NEI, M., MARUYAMA, T. & CHAKRABORTY, R. (1975): The bottleneck effect and genetic variability in populations. *Evolution* 29: 1–10.

SEAL, U. S. (1984): An analysis of the demography and genetics of captive Amur tigers and a preliminary captive propagation plan (*Panthera tigris altaica*). In *Internationales Tigerzuchtbuch 1984*: 5-18. Seifert, S. & Müller, P. (Eds). Leipzig: Zoologischer Garten Leipzig. SOULÉ, M. E. (1980): Thresholds for survival: maintaining fitness and evolutionary potential. In *Conservation biology*: 151–169. Soulé, M. E. & Wilcox, B. A. (Eds). Sunderland, MA: Sinauer Associates.

WEMMER, C. (1983): Sociology and management. In The biology and management of an extinct species, Père David's deer: 126–132. Beck, B. B. & Wemmer, C. (Eds). Park Ridge, NJ: Noyes Publications.

Int. Zoo Yb. (1986) 24/25: 174-179

Goals of captive propagation programmes for the conservation of endangered species

U.S. SEAL

VA Medical Center, Minneapolis, Minnesota 55417, USA

Interest by the conservation community in the use of captive propagation for the conservation of endangered species of vertebrates has increased during the past five years (Conway, 1980; Soulé & Wilcox, 1980; Frankel & Soulé, 1981; Schonewald-Cox et al., 1983). Wild populations are under severe pressures. Conservation measures are providing temporary relief, but many populations are becoming so diminished and fragmented that they are not viable for two to ten generations much less on an evolutionary time scale. The survival of the Amur/Siberian tiger Panthera tigris altaica, the European bison Bison bonasus, the Sumatran rhinoceros Dicerorhinus sumatrensis, and many others will depend upon captive populations and propagation programmes.

Organised collaborative captive breeding programmes sponsored by professional zoo organisations are developing in North America (Foose, 1983) and the United Kingdom. Others organised around particular species are developing in Europe and Australia. A series of propagation plans, meetings on population genetics of small populations, and workshops on the application of these principles to the practical problems of a captive population have begun to delineate agreement on the scientific fundamentals for the development of workable species survival plans.

The clear and explicit definition of the goals of a captive propagation programme in the conservation of a species is the first task in every case. It is the single most important policy decision to be made and it will influence every aspect of the work. Confusion over goals will be detrimental to the efficient long-term captive propagation of the species and ultimately, therefore, to its survival. The options range from maintenance of stock suitable for wild habitat stocking and reintroduction to production of zoo-adapted 'domesticated' species.

The goal of a programme designed to maintain stock suitable for return to wild habitats may be stated as 'maintenance of the maximum amount of genetic diversity available in the founder stock that has evolved in the wild populations' (Flesness, 1977; Foose, 1983). The captive and wild populations must be managed to provide an effective population size which is sufficient to allow maintenance of a specified amount of genetic diversity for the planned duration of the programme (Denniston, 1978; Franklin, 1980; Senner, 1980), together with sufficient numbers of animals within the appropriate sex and age distributions to protect against loss due to demographic fluctuations (Foose, 1980; Goodman, 1980).

Calculation of the rates of loss of genetic diversity, generation by generation, for any given set of starting conditions can be made rather easily. However, the time scale of a captive propagation programme has rarely been a definite part of policy for development of the detailed plan. The decision on the time scale of the programme and the allowable rates of loss of genetic diversity will determine the population size (N) that must be maintained to achieve these goals.

This policy implies a criterion for termination of a programme based upon the secure existence of wild populations of the taxon of such size as to allow long-term survival and for evolution by natural selection of the taxon.

How are such goals to be defined and achieved?

Two biological problems must be confronted if we are to develop captive breeding programmes for preservation of endangered species.

1. The first is an assessment of priorities for selection of taxa and allocation of resources to the taxa in greatest need of sanctuary in zoo-based captive breeding programmes. The captive habitat - our ark - is limited. The criteria for selection include: the animals' rarity in the wild, their taxonomic uniqueness, and their fitness for captivity. The development of criteria that can be used for quantitative evaluation of candidates for captive propagation that is being undertaken by the IUCN Captive Breeding Specialist Group and other organisations using information from the IUCN Red data books and ongoing field studies.

2. The second important consideration is the management of the captive collections as biological populations. A necessary beginning is the determination of our captive carrying capacity. The components of carrying capacity include logistic, conservation and genetic criteria. The logistic criterion perhaps places an upper limit on the 'mega' of the charismatic 'megavertebrates' since the Blue

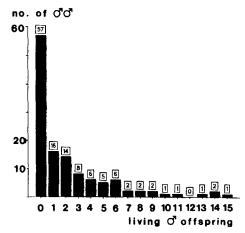


Fig. 1. Variation in number of living 3 Siberian tiger *Panthera tigris altaica* offspring born before 1974 from 3 parents. Only 33 aged eight years and over were considered for tabulation in the zero offspring category.

whale Balaenoptera musculus is not yet on exhibit. The conservation interest appears to be an attempt to conserve as many species as possible within, as yet, undefined limits. A crucial aspect of carrying capacity is the minimum number of animals of a species necessary to meet our propagation objectives. A key concept is 'effective population size' (N_e) , a measure of that proportion of the census population which is contributing to the next generation.

Factors affecting the effective population size are (1) the number of 33 and 99 that reproduce, (2) the sex ratio of the breeding animals, and (3) the variance in the life-time family size of the reproducing animals. The most critical factor in most 200 populations is variance in family size. Examples of severe variation in family size are available from the studbooks for the Tiger Panthera tigris ssp and the Gorilla Gorilla gorilla (Seifert & Müller, 1983; Kirchshofer, 1982). Among the tigers there have been many 33 which have sired no offspring and of the remainder only a few with many surviving young (Fig. 1); the picture for $\mathcal{Q}\mathcal{Q}$ is similar but not quite as extreme. The result is that this species is being managed at about 30% of the possible genetic efficiency. This means that much of the space used to house Siberian tigers is

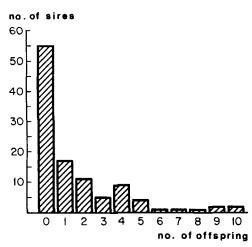


Fig. 2. Variation in number of Gorilla Gorilla gorilla offspring of both sexes from 3 parents. Only 33 aged ten years and over were considered for tabulation in the zero offspring category.

being wasted from a conservation point of view. A similar disparity in family sizes has occurred in the Western lowland gorilla G. g. gorilla although for different reasons. The result, however, is the same in terms of the \Im gorillas in North America 53 have sired 173 offspring with seven \Im responsible for 59 of the births (Fig. 2), and 55 \Im have never produced offspring. The family size of \Im gorillas is less skewed, although 12 \Im have produced 60 births and 53 \Im have not produced offspring.

What are some of the reasons and consequences of these unequal family sizes? As the International tiger studbook records (Seifert & Müller, 1976–1983), the number of living Siberian tigers in zoos has increased to about 1200 animals. Nearly all of these are captive born and most of the wild-caught animals are in the USSR. The number of potential founders or wild-caught animals is more than 60. However, the distribution of founder representation in the living tiger population shows that six animals have contributed about 70% of the genes (Seal, 1984). This means that much of the original genetic diversity is either lost or very poorly represented. One consequence has been a

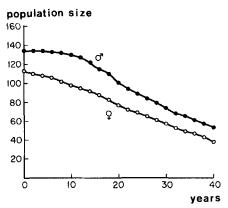


Fig. 3. Demographic projections for the Gorilla population in North America based on mortality and fecundity figures derived from this group with particular emphasis on its most recent five years.

relatively high level of inbreeding in the population dating from 1965.

The gorillas present a different picture. Demographic analysis of data from the studbook (Kirchshofer, 1982) and from ISIS for more recent years, indicates that gorillas are in serious trouble in North America with a forecast of a declining population (Fig. 3). Why? The population age and sex structure shows a steady recruitment of captive-born young into the population but not in sufficient numbers to match the projected losses. The population includes a number of gorillas older than 20 years. Examination of the age distribution of sires makes it evident that most of the production is by younger animals and that few young have been produced by animals older than 20 years. The picture has been strikingly similar for $\mathcal{Q}\mathcal{Q}$ with few animals older than 20 years giving birth. If we plot the age distribution of those individuals that have never produced young and look at that portion in the mature age groups we find that many of the older gorillas have been totally non-productive (Fig. 4). The effective population size is smaller than the census population and a reproductive failure of both sexes appears to be a major factor.

A second determinant of the size of populations that must be maintained is 'for how long do we plan to preserve the species by captive propagation?' We can calculate the

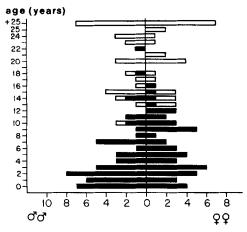


Fig. 4. Age structure of living non-reproductive \Im and \Im Gorillas in North America based on the international studbook (Kirchshofer, 1982), ISIS figures and a current survey of institutions. The captive-born proportion is indicated by black bars, and the wild-born proportion by unshaded bars.

decline of genetic diversity for different N. over many generations. The number of years, the number of founders, and the size of the stable population chosen as an objective for the programme will determine the number of generations and the rate of decline. Thus, if we choose to plan for 200 years then the number of elephant generations may be only eight or nine whereas for tigers it may be about 40 and for mice 300 to 400 generations. If we set a criterion of maintaining 90% of the available genetic diversity in the population from the time it reaches the effective population size, then the population size required for tigers may be 180 to 200, for elephants about 25 to 50, and for mice perhaps 1300 + .

These results indicate that efficient genetic management can increase the number of taxa that can be propagated in zoos for conservation. International collaborative programmes can further increase the number of species that can be propagated. Indeed if full use were made of available resources, perhaps all of the endangered species of megavertebrates could be maintained.

Another early step is the estimation of the amount of captive habitat available. Estimates

for North American zoos have been constructed from ISIS data and are being constructed for the world's zoos with the data from the International zoo yearbook. By way of example, at one time approximately 82% of 32 000 mammal specimens in ISIS were primates, ungulates, or carnivores. Of the 5600 carnivores about 51% (3880) were felids and 60% (1750) of these were big cats. If we further examine the last figure we find that nearly half of the available living spaces were occupied by some 450 tigers and 380 lions. There are 82 extant named subspecies of the big cats and 45 of these are listed in the Red data book. Thus if we choose to maintain an effective population size of 100 animals we might maintain 18 forms in these same zoo spaces whereas only seven forms can be propagated if we require an effective population size of 250. The problem is more severe if we cannot manage with the effective population (N_{a}) size about equal to the census population (N), an objective number which has not been accomplished very often with traditional management procedures.

The tigers provide an example of the complex dilemma faced by captive breeding for conservation (Seal & Foose, 1984). There are eight named forms of the tiger. Should all of these forms be maintained in captive populations? How many? Which ones? A mixture? How to choose? When to choose? North American zoos currently maintain about 500 tigers with half *P. t. altaica*, about 40% *P. t. tigris*, a few *P. t. sumatrae* and *P. t. corbetti*, and the remainder of unknown or mixed ancestry.

The subspecies problem will become increasingly serious as each new request for captive breeding for conservation is examined. It will require additional research and the use of available techniques including chromosomal analyses, molecular studies (Ryder *et al.*, 1981, see also this volume; O'Brian *et al.*, 1983), and careful genetic analysis of pedigree information seeking evidence for inbreeding and heritability effects on components of fitness (Ralls *et al.*, 1979; Templeton & Read, 1984).

All of these analyses and programmes depend on the consistent collection and

reporting of data. The correct kinds of data are essential (Seal & Flesness, 1979); essential elements for genetic and demographic analysis, and for management are (1) birth date, (2) death date, (3) sex, and (4) parentage (including parents' age at birth of offspring). This requires identification of individuals. The main collective sources of these data are the international studbooks and ISIS.

All management programmes are going to require the continued development of the international studbooks including the use of available technology for collection, distribution and analysis of the data that are necessary for scientific captive population management. Given the current projections for the rate of loss of habitat through expansion of human populations one can predict that by the year 2000, zoos will be almost entirely dependent upon captive breeding to supply their exhibit animals and that most captive species will need to be carefully managed. This implies the need for about 500 studbook-like programmes: overwhelming perhaps, but possible.

Indeed, if we agree that the preservation of genetic diversity (IUCN, 1980) is our unique responsibility to our children's children, then we will need to spend the time necessary to work through the practical problems until our friends, the reproductive biologists, can provide us with a full zoo in the freezer, and the surrogates to produce new specimens at that time in the future when reintroductions will be possible. It is the intention of the Captive Breeding Specialist Group of the IUCN/SSC to provide an international forum for the development of collaborative plans for captive propagation programmes designed for species survival.

Not to act is to act. The necessity for action always presents the possibility of unpleasant alternatives but it is possible to construct a safe-to-fail strategy which allows the opportunity for many trials and failures. The rewards are for us, our children and grandchildren.

REFERENCES

CONWAY, W. G. (1980): Where we go from here. Int. Zoo Yb. 20: 184–189.

DENNISTON, C. (1978): Small population size and genetic diversity: implications for endangered species. In Endangered birds: management techniques for preserving threatened species: 281–289. Temple, S. A. (Ed.). Madison: University of Wisconsin Press.

FLESNESS, N. R. (1977): Gene pool conservation and computer analysis. Int. Zoo Yb. 17: 77-81.

FOOSE, T. J. (1980): Demographic management of endangered species in captivity. Int. Zoo Yb. 20: 154-166.

FOOSE, T. J. (1983): The relevance of captive populations to the conservation of biotic diversity. In *Genetics and conservation*: 374-401. Schonewald-Cox, C. M., Chambers, S. M., MacBryde, B. & Thomas, W. L. (Eds). Menlo Park, CA: The Benjamin/Cummings Publishing Co. Inc.

FRANKEL, O. H. & SOULÉ, M. E. (1981): Conservation and evolution. Cambridge: Cambridge University Press.

FRANKLIN, I. R. (1980): Evolutionary change in small populations. In *Conservation biology*: 135–149. Soulé, M. E. & Wilcox, B. A. (Eds). Sunderland, MA: Sinauer Associates.

GOODMAN, D. (1980): Demographic intervention for closely managed populations. In *Conservation biology*: 171-195. Soulé, M. E. & Wilcox, B. A. (Eds). Sunderland, MA: Sinauer Associates.

IUCN (1980): World conservation strategy. Gland: International Union for the Conservation of Nature and Natural Resources/United Nations Environmental Program/World Wildlife Fund.

KIRCHSHOFER, R. (1982): International studbook of the gorilla Gorilla gorilla (Savage and Wyman, 1847). 3. Frankfurt: Frankfurt Zoological Gardens.

O'BRIAN, S. J., WILDT, D. E., GOLDMAN, D., MERRIL, C. R. & BUSH, M. (1983): The cheetah is depauperate in genetic variation. *Science, Wash.* 221: 459–462.

RALLS, K., BRUGGER, K. & BALLOU, J. (1979): Inbreeding and juvenile mortality in small populations of ungulates. *Science, Wash.* 206: 1101–1103.

RYDER, O. A., BRISBIN, P. C., BOWLING, A. T. & WEDEMEYER, E. A. (1981): Monitoring genetic variation in endangered species. In Evolution today: Proceedings of the second international congress of systematic and evolutionary biology: 417-424. Scudder, G. G. E. & Reveal, J. L. (Eds). Pittsburgh, PA: Hunts Institute for Botanical Documentation, Carnegie-Mellon University.

SCHONEWALD-COX, C., CHAMBERS, S. M., MACBRYDE, B. & THOMAS, W. L. (Eds) (1983): Genetics and conservation: a reference for managing wild animal and plant populations. Menlo Park, CA: The Benjamin/Cummings Publishing Co. Inc.

SEAL, U. S. (1984): An analysis of the demography and genetics of captive Amur tigers and a preliminary captive propagation plan (*Panthera tigris altaica*). In *Internatio-nales Tigerzuchtbuch 1984:* 5–18. Seifert, S. & Müller, P. (Eds). Leipzig: Zoologischer Garten Leipzig.

SEAL, U. S. & FLESNESS, N. R. (1979): Noah's ark — sex and survival. *Proc. AAZPA Conf.* 1978: 214–228.

SEAL, U. S. & FOOSE, T. J. (1984): Siberian tiger species survival plan: a strategy for survival. *J. Minn. Acad. Sci.* 49: 3 9. SEIFERT, S. & MÜLLER, P. (1976–1983): Internationales Tigerzuchtbuch 1976–1983. Leipzig: Zoologischer Garten Leipzig.

SENNER, J. (1980): Inbreeding depression and the survival of zoo populations. In *Conservation biology*: 209–224. Soulé, M. E. & Wilcox, B. A. (Eds). Sunderland, MA: Sinauer Associates. SOULÉ, M. E. & WILCOX, B. A. (Eds) (1980): Conservation biology: an evolutionary-ecological perspective. Sunderland, MA: Sinauer Associates.

TEMPLETON, A. R. & READ, B. (1984): Factors climinating inbreeding depression in a captive herd of Speke's gazelle (Gazella spekei). Zoo Biol. 3: 177–199.

Int. Zoo Yb. (1986) 24/25: 179-188

The reintroduction of the Arabian oryx

Oryx leucoryx

into Oman

M. R. STANLEY PRICE

Office of the Adviser for Conservation of the Environment, P.O. Box 246, Muscat, Oman

The Arabian or White oryx Oryx leucoryx has for many years symbolised man's success at exterminating a species from the wild by direct persecution, usually hunting. The last herd in Arabia was eliminated in Oman in 1972 (Henderson, 1974). The steps which were taken ten years before, in anticipation of this event and which led to Operation Oryx and the establishment of the World Herd in the USA, are fully described by Fitter (1982). He also summarises the actions leading up to and following the decision to release oryx into the deserts of central Oman with the aim of re-establishing a free-living, viable population. This paper describes this project from the arrival of the first oryx back in Oman in March 1980 to August 1984.

THE REINTRODUCTION AREA

The Jiddat-al-Harasis is a flat plain of Cretaceous limestone occupying much of central Oman (Fig. 1), lying between the wadis which drain the north side of the Dhofar mountains and the wadis flowing south from the interior face of the Jabal Akdhar range. To the north and west, the Jidda' is bounded by the sand seas of the Rub'-al-Khali, and to the east by the Huqf escarpment. Between the Jidda' and the Indian Ocean is a narrow coastal plain.

The reintroduction area is a distinct ecological unit of about 25 000 km² at the eastern side of the Jiddat-al-Harasis. It is distinguished by its well-developed vegetation which dwindles to the west, to be replaced by relatively barren desert.

This area, which is by no means the total oryx habitat in Oman, is a stony desert with little surface sand. It has no natural permanent water source except for a few brackish seepages and hand-dug wells at the foot of the Huqf escarpment. It has an internal drainage system, and water retention following rain is often poor because of sink-holes in the numerous pans and depressions. The only sources of potable water are at Al-Ajaiz and Haima. The latter is a Tribal Administrative Centre on the main road through the country. The project camp is at Yalooni, 80 km due east of Haima.

The climate is extreme, and rainfall so erratic in time and place that averages mean little. The air temperature varies by $15-20^{\circ}$ C each day of the year, and the mean summer minimum is approximately the mean winter maximum (Fig. 2). Recorded extreme shade temperatures are 7° and 48° C. Especially in