the intensity of genetic management (e.g. by encouraging tighter compliance with breeding recommendations);
- improving husbandry practices or investing in husbandry, behaviour, nutrition and veterinary research to improve reproductive performance;
- importing additional founders from the wild or other regional programmes.

4.3 Science of population management

Population management includes demographic management, genetic management, veterinary care and husbandry. Coordination among these fields is absolutely necessary since each places constraints on the others. For example, husbandry and behavioural concerns often limit genetic management, and veterinary concerns may remove animals from breeding situations or prevent some desired transfers between institutions.

Demographic management is concerned with monitoring the age, social and sex structure of the population, and number of conspecifics, to ensure reliable reproduction, as well as determining the number of animals that need to be bred to achieve a desired growth rate. Analytical software using studbook data is used to estimate this. Two major concerns facing demographic management are managing population growth rates and limited resources.

As populations grow animals may need to be sent to other responsible zoos and institutions, and reproduction limited, ideally to achieve zero population growth. This puts considerable strain on population management, since placing animals in non-breeding situations is often difficult from a husbandry perspective; it may take up valuable space and be unnatural with regard to normal social groupings. While contraceptives have frequently been used to regulate reproduction, this is often not ideal and can lead to health and social problems in some species. Nevertheless, contraceptives are the primary method used to control population growth in many zoos, and further research is needed to develop safe, reversible contraceptives for the large variety of species under zoo care. Euthanasia can be another method of population control for some populations, but not all, and may raise ethical and cultural concerns. (See also Chapter 9.)

Limited resources, particularly enclosure spaces, also place constraints on population management. While scientific criteria can be used to determine ideal population

sizes, for many species there are simply not enough enclosure spaces available, even on a global scale, to establish viable long-term populations.

Genetic management is concerned with verifying the taxonomic identity of animals, and designing breeding programmes to meet the primary genetic challenges facing zoo populations: the deleterious effects of inbreeding; genetic adaptation to the zoo or aquarium environment (akin to domestication); loss of genetic diversity; and the appearance of deleterious traits. Breeding strategies the primary objectives of which are to minimize loss of genetic diversity (e.g. minimizing mean kinship) in general, address all of these concerns.

Two major challenges to genetic management are uncertainty of the taxonomic status of specimens due to lack of information on their place of origin, and lack of information on relationships among individuals because of missing pedigree information. Inexpensive molecular techniques (e.g. mitochondrial DNA and microsatellite nuclear DNA analysis) are now available for evaluating the systematics of living collections using easily collected samples such as hair and faeces. No doubt the future will bring more techniques that will continue to simplify these analyses, making them increasingly available to institutions worldwide.

The best breeding strategies for maintaining genetic diversity have been developed for populations where relationships among individuals are known and can be calculated from complete pedigrees. However, it is difficult to apply these strategies to populations where parentage is uncertain. Molecular genetics can be used to resolve many of these unknown relationships if there is enough genetic variation and if the critical animals (potential parents and offspring) are still accessible for genetic sampling. When there is little genetic variation, or when samples from key individuals are not available, molecular genetics is often of little help in defining relationships among individuals.

In populations with incomplete pedigrees or species that live in groups where individuals are difficult to distinguish (e.g. in aquariums, in some *ex situ* populations), managing the group, rather than individuals, is often the only option. Population managers are just beginning to develop and evaluate strategies for these group situations. In the future, population management will rely heavily on group management strategies for many populations, both *ex situ* and *in situ*.

Two other genetic issues will become increasingly problematic in future population management. These are the problems of adaptation to the zoo or aquarium environment and the likely increase in appearance of deleterious traits as populations become more inbred.

Genetic adaptation to controlled breeding has long been recognized as an important consideration in population management, yet it is not well understood. Artificial selection, conscious or unconscious, will tend to domesticate animals to some extent over time. Traits under selection may be subtle though significant, such as a

decreased fear response, decreased aggression, or digestion efficiency of an artificial diet. Collection-based environments as well as husbandry techniques have the inadvertent potential to duplicate some of the criteria intentionally used in artificial selection of domesticated stock. This is one of the main reasons that breeding decisions should be based on pedigrees, using strategies like mean kinship to maximize genetic diversity, rather than based on selecting for certain traits. Despite these breeding strategies, artificial selection is still likely to be occurring. Future research will be needed to better understand the potentially critical effect artificial selection has on the long-term future of zoo-based populations and how they contribute to successful conservation of the species (e.g. success of reintroduction programmes).

The appearance of deleterious traits will be increasingly common as populations become inbred over time, as these deleterious recessive genes are a normal part of the genetic variation in populations. Managers must first determine if the appearance of unhealthy traits is due to genetics or environmental effects. Managers should also not immediately assume that the most appropriate strategy is to select against known and potential carriers of the trait. Doing so risks simultaneously removing other desirable genetic variation in the population. Pedigree analyses should be conducted to determine the best strategies for dealing with deleterious traits that appear as populations become increasingly inbred.

Population management cannot succeed without sound veterinary and husbandry management. Successful reproduction usually requires healthy, well-cared-for animals in appropriate environments. Behavioural needs of animals must be met through correct social group structure, exhibit design and enrichment programmes. This is likely to require behavioural research, especially for little-known species. Movement of individuals between institutions intensifies veterinary concerns. Animal transfers are a critical component of population management and involve significant risks of spreading disease. Most species of animals have co-evolved with a suite of organisms that may or may not cause a high level of morbidity or mortality. This normal situation may be altered by placing animals in suboptimal situations (physically, psychologically, nutritionally, etc.) or by exposure to new pathogens from other species (including humans) or conspecifics originating from a different location. Uncompromising care must be taken to reduce exposure of animals to other species or organisms that they would not naturally encounter. Assessing new pathogens requires ongoing research and screening programmes. Zoos and aquariums need well-managed quarantine facilities and protocols to address these concerns adequately.

As with population management in general, regional or multiinstitutional approaches to health screening and management can enhance success and reduce the risks and burden of effort on a particular institution. A tremendous and growing body of knowledge is available through networks of health professionals, such as the IUCN Veterinary Specialist Group, an international network of wildlife and zoo veterinarians, and regional zoo vet organizations (e.g. American Association of Zoo

Veterinarians and the European Association of Zoo and Wildlife Veterinarians).

4.4 Population management tools: databases, ISIS, studbooks and ZIMS

Each zoo or aquarium participating in a population management programme needs to record information on individual animals in its collection in the same manner, using standardized software packages, e.g. Animal Record Keeping System (ARKS) developed by ISIS. The basic data recorded will include place of origin, dates of birth and death, parentage, and offspring, but also information on diet and feeding, health, medical treatments, and breeding habits. This information is essential for a population management programme and often also provides details of the basic biology of little-known species.

ISIS provides the central computer base for animal records collected from, and shared by, its world membership of over 600 institutions (Box 3.2). By using ARKS, member institutions can electronically transfer data direct to the ISIS database.

Records for particular species are also kept in studbooks, either internationally, regionally or nationally. Studbooks are often the most accurate datasets for species because they are maintained by a studbook keeper who is responsible for collecting, verifying, editing and publishing the studbook. International studbooks come under the jurisdiction of WAZA, and regional or national studbooks are the responsibility of the relevant zoo association. ISIS annually produces and distributes a CD-ROM that contains the latest editions of studbooks sent in by studbook keepers. The 2003 Studbook CD-ROM contained data from 281 institutions in 47 countries and lists 903 regional and 167 international studbooks, plus 87 husbandry manuals. This is a considerable increase since the 1993 World Zoo Conservation Strategy and is partly a reflection of an increase in questionnaire response but it also reflects a real increase in the number of studbooks.

In addition to the software used to manage animal data, there are various specialized software packages for analyzing studbook data and developing management recommendations, e.g. REGASP, PM2000 and MateRx.

The current system of maintaining multiple duplicate databases is an inefficient use of resources and there is now an exciting new development, to be run by ISIS, for a comprehensive and integrated web-based information system to support a wide range of animal management and conservation activities. This system, the Zoological Information Management System (ZIMS), will be accessible online and through stand-alone record keeping stations. (See Chapter 3, and Box 3.2)

4.5 Organization of cooperative breeding programmes

Cooperative breeding programmes can be organized and administered at global or regional levels. Regional programmes are often preferred as animals are usually more easily transferred within regions (e.g. within the European Union). Zoos and aquariums in different regions may have different conservation priorities.

Several regions also actively develop regional collection plans that identify priority taxa to breed and to allocate regional resources. Target population sizes are defined for each taxon in the plan to optimize the use of zoo spaces, and participating institutions incorporate these regional collection plan guidelines into institutional collection planning. Priorities for selecting species may include many factors such as:

- degree of threat to the wild populations, i.e. IUCN categories of threat;
- taxonomic uniqueness;
- species native to a region;
- species with established husbandry protocols;
- species with already established and healthy populations;
- flagship species;
- educational and research value.

The software REGASP (Regional Animal Species Collection Plan) was developed by the Australasian Regional Association of Zoological Parks and Aquaria, to assist zoos with institutional collection planning. REGASP combines information from institutional animal records with data on regional collection goals so that zoo and aquarium managers can find regionally and globally produced collection recommendations during their planning process. REGASP is distributed worldwide as part of the ISIS suite of animal management software.

The IUCN Species Survival Commission has a network of Specialist Groups which deal with particular taxa and assist in setting priorities for conservation activities.

4.6 Global cooperative breeding programmes

Global cooperative breeding programmes, which exist for some species, have international studbooks and an international species coordinator, who evaluates the roles of individual animals, institutions and regions from a global perspective. These programmes may be operated under the authority of a national government that may own all or most of the animals in the breeding programme.

Global programmes can maximize the management potential of collection populations by avoiding possibly conflicting or even competing goals and recommendations among regions. For example, attempts to establish regional programmes for some species in range regions could be jeopardized by the removal of genetically important animals to supply programmes in other regions. Likewise, one regional programme may send surplus stock (and genetically unimportant animals) to other regions that, when they mobilize their resources to set up their own regional management programmes, suddenly discover that their founder stock is of little genetic value from a global perspective. In some taxa, it may be that a coordinated effort by several regions is needed to maintain a healthy and viable population. In other cases, each region may be able individually to maintain a viable population of one subspecies or species of a broader taxon for which several taxa are in need of management. Coordinated allocation of resources among the world's zoos and aquariums is needed to avoid fragmentation of resources or unnecessary duplication of effort.

4.7 Ownership and population management

Ownership of animals continues to be an important aspect of the structure and implementation of cooperative breeding programmes. With some programmes, ownership remains with the government of the range states and the original stock and all descendants are on loan; ownership is therefore not usually an issue in population management. Other programmes make animal transaction recommendations but ignore ownership, leaving it up to the individual institution involved to determine if animals are lent, traded or sold/purchased. The benefits of lending animals include retaining ownership of genetically valuable specimens and engaging in reciprocal loan agreements between institutions, thereby increasing access to a larger variety of specimens for the collection.

Some zoos however, have to rely on the revenues from the disposal of animals to finance, at least part of, their breeding programmes. This complicates transactions between institutions and may limit the efficiency of cooperative breeding programmes, as these zoos may prefer to sell animals rather than turn them over to the coordinator's management authority. Strong conflicts of interest may develop in zoos and aquariums with high financial interests in the population under management. They may be unwilling to follow through on recommendations to stop breeding, or to send specimens to other institutions to breed with non-owned specimens. These issues are particularly pertinent when cooperative breeding programmes include private individuals. Species coordinators need to evaluate the costs and benefits of including in the programme those institutions, public or private, with commercial interests in the species being managed. While such participants may hold and make available (at a cost) genetically valuable stock, their commercial interests may otherwise complicate or even damage the credibility of the programme. (See also Chapter 9.)

4.8 Confiscated and abandoned animals

A problem for some breeding programmes is confiscated or abandoned animals. These may have been illegally held as pets or confiscated as illegally imported. They may be animals rescued and turned over to wildlife authorities or they may be problem wild animals removed by wildlife authorities to avoid human/animal conflicts. When assimilating confiscated and abandoned animals into a breeding programme the following points should be considered:

- questionable health, disease risks;
- questionable origin because of lack of a life history (wild born, wild-caught, taxonomy);
- questionable relationships among individuals in confiscated groups.

On the other hand, healthy confiscated or rescued wild-caught animals can provide a breeding programme with an opportunity to refresh the founder stock, or replace post-reproductive old animals with young breeders. Most breeding programmes have not been established with an adequate number of founders and the periodic inclusion of new unrelated animals may be a bonus for such programmes. Every effort must be made, however, to

ensure that any individuals that are included are healthy, of known taxonomy, wild born (or, if collection born, their relationship to the population is known) and appropriately placed. WAZA and the IUCN have developed detailed guidelines for zoos and aquariums, and wildlife authorities, for dealing with confiscated animals (available from WAZA, and at the IUCN web site www.iucn.org).

4.9 National and international regulations

Intensive population management serving conservation goals requires transfers of animals. This includes: exchanges of animals between the sub-units of the *ex situ* population; introduction to existing *ex situ* populations of animals from the wild for genetic reinforcement; establishing new *ex situ* populations with wild animals; and the interactive exchange of animals between *in situ* and *ex situ* populations for mutual reinforcement. Many of these transfers - planned in the framework of species conservation - involve the crossing of national and continental borders.

Zoos and aquariums must comply with national and international legislation with respect to animal transfers. However, for the sake of effective population management, which is crucial to species conservation, existing and pending legislation should be adapted and developed to leave open ample possibilities for the transfer of animals and genetic material between registered zoos and aquariums and between *in situ* and *ex situ* populations. It is the processes required for the implementation of legislation, such as those listed below, that can unfortunately be time-consuming and complicated, and thereby cause unnecessary delays:

- CITES regulations and related national and international legislation, regulating imports and exports of animals of endangered species;
- national legislation restricting the imports of animals (both domesticated and wild) in order to prevent the introduction of diseases;
- national legislation or conservation codes regarding the removal or reintroduction of animals from or to a natural habitat;
- national legislation developed as a result of the Convention on Biological Diversity (CBD) concerned with the control of bio-piracy, and a nation's sovereign rights over biodiversity;
- national legislation aimed at preventing the introduction of alien species that have invasive potential.

4.10 *In situ* and *ex situ* population management: metapopulation management plans

A primary goal of cooperative *ex situ* breeding programmes for threatened and endangered species is to support *in situ* conservation. This may be through rescue of species imminently threatened with extinction in the wild, through research, education, or promotion efforts that support *in situ* populations, or simply as genetic and demographic reservoirs serving as backups for endangered wild populations.

A useful model for describing the potential relationships between *ex situ* and *in situ* population management is the metapopulation management model, a set of interacting populations being managed under one conservation goal

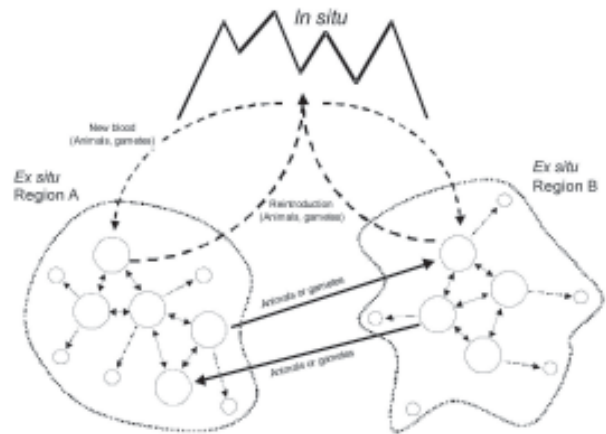


Figure 4.1. Metapopulation management involves managing a set of interacting populations, both *in situ* and *ex situ* under a common conservation goal. This may involve any number of components: exchanges among larger breeding institutions (large circles); disposition of post-reproductive or nonbreeding animals in peripheral institutions (smaller circles and dotted lines); transfer of animals between regions; reintroduction of zoo-born animals into native habitats; and periodic transfer of wild animals to the *ex situ* population. With future advances in reproductive technology, transfer of genes among units of the metapopulation could be through animal or gamete transfer.

(Figure 4.1). Components of a metapopulation management plan may include multiple regional *ex situ* populations (or a global *ex situ* population), in-country breeding programmes, multiple wild populations, reintroduced populations, vacant habitat suitable for reintroductions and even genome banks. Population management is accomplished through transfers between institutions in the *ex situ* population as discussed above, reintroduction of zoo-bred animals into the wild, translocation of animals among wild populations, and, for genes, artificial insemination, or embryo transfer technologies. The role of the *ex situ* populations can vary from simply serving as a static genetic and demographic reservoir for the species, with little interaction with wild populations, to populations with extensive gene flow in both directions (reintroduction and periodic acquisition of new founders).

In situ populations often face problems similar to those of *ex situ* populations – small founder base and overall population size, limited gene flow, possible hybridization issues, overpopulation (exceeding carrying capacity) and the need for human intervention. The science of small population management developed primarily for managing *ex situ* populations will need to be applied to these *in situ* populations to enhance their viability. Zoos and aquariums will be in a strong position to supply this expertise and should look for opportunities to do so.

Reintroduction is an obvious and important component of the relationship between *ex situ* and *in situ* conservation, though it remains a challenging task. (See also Chapter 2.)

Recommendations

The World Zoo and Aquarium Conservation Strategy (WZACS) recommends that all breeding programmes for

threatened species in zoos and aquariums be managed as global or regional cooperative programmes with participating zoos and aquariums sharing a set of specific programme objectives. Regional programmes should link together to address global conservation strategies. Global or regional studbooks or equivalent databases need to be maintained for these species. Where resources allow, breeding programmes for non-threatened species should also be monitored and managed.

The WZACS recommends that all breeding programmes in which zoos or aquariums are involved should be quantitatively and objectively evaluated in terms of their objectives, status and viability.

The WZACS strongly recommends that all breeding programmes should be based on sound science and management using the latest available knowledge on population management, reproductive biology, genetics, animal behaviour, nutrition, veterinary care and husbandry standards.

The WZACS reminds all zoos and aquariums and local, regional and national authorities that they would find it useful to consult the 'WAZA Guidelines on the acceptance of seized or confiscated animals' before accepting confiscated animals.

The WZACS urges all zoos and aquariums to continue to support the scientific development of population management, particularly for taxa held in group situations (e.g. fish, invertebrates and micro-organisms), or species facing specific challenges, such as disease.

The WZACS reminds all zoos and aquariums that they are expected to maintain critical animal records on their collections and contribute these data to the ISIS database and studbooks in a timely and comprehensive manner. The WAZA and regional associations must continue to explore economically viable methods for institutions in developing countries to participate fully in this process.

The WZACS calls on all zoos and aquariums to link their collection planning with regionally or globally identified conservation priorities working in collaboration with the IUCN Species Survival Commission's taxonomic and species advisory groups.

The WZACS calls upon legislators and enforcers to make sure that the processes of implementation involved in the transfer of animals and genetic materials between zoos and between aquariums are completed as speedily as possible.

WZACS is, or should be, for ALL Zoos (or) Let's take the "Con" out of zoo conservation

Zoo Outreach Organisation and the South Asian Zoo Association, both members of WAZA, have taken a very active role in trying to promote WZACS and its implementation to South Asian zoos and aquaria. We now have a special mission to promote the notion that ALL zoos, not just zoos with a surfeit of resources, and, at least, all those zoos that WANT to be ethical and caring and "righteous", need to be *active partners* in all aspects of this movement.

Therefore, the interpretation of what WZACS says is very important. WZACS has adopted an IUCN definition of conservation which is "*Conservation is the securing of longterm populations of species in natural ecosystems and habitats wherever possible.*"

This definition is more or less what we often refer to as "field conservation" or *in situ* conservation. How do zoos from our part of the world achieve that? When zoo personnel continue to think that just by holding an animal they are "conserving" it, no matter where it came from (a trapper, dealer or a bad zoo), and no matter its living conditions, some zoos will see no discrepancy. There is, however, a big difference in merely having wild animals and contributing to conservation. The purpose of this article is to set right misguided thinking on this issue.

The environmental and wildlife crises which are taking place now all over the world should suggest to all zoo, wildlife and environmental institutions that they should

make the most of their unique ability to promote awareness and lend whatever their expertise to the goal of protecting, renewing and/or sustaining habitat and the wildlife within.

As mentioned before WZACS more or less defines conservation as "field conservation". According to Miranda Stevenson, Director of the British Association of Zoos and Aquaria and also the Coordinator of WZACS, "the reason for the emphasis on *in situ* conservation in WZACS is two-fold (i) true conservation can only take place in the natural environment and therefore the 'securing of long-term populations, etc. must be the long term goal of any programme, and (ii) keeping animals in captive environments without this goal can hardly be considered conservation – more accurately this would be preservation only! Some preservation efforts (Pierre David's deer, Przewalski's horse, etc.) started off as preservation and ended up as conservation, however, zoos have been criticized by the anti-zoo lobby and even some conservationists for putting the "con" into conservation, and where a zoo claims to be doing conservation simply by holding a species – there is some justification for this criticism! Also as Sally describes subsequently, buying animals from dealers and irresponsible breeding can be actually detrimental to conservation, as can keeping them in inadequate captive environments."

WAZA is right to promote this definition. Keeping wild animals in institutions, when their habitat has been allowed to degrade and disappear, makes very little or no sense at