THE CONTROL OF ZOO POPULATIONS WITH SPECIAL REFERENCE TO PRIMATES

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Modern zoos are increasingly successful in maintaining and breeding exotic species. Many of the animals bred in captivity cannot be housed in their natal zoo nor in other recognized zoos in the region. These 'surplus' animals create a problem as zoos only have limited space at their disposal. The options open in this situation are to avoid the problem by preventing the animals from breeding (sterilization or contraception) or to dispose of the surplus animals (euthanasia; or transfer either to institutions not recognized by any national zoo federation or to a zoo outside the region, possibly using the services of an animal dealer). The pros and cons of all these options are evaluated in terms of practicality, welfare and ethics. In many cases, the judicious use of a combination of contraception and euthanasia would seem the most acceptable choice from an animal welfare point of view. Nevertheless, it is believed that considerably more research is needed into the methods and welfare aspects of contraception and sterilization.

Keywords: *animal welfare, contraception, euthanasia, zoo population control*

Introduction

Zoos have traditionally been regarded as institutionalized consumers of wildlife: organizations which import animals from the wild for motives of public entertainment and profit. This was certainly true in the past, when the import of newly captured animals from the wild was relatively unrestricted. The ease with which replacement stock could be imported meant that there was no incentive for zoos to breed animals, so they often did not even try. However, the situation has changed radically in the last 20 years. The ratification of the International Convention on the Trade in Endangered Species (CITES) by most nations has forced even the most recalcitrant zoos either to revise their policy on captive breeding or go out of business. Today, the majority of animals which visitors encounter on a typical zoo trip have never seen the wild. They have been born in a zoo setting, possibly as the result of one of the many dedicated breeding programmes.

Over the years, zoos have developed considerable expertise in the management and breeding of exotic species. This skill means that today's zoo animal generally breeds better and lives longer than its forbears, even those which lived in the wild. While on the one hand this represents a very positive achievement for the zoo community, on the other it is fast becoming a burden as finding suitable accommodation for zoo-born animals is becoming

increasingly difficult. Animals which cannot be kept in their current zoo and for which no acceptable accommodation can be found in other zoos, are defined as surplus[1]. Lindburg (1991) identified the problem of surplus animals as *the zoo issue* of the 1990s. In the following article the various ways of dealing with this problem will be evaluated.

Contraception obviously plays a key role in controlling zoo populations. Reviews of the various available alternatives already exist in the literature (Munson 1993; Gerlofsma 1994; Porton 1995; Asa *et al* 1996) and will not be repeated here. One such review, Sainsbury (1997), even deals specifically with the problem of population control in captive primates. However, as it focused on the callitrichids, the conclusions and recommendations are only of limited application to other (primate) taxa.

The marmosets and tamarins are unusual among zoo animals as they represent a group of small-bodied species which are best maintained in monogamous family groups. In these families, the reproduction of subordinate adults is naturally suppressed. As a consequence of their biology, 'surplus' callitrichids can remain in their natal groups for some considerable time. A similar social organization (ie young remaining with the natal group for several years as non-breeding members) is found in some other taxa: among canids(in the wolf, *Canis lupus*, the African hunting dog, *Lycaon pictus*, and in some jackals; see Moehlman 1989); in the gibbons, *Hylobates* spp; and, in its most extreme form, in the naked mole rat, *Heterocephalus glaber* (Jarvis 1981). However, most of these are large-bodied species which means that, when offspring are eventually evicted from the natal group, they cannot be as easily or cheaply housed in 'temporary' accommodation as a callitrichid.

The majority of species held in zoos do not lend themselves to this type of management. Not only are they physically larger and stronger than callitrichids, but they may not suffer the presence of the sexually mature offspring. The ursids are a good example of this. In those species where maturing offspring are tolerated by their parents, reproduction may not necessarily be suppressed. For example, in species which have a 'harem' social structure (eg gorillas, *Gorilla gorilla* spp; various langurs, *Presbytis* spp and the majority of ungulates) adult daughters are often tolerated by their parents. In zoos they are often left in their natal group but they have full reproductive capacity and can breed – even with their fathers.

A further consequence of the harem social structure is that maturing males are not usually tolerated by their fathers. In captivity, they must be removed from their natal group to avoid severe aggression. The fact that only one male can be housed with a group of females means that the majority of zoo-born males will never be required to join a breeding group and are, therefore, 'surplus'.

Ways to decrease or avoid the problem of 'surplus' animals

Simply stated, there are two ways in which a zoo can overcome the problem of surplus animals: they can eliminate excess animals, or avoid producing animals which are not required. Organized breeding programmes are particularly relevant in the latter context, as they control the production and distribution of animals.

[1] Reintroduction is not specifically mentioned here as this is generally not a valid option. If reintroduction were feasible most zoos would certainly consider it.

Breeding programmes

Cooperative breeding programmes have been established to ensure the long-term survival of particular species in captivity. They are based on sound genetic and demographic principles and are designed to ensure that a viable, genetically diverse population is maintained for a predetermined number of generations. These breeding programmes are organized on a regional basis (eg within Europe or North America). Within each region a selected group of experts coordinates the programme for a particular species. This team recommends which animals should go to which zoo, how many young are produced and from which parents. Zoos participating in such programmes do so on a voluntary basis and animals are often lent to participating institutions rather than being traded commercially. Where such programmes are active, they usually ensure that young are born in response to the needs and requirements of the zoo population as a whole, rather than on the whim of a particular holding institution. This approach substantially reduces, but does not eliminate, the production of surplus animals.

Unfortunately, these coordinated breeding programmes are essentially restricted to the management of rare or endangered species, where there is a perceived need to protect against extinction. They deal only with a small percentage of zoo animals; for example, in 1993 there were 267 primate taxa maintained in European zoos (Schmidt & Stevenson 1993), of which only 23 (9%) were managed by breeding programmes (Rietkerk *et al* 1995). Breeding programme management is relatively labour-intensive – with each programme coordinated by a team of 8-10 people. Given this level of involvement, some 2500 people would be required to coordinate the programmes just for the primates. Although breeding programme management is not a full-time occupation, clearly this is still not feasible; the zoo workforce is insufficient to carry the burden.

Creating more space

There is current discussion of ways to rationalize zoo collections. The favoured idea is to hold larger populations of fewer species. This would lead to better management and healthier populations. Groups of experts referred to as Taxon Advisory Groups (TAGs) would advise zoo managers on which species they should maintain and which to phase out. It is often suggested that such a step might eliminate the problem of surplus animals by making more space available to remaining species. However, this is a short-term view. In the first place, this rationalizing process will create surplus animals in the form of those species selected to be 'bred to extinction'; and in the second, it will merely delay the onset of the surplus problem in the remaining species.

Another temporary solution to the surplus problem was offered by Lindburg (1991)who suggested that zoos should be obliged to direct some of their budgets to financing low-cost, off-site accommodation or retirement sanctuaries to house surplus animals. This is an appealing solution to the problem of surplus animals but it is merely a palliative and not a cure. The problem of surplus animals will always arise where captive management is so successful that birth rates exceed death rates. Even where there are breeding programmes in force or where extra space or retirement homes are provided, steps will still have to be taken to reduce population growth to avoid production of surplus animals. Furthermore, regardless of any steps taken, the production of surplus males cannot be avoided in species where fewer males than females are required for breeding.

Avoiding the production of surplus animals

In many ways it seems preferable to prevent the problem of surplus animals through the judicious use of contraception and sterilization. However, the effects of these procedures on other aspects of the health and welfare of the animals are often only superficially considered. The influence which the suppression of reproduction could have on the social behaviour and activity of primates or other social species needs to be examined. Not only do young animals frequently provide enrichment for the adults in such species (Van Hooff 1991; Holst 1998; in press), but they also facilitate the development of social bonds between adults (Ogawa 1995; Silk *et al* 1996; Zhao 1996). There can be no doubt that maintaining social species in a non-breeding situation for a prolonged period results in an impoverished environment.

When selecting an appropriate means of population control it must be remembered that, if the production of surplus animals is to be avoided, most zoo animals will have to spend the majority of their adult life in a non-breeding state. As zoo populations reach carrying capacity, females may only be required to breed once or twice in their entire lives. Reproductive effort may be confined to the first few years of adulthood, or it may be required from older individuals. There are three ways in which the production of surplus animals can be avoided: contraception, sterilization or housing animals in single-sex groups. The selection of the appropriate method depends on the biology of the species concerned, the space available and the demography of the population.

Contraception

This article will evaluate the welfare and ethical considerations associated with the various population control methods. For detailed discussion of the pros and cons of the available contraception techniques the reader is referred to the many reviews of the topic available in the literature (Asa & Porton 1991; Munson 1993; Porton 1995; Asa *et al* 1996; Sainsbury 1997).

Hormone-mediated contraception

Progestins are often used in fertility control in zoo animals; MGA (melengestrol acetate) and MPA (medoxyprogesterone acetate) are commonly used compounds. Administration can occur via implant, injection or oral routes. However, the prolonged use of progestins for contraceptive purposes should be treated with caution as various side-effects have been associated with their use. These include: diabetes mellitus, Cushing's disease, weight gain, increased aggression; and various mammary and uterine abnormalities (Seal *et al* 1976; Kollias *et al* 1984; Raphael *et al* 1990; Kirkpatrick & Turner 1991; Munson & Mason 1991; Gerlofsma 1994)

A second point which should be considered when using hormonally mediated contraception is that it suppresses oestrus and proceptive behaviour in females. Thus, in those animal groups in which females are maintained on this form of contraception, courtship or mating behaviour will not be exhibited. It is not known what long-term impact this may have on activity and social structure.

Immunocontraception

This is based on the principle of stimulating an animal to produce antibodies to a particular protein necessary for the reproductive process. Porcine zona pellucida vaccine (PZP) is used to stimulate the production of antibodies against the receptor for sperm on the zona pellucida. In other words, a female is immunized against fertilization. PZP does not have the negative effects normally associated with steroidal contraception. In addition ovarian cyclicity, and therefore normal sexual behaviour, is retained. However, PZP can only be used for a limited period; use for periods exceeding 3 years can lead to permanent changes in the ovary (Mahi-Brown *et al* 1985; Dunbar & Schwoebel 1988). This method of contraception is essentially confined to ungulates and carnivores (with varying degrees of success) and has not, to date, been used on primates.

Intrauterine devices

Intrauterine devices (IUDs) have been used successfully in some apes, chimpanzees (Mundy *et al* 1992) and a gorilla in Rotterdam Zoo (W Schaftenaar personal communication 1991). However, they are not suitable for use in the smaller-bodied primates and have not been employed with other taxa. IUDs have the advantage that they do not suppress normal courtship or mating behaviour. They have not been reported as having adverse effects on health in apes. However, in women there are reports of secondary infection and uterine penetration. In addition, they have to be introduced under anaesthesia and they can be expelled from the body unnoticed, which could lead to an unwanted pregnancy.

Sterilization

When particular individuals are no longer required for breeding purposes, sterilization may be considered an attractive option. Either vasectomy or tubular ligation can be performed (castration is discussed separately below). Neither procedure is known to have side-effects on the health or behaviour of the animals. However, both operations are essentially irreversible and therefore should only be considered when it is certain that the animal will never be used for breeding purposes. Unfortunately, given the demographic structure of most zoo populations, this could mean that sterilization is not a viable option until quite late in an animal's life.

Castration

One of the more common ways in which zoos deal with the problem of surplus animals is castration – or the female equivalent, ovariohysterectomy. While these procedures prevent breeding, castration can also be used to feminize males to reduce their aggression. As aggression is seen as the prime reason why young males cannot be left in their natal group, this operation could offer a solution. However, aggression is not always reduced by castration, and in fact the effects of castration on aggression are very variable depending on the species, age at castration and the individual. Bouissou (1983) reports that in domestic cattle castrated males may dominate complete bulls. Similar observations have been made for horses (Tyler 1972) and reindeer (Espmark 1964). In primates in particular, castration generally has no effect on aggression or social relationships (Wilson & Vessey 1968; Dixon & Herbert 1977; Epple 1978;1981). As Huntingford and Turner (1987) point out, the effect of altered androgen levels on aggression is by no means universal among male mammals. Castration has a much less marked effect on this aspect of behaviour when the subject is on

its home territory – as is the case in the captive environment. Even where castration reduces aggressive contacts with intact males, it may lead to elevated levels of aggression with females (Dixon 1993). This means that the castrated individual may still need to be removed from the group. Furthermore, there are the ethical considerations of surgically altering behaviour as well as the welfare questions relating to the integration of a neutered individual into a natural social group.

Separation of the sexes

The only non-invasive way to avoid breeding is to separate adult males and females, either by keeping them in single-sex groups or by separation of the sexes during the breeding season. The latter option is obviously only appropriate for those species which are strictly seasonal in their reproduction. However, despite being non-invasive, this approach can cause extreme disturbance to normal social behaviour, except when applied to species which are relatively solitary in their behaviour.

Single-sex groups

Single-sex groups are a particularly interesting option when dealing with the problem of surplus males. However, zoos pride themselves on breeding animals and zoo visitors enjoy seeing baby animals. This means that few zoos want to commit themselves to holding all-male groups, even when such groups are a natural phenomenon. This problem is compounded in those species where suitable accommodation is expensive to construct – as is the case, for example, with gorillas.

One advantage of all-male groups is that they function as reservoirs of potential breeding males for future use. However, for such a group to function well, a good understanding of the behaviour of the species is required: males would have to be added or removed from the group periodically; this must be achieved with the minimum of aggression.

Ways of disposing of surplus animals

Animal trade

There are only two choices open to a zoo with surplus animals: transfers to a new home or euthanasia. Unfortunately, finding suitable accommodation for many zoo-born animals is not easy, particularly when certain minimum standards must be met. There are two main channels available to a zoo needing to place animals: the regular circulation of 'surplus and wanted lists' to colleagues; or employing the services of an animal dealer.

The first of these options is preferable, as the zoo retains discretion over the animal's destination. However, the process can be slow and success is not guaranteed. The use of an animal dealer is often quicker and, unfortunately, there are still zoos which resort to their services (Brouwer 1993) despite the fact that the *World Zoo Conservation Strategy* (IUDZG/CBSG[IUCN/SSC]1993) specifically advises against them. The problem with using a dealer to dispose of surplus animals, is that the zoo concerned usually has to relinquish control over the animal. This means that animals can then be disposed of in ways (or to institutions) that would be unacceptable to the original owner. A further complication derives from the fact that some dealers are suspected of illicit trading. By supporting legitimate dealers, zoos may inadvertently lend an aura of acceptability to the trade as a whole.

It must also be remembered that quarantine is often an intrinsic part of any transfer to a new home. The welfare implications of this are rarely considered, although it can be a relatively stressful experience. This means, that even when new accommodation can be found for surplus animals, they may be subject to a quite traumatic transfer process.

Euthanasia

Euthanasia in zoos is a difficult topic: it is the ultimate solution to any surplus problem but it brings with it some very complex ethical issues. There are many people, including veterinarians and zookeepers as well as the general public, who have objections to killing healthy animals. In some European countries, for example Germany, such a practice is illegal. With the exception of Lacy (1991) and Graham (1996) few consider the welfare aspects of applying euthanasia as a means of population control. However, given the negative aspects of the other options outlined above, it merits serious consideration.

When compared with the welfare implications of keeping animals in sub-standard conditions for prolonged periods or those resulting from the protracted use of contraception, euthanasia can seem a preferable method of population control. The judicious application of euthanasia could allow zoo animals to lead more natural lives where courtship, mating and parental behaviours are all expressed.

To derive the greatest behavioural benefits from such a policy, young animals would have to be euthanased at the age when they would naturally leave the natal group. Removing animals at this age would minimize social disruption, prolong the period in which the group could benefit from the social stimulation of the young animals and also exploit the contraceptive benefits of lactation. However, such a policy would conflict with existing ideas that euthanasia should take place immediately after birth or when an animal has fulfilled its reproductive 'duties'. Euthanasia is generally more readily accepted by zookeepers if applied to young animals immediately after birth, as the newborn are considered barely aware. However, given that euthanasia is painless, unless we assume that older animals are in some way cognizant of death, the age at which it occurs is irrelevant.

The second point of view is more pragmatic. It assumes that space is better allocated to animals which might be needed to breed in the future than to those which will not. Lacy (1991) argues that it is preferable to support two healthy animals for 10 years than to allow one animal to live for 20 years. However, he neglects the fact that demographic considerations are important to the development of a socially normal, viable population. In my experience, non-reproductive females may fulfil an 'aunt' role within groups of various species, eg gorillas and elephants; and in Japanese macaques, *Macaca fuscata,* older females can have an impact on the dominance status of their descendants (Chapais *et al* 1997). Older, non-dominant male long-tailed macaques, *Macaca fascicularis,* may also fulfil a 'grandfather' role (Louwerse personal communication 1998).

However, despite the potential welfare benefits of controlling zoo populations by euthanasia, such a policy would be a minefield from both ethical and political standpoints. It would be very difficult to get such an idea accepted by the general public and, in some instances, by the zoo staff. Even were it to be accepted in principle, it is also unlikely that euthanasia could ever be applied uniformly to all species – and that what might be acceptable for ungulates would not necessarily be so for primates, particularly the great apes.

Discussion and animal welfare recommendations

It is clear from this review that the problems associated with surplus animals are very complex and that there is no clear solution. All the options that have been mooted have their disadvantages. In practice this dilemma has lead to an increase in the use of contraception and sterilization (including castration) by zoos. At the same time, the idea that natural behaviour is important of itself (IUZDG/CBSG[IUCN/SSC]1993; Hosey & Glatston 1997) and to the welfare of zoo animals (Van Hooff 1993; ; Westerveld & van Herk 1996; Holst 1998; in press) is growing. Furthermore, zoo educators believe that the opportunity to observe natural behaviour is an integral part of the zoo experience (Westerveld & van Herk 1996). These two approaches to captive management are contradictory. Given that behavioural enrichment is the current buzzword in captive management, the philosophy of facilitating natural behaviour is gaining credence. This could lead to reduced reliance on contraception and a change in traditional attitudes towards euthanasia.

A two-pronged approach is needed to solve the dilemma which zoo managers confront when dealing with surplus animals: policy development and research. There is clear need for a rationalized policy regarding surplus animals and the control of zoo animal populations. Such a policy needs to be founded on good research into welfare issues as well as on ethics. It should also integrate all the existing methods of population limitation into a functional whole. The actual combination of methods should be tailored to the natural social structure and behaviour of the species concerned. It might, therefore, be useful if the zoo community were to develop a key for use when addressing the problem. An example of a simple key is presented in Table 1.

Research is of major importance to the future development of population control methods in zoo animals. Studies are required to produce new and improved methods of contraception which have fewer side-effects and do not impact on reproductive behaviours. Reversible sterilization techniques represent one such possibility. However, research is not just needed in the field of fertility control; thorough studies on the welfare implications of the various population control methods currently in use are also essential. We may speculate on the welfare aspects of reproduction and its control but we do not know how far the ability to breed promotes the well-being of animals in captivity. Article 5 of European Directive 86/609 and Section 3.2 of the 1996 *Code of Practice for the Housing and Care of Animals in Designated and Breeding Establishments* state that captive animals should be able to perform most of their natural behavioural repertoire. Breeding behaviour in all its aspects is obviously a part of that repertoire, therefore by preventing captive animals from producing and rearing young we would seem to be flouting these guidelines.

The extra problem of surplus males cannot be solved by the judicious use of contraception alone. The options discussed in this paper for dealing with this issue also need further research. Castration as a means of reducing intragroup aggression needs to be evaluated, as do the welfare implications of maintaining castrated animals in social groups. The establishment of all-male groups is the best solution to the surplus male problem, assuming zoos can be found which are willing to hold all-male rather than breeding groups. Given that such zoos exist, research is needed on a variety of species regarding the establishment and maintenance of such groups.

Table 1 Key to the appropriate method of population control.

1) Does the species concerned have an active breeding programme management (SSP, EEP etc)?	
- yes	follow advice
- no	go to 2
2) Do you have, or know of, a location for any future offspring?	
- yes	breed if wanted
- no	go to 3
3) Is the species solitary, with a clear or delimited breeding season?	
- yes	separate sexes during breeding season
- no	go to 4
4) Do the young play an important role in the group?	
- yes	programme C
- no	go to 5
5) Do the animals represent rare bloodlines which could be important to captive populations in the future?	
- yes all	go to 6
- yes female(s)	vasectomize male
- yes male	tubular ligation/hysterectomy of female(s)[1]
- no	vasectomize male
6) Do you expect to breed from the animals in the near future?	
- yes	programme A
- no	programme B

Programme A
Use appropriate contraceptive methods. Where possible use those which allow retention of courtship and mating behaviour. Set an acceptable time limit on use.

Programme B
There are two options: i) breed and construct temporary accommodation to house the young until needed; ii) if appropriate, collect genetic material and then vasectomize the male.

Programme C
Design a contraception programme allowing each female to breed in turn. Only one female at a time should be reproductively active. The young should be retained in the group until the natural age of dispersal. If accommodation is still unavailable[2] euthanasia is the best option.

[1] The choice of hysterectomy or tubular ligation with the possibility of phantom pregnancies is species dependent.

[2] Accommodation may become available in the interim period.

One final option for counteracting the problem of surplus males would be to look at ways of altering secondary sex ratios (sex ratios at birth). There are reports of a number of species in which the sex of infants appears to be related to the dominance status of the mother. In some species dominant females are reported to produce more female than male offspring, eg bonnet macaques, *Macaca radiata*, (Silk 1981) and savannah baboons, *Papio cynocephalus*, (Altmann *et al* 1988); while in others, eg long-tailed macaques, *Macaca fascicularis*, (Van

Schaik *et al* 1989) and Japanese macaques, *Macaca fuscata*, (Aureli *et al* 1990) the converse is true. In gorillas, the age of the mother has been reported as influencing the sex of her offspring with older mothers producing more males (Mace 1990; Graham 1997). Should these kinds of phenomena prove predictable, it might be possible to adjust sex ratios by use of selective contraception; females more likely to produce male infants would not be allowed to breed as frequently as those expected to produce female offspring. Such a policy could shift the sex ratio of the births in a specific group towards females. The feasibility of such an approach needs to be examined.

So far ethical considerations have been omitted from this discussion. Nevertheless, ethical issues will play an import role in any final decisions taken. Zoos need to decide which approach to population control is most acceptable: is euthanasia preferable to life in an impoverished environment; are the risks of contraception acceptable; and is it ethical to castrate animals for our own convenience? Furthermore, how can a zoo weigh the risks of hormonal contraception to a mother against the (quality of) life of her offspring? To what extent is it acceptable for institutions which claim education as one of their primary goals to deliberately avoid showing their visitors reproductive and parental behaviours? Should all species be treated equally; ie can the same euthanasia policy be applied to the great apes, as to prosimians and even to non-primate species?

As a final point, it must be remembered that zoos have an obligation to consider the sensibilities of their visitors. If any zoo management were to agree a policy of population control in primates or any other species without public support, its implementation would be unfeasible. If the zoo management went against public opinion in such a matter, they would undoubtedly suffer from an immediate fall in gate numbers. The financial implications of this would, in turn, have an adverse effect on all the animals living in the collection.

From the above, it can be seen that the zoo community finds itself in an insoluble dilemma over the best means to limit zoo populations. Should they use contraception – with all its welfare implications – or should they euthanase surplus animals and weather the inevitable criticisms from the media, a concerned public and various welfare organizations? As long as primates and other exotic animals are kept in captivity these kinds of problems will arise. It can only be hoped that a combination of research and open discussion will provide an optimal solution which will promote the best welfare for all the animals involved. It is only through the development of a well-considered population control policy, founded on a sound scientific basis and complemented by a wide-reaching public information campaign, that zoos can hope to overcome the dilemma of dealing with surplus animals.

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