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A review of population control methods in captive-housed primates

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Abstract

The success of breeding primates in captivity has led to a surplus number of animals in collections. This review examines published journals and key books to investigate the various methods of primate population control. Hormonal, surgical and separation methods are discussed and evaluated with regards to behavioural and welfare implications. Methods of dealing with surplus animals are also reviewed. It is concluded that the successes of contraception methods vary significantly between species, and in some cases not enough is known to conclusively state that one method is preferable to another. The behavioural effects of contraception should be evaluated, as social status and sexual behaviours can be negatively affected by contraception. Non-reversible sterilisation methods, such as castration, should not be used without thorough evaluation due to the behavioural effects on the individual and group as a whole. Overall, the zoo community should share information of successes and failures of contraception in different species, and professional advice should be sought to ensure that the welfare of primates in captivity is not compromised.

Keywords: *animal welfare, contraception, euthanasia, population management, primates, surplus stock*

Introduction

Primates are kept in captivity for many reasons, including for educational purposes, to support conservation through captive breeding and also to allow for research, as well as gaining a better understanding of their behaviour, social systems and biology. Due to the large number of primates being kept in captivity the way in which groups are managed is of the utmost importance for their welfare and therefore one of the main goals of zoos and research facilities should be population management, through a balance of selective breeding and fertility control (Hosey *et al* 2009). The breeding of primates in captivity became more common after the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) came into force, regulating the removal of animals from the wild (Glatston 1998; Bourry *et al* 2005). Captive-born primates tend to live longer, outgrow the available space and breed very successfully due to improved husbandry, nutrition and medical care (Asa 1997; Plowman *et al* 2004). A study by Hill *et al* (2001) showed that wild chimpanzees (*Pan* spp) tend to have a life expectancy at birth of less than 15 years, and an average adult lifespan of approximately 15 years, however, the maximum age of captive chimpanzees recorded by Dyke *et al* (1995), was 60 years, which is older than the estimated age of any individual in the wild study site (Hill *et al* 2001). In many cases, this increased captive lifespan has led to the birth rate exceeding the death rate of animals. Where collections do not have the financial means or space to house the surplus animals their welfare may be compromised (Sainsbury 1997; Bourry *et al* 2005). This is especially problematic in species where the offspring cannot stay with the natal group (Glatston 1998). Although the problem varies from species-to-species, male offspring tend to cause more of an issue than females, as social groupings often favour more females, and have only one or two dominant breeding males.

The artificial longevity of captive primates is itself an interesting point. Without natural threats, such as predation, disease and starvation, the process of natural selection is prevented. In its place, there are keepers and conservationists deciding which individuals are the 'fittest' through the use of studbooks and genetics, with only these animals passing on their genes to improve the overall population. This can allow for well-managed populations, reducing the chance of inbreeding, however issues can arise for collections as often the effective population of a captive species is under 100 individuals, making the likelihood of inbreeding problems high whilst reducing the genetic diversity of the population (Hosey *et al* 2009).

Artificial longevity, as seen in captive gorillas (*Gorilla gorilla*), has also highlighted possible issues, as older females tend to produce more male offspring than female (Graham 1996). As stated previously, one of the main issues with surplus animals is the high number of males, therefore, this sex bias strengthens the case for managing those animals which are 'allowed' to breed. It has also been hypothesised from the results of a study by Alberts *et al* (2013) that artificial longevity due to captivity may allow female primates to become menopausal, whereas in the wild they do not tend to live long enough to reach this lifestage. Menopause in humans is linked to a range of physiological changes, such as osteoporosis and osteoarthritis. Due to the possibility of these conditions being mirrored in non-human primates, Margulis *et al* (2007) suggested that for gorilla, small changes to husbandry, such as amended diets and additional supplements may be beneficial, and should be commenced when they become peri-menopausal, at around 30 years old (Margulis *et al* 2007). Other species where menopause has been recorded include baboon (*Papio* spp), rhesus macaques (*Macaca mulatta*) and chimpanzees (Bellino & Wise 2003). Where females become peri-menopausal or reach menopause in captivity, contraception and husbandry requirements should be re-assessed to prevent any unnecessary procedures which can affect welfare negatively.

The welfare of captive primates and population management are very closely linked. There are arguments for facilitating the breeding of captive animals, as it is meeting one of the Five Animal Needs as stated in the Animal Welfare Act 2006: "its need to be able to exhibit normal behaviour patterns" (Animal Welfare Act 2006 [England and Wales]). Allowing primates to breed in captivity will allow not only maternal/paternal behaviours to be exhibited, but also other, intricate social behaviours that would not otherwise be displayed.

From a conservation perspective, in social groups where no breeding has taken place for some time, if individuals are required to start breeding again, the lack of infants and reproduction prior to this will limit the behavioural experience of the group, and may have a serious effect on the survival rates of the offspring (Munson *et al* 2005). This is apparent in species which display alloparental behaviours, such as the cotton-top tamarins (*Saguinus oedipus*) and other callitrichidae species (Burkart & van Schaik 2010), amongst others. Studies on cotton-top tamarins found that infant mortality was significantly higher in individuals which had no experience of helping to raise siblings, as their parenting skills were poorer (Leong *et al* 2004). Other than learnt social behaviours, allowing reproduction and the raising of offspring is also considered to be a form of enrichment for primates, this should be considered when deciding on methods of population control (Hosey *et al* 2009).

There have also been cases made against allowing animals in captivity to breed. The UK Government Department for Environment, Food and Rural Affairs (Defra) states that the breeding of primates should not be undertaken unless the keeper is confident that the offspring can be rehomed with owners who can provide appropriate care, in any other case contraception should be used (Defra 2010). This guidance chiefly concerns owners of privately owned primates; the underlying rules should be the same whether kept as pets or in a collection with public access. It is also considered by some to be unethical to breed animals where they are not required, or where their welfare may not be paramount. This review aims to support the above-mentioned theories and guidances, and discusses methods of population management and dealing with surplus animals, with a specific emphasis on welfare and behaviour.

Materials and methods

An online literature search of peer-reviewed papers written between 1970 and 2015 was conducted to understand the population control methods utilised by zoos and other collections which house captive primates. The main search engines used included Wiley, Science Direct, Google Scholar and Ingenta Connect. Keywords used included variations on the following: 'Primates and contraception'; 'Captive primates and population control'; 'Zoos and captive breeding'; 'Zoos and primate contraception'; 'surplus stock and primates'.

From these searches, a number of key texts were found, and these have been used to create a review of contraceptives and population management strategies in captive primate populations. As far fewer articles were found than expected, key textbooks have also been consulted.

Once papers and key texts were located, the keywords were again searched for and relevant data extracted to form a review of the processes and methods of population control for captive primates. In addition, information from the AZA (Association of Zoos and Aquariums) Wildlife Contraception Center (WCC) database is included for contraception products and important results not yet represented in the published literature. Tables 1–4 detail data collected by the WCC on contraceptive methods and species of primate treated. Data have been included for New and Old World monkeys, prosimians, and apes. Table 5, available as supporting material (see supplementary material to papers published in *Animal Welfare* on the UFAW website: http://www.ufaw.org.uk/the-ufaw-journal/supplementary-material), presents a detailed summary of available contraception products used in primate species in the US, including manufacturers and brand names.

Results

Table 6 shows a summary of the population control methods discussed in this review. Further detail on each method can be seen in the text below, and information on individual species relating to each method can be found in Tables 1–4.

Contraception

Depending on the primate species discussed, contraception can seem to be a simple and effective management strategy. By 2005, the WCC database held information on 87 species of primate that had been treated by one or more of 40 different contraceptive products (Porton & DeMatteo 2005), although most of those were merely various commercial brands of combination birth-control pills. A further complication in summarising their use is that contraceptive products available in one country or region may not be available in another. Recognising the complexity of choosing an appropriate method for a particular species and

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Table 1 **Contraceptive methods used in prosimian species reported to the AZA Wildlife Contraception Centre.**

Species	Combination pill	Depo-Provera®	Implanon®	MGA implant	Megestrol acetate	Norplant®	PZP	Suprelorin®
Daubentonia madagascariensis		X		X				
Eulemur spp		X		X			X	X
Hapalemur griseus		X	X	X				X
Lemur catta	X	X		X	X			X
Nycticebus coucang		X		X				
Nycticebus pygmaeus		X		X				X
Otolemur spp		X		X			X	
Perodicticus potto		X						
Prolemur simus		X						X
Propithecus spp		X		X				
Varecia variegata	X	X	X	X	X	X	X	X

Table 2 **Contraceptive methods used in New World primate species reported to the AZA Wildlife Contraception Centre.**

Species	Combination pill	Depo-Provera®	Implanon®	MGA implant	MGA liquid	Jadelle®	Megestrol acetate	Norplant®	PZP	Suprelorin®
Alouatta spp	X	X	X	X			X	X		X
Aotus spp		X	X	X			X		X	X
Aotus azarae				X			X			X
Ateles spp	X	X	X	X		X		X		X
Callicebus spp		X		X						X
Callimico goeldii		X		X					X	X
Callithrix spp		X	X	X						X
Cebus spp		X	X	X		X				X
Chiropotes chiropotes										X
Lagothrix lagotricha	X			X			X			X
Leontopithecus spp		X	X	X				X		X
Pithecia pithecia		X	X	X	X			X		X
Saimiri spp		X	X							X
Saguinus spp		X	X		X		X	X	X	X

individual, the WCC was established in the US in 1990 and, more recently, a similar programme has begun in Europe, the EAZA (European Association of Zoos and Aquariums) Group on Zoo Animal Contraception (EGZAC). Both programmes have websites with extensive information about contraceptive products and their use (www.stlzoo.org/contraception and www.egzac.org), and are important ways of information-sharing within and beyond the zoo community. In order to ensure that data are up to date and accurate, collections should engage with the programmes, contributing their experiences and methods to the system. This is imperative and will assist in maintaining high standards of animal welfare and effective population management for the future.

Methods of contraception vary and can prevent ovulation, fertilisation, implantation or the success of a pregnancy, terminating the foetus (Gray & Cameron 2010). Criteria for the ideal contraceptive proposed by Kirkpatrick and Turner (1991) include: a high degree of effectiveness; a lack of harmful side-effects for the individual being treated;

Table 3 Contraceptive methods used in Old World primate species reported to the AZA Wildlife Contraception Centre.

Species	Combination pill	Depo-Provera®	Implanon®	MGA implant	Jadelle®	Lupron®	Megestrol acetate	Norplant®	PZP	Suprelorin®
Allenopithecus nigroviridis		X		X						X
Cercocebus spp		X		X			X			X
Cercopithecus spp		X	X	X			X	X	X	X
Chlorocebus spp			X	X			X			
Colobus spp		X	X	X				X	X	
Erythrocebus patas		X	X	X	X			X	X	X
Lophocebus spp		X		X			X			
Macaca spp		X	X	X		X	X	X		X
Mandrillus spp	X	X	X	X		X	X			X
Papio spp	X	X	X	X	X	X	X	X		X
Pygathrix nemaeus		X		X						
Semnopithecus entellus		X		X						
Theropithecus gelada		X				X				
Trachypithecus spp	X	X	X	X				X		X

Table 4 Contraceptive methods used in ape species reported to the AZA Wildlife Contraception Centre.

Contraceptive method	*Gorilla gorilla*	*Hylobates* spp	*Pan* spp	*Pongo pygmaeus*
Combination pill	X	X	X	X
Progestin-only pill	X	X	X	X
Megestrol acetate		X	X	
Delvosteron®	X	X	X	
Depo-Provera®	X	X	X	X
MGA implant	X	X	X	X
Implanon®	X	X	X	X
Jadelle®			X	X
Norplant®	X	X	X	X
Lupron®	X			X
Suprelorin®		X	X	X
PZP			X	X
IUD	X		X	X

treatment should be flexible and reversible, without limiting or damaging the reproductive ability of the individual; treatment should be affordable; it should not affect the social structure of the individuals involved; and it should be administered remotely, with a single administration. These criteria were written originally for free-ranging animals, and can therefore be difficult to meet in captivity. For example, it may be preferable to capture and restrain an animal to inject a contraceptive, ensuring a full dose is administered, rather than administer it remotely where there is the risk that only a partial dose is received. Also, in some cases, one method that meets most of the above criteria in one species, will not do so in another. As no contraceptive method is ideal for all species (Bourry *et al* 2005), approaches have to be trialled and information shared within the zoo community. Some platforms where zoos and research facilities can communicate and share information about contraceptive records effectively include record-keeping systems, such as the International Species Information System (ISIS) and the software packages that have been designed by the ISIS developers, including ARKS (the Animal Record Keeping System) and SPARKS (Single Population Analysis and Records-Keeping System) which is used to assist studbook keepers with managing small populations. A relatively new platform, the ZIMS database, is the main system which allows real time information-sharing as it is web-based. The other databases mentioned above work independently of each other and therefore can be time-consuming and require much duplicative work when sharing information with other collections (Hosey *et al* 2009). As mentioned previously, the most effective way in which contraceptive information can be shared and distributed is either the AZA Wildlife Contraception Center (AZA WCC), with guidelines generated from a database of more than 30,000 entries and the EAZA Group on Zoo Animal Contraception (EGZAC). EGZAC recommendations diverge from those of the WCC, because some North American contraception methods are not available within

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Table 6 Summary of population control methods used in captive primates species.

Method	Male/ Female	Form/Method of administration	Reversible	Side-effects/Welfare implications	Comments
Hormonal					
Synthetic progstagens, eg MGA	Female	Implant, injection or pill. May require anaesthesia	Yes	Side-effects include weight gain and vary amongst species. Implants can be removed through grooming	Does not affect behaviour as much as other methods. May compromise future fertility in prosimian and New World monkeys. Not recommended in Goeldii's monkeys. One implant can prevent pregnancy for 2–5 years
Progstagen plus oestrogen, eg combination birth-control pill	Female	Daily tablet	Yes	Must be taken daily via oral administration, missed pill could result in pregnancy	Commonly used in apes. For smaller primates advice should be sought regarding dosage
GnRH agonists	Both	Implant/Injection	Yes	Effects are similar to gonadectomy with regards to behaviour	Prevents the production of gonadal hormones. Unknown time-frames for reversibility in primates
Immunocontraception					
PZP vaccine	Female	Injection	Yes	Oophoritis in macaques, reduced follicular development in baboons. Long-term use led to increased follicular atresia (Munson *et al* 2005)	Allows females to continue to cycle. Variable effectiveness, if immunosuppressed the effectiveness may be impaired (Morgan & Tromborg 2007)
Mechanical					
IUDs	Female	Mechanical device inserted into uterus under anaesthesia		Device can be expelled by individual	Used in ape species. Strings should be cut short to prevent removal by individual. Device can be difficult to remove by staff due to the need for the short string
Physical separation					
Separating the sexes	Both	Housing males and females separately	Yes	Aggression may be seen in bachelor groups post-separation. May cause welfare issues during reintroductions	Non-invasive, can utilise natural social groupings. Requires additional housing for animals. Immediate effectiveness
Surgical					
Castration	Male	Surgery. Anaesthesia required	No	Removal of hormones affects behaviours, may lead to individual being subjected to aggression. Time away from group required for post-operative care	Invasive. Post-operative wound management required. Male behaviours are reduced allowing bachelor groups to be housed together
Vasectomy	Male	Surgery. Anaesthesia required	Possible	Time away from group required for post-operative care	One time administration therefore minimal handling/capture time. Invasive. Takes about 6 weeks for sperm to be eliminated from system. Levels of testosterone are not affected so behaviours and secondary sexual characteristics remain the same
Ovariectomy/ ovariohysterectomy	Female	Surgery. Anaesthesia required	No	Invasive. Female behaviours can be altered. Time away from group required for post-operative care	Post-operative wound management required. Groups can be housed in a natural way

the EU and *vice versa* (EGZAC 2014). These sharing platforms should help maintain a high standard of welfare in captive animals through effective population management.

Contraception is thought to be beneficial and increase the welfare of young females which either cannot sustain a pregnancy, or may breed but do not have the mothering skills to raise offspring successfully (Bourry *et al* 2005). As stated previously, one of the reasons for infant mortality in captive populations is inexperienced mothering (Wheaton *et al* 2011). Methods of contraception can include separating the sexes, hormonal contraceptives and surgical procedures (Graham 1996). Each method will have an effect on the behaviour and welfare of the primates involved.

Separating the sexes

Separation of males and females is an effective, non-invasive way to prevent reproduction that should be fully reversible (Glatston 1998). However, females that do not reproduce for extended periods of time may develop uterine abnormalities, such as fibroids, that reduce fertility (Walker 2001). Separation may be permanent or for the duration of the breeding season. It is thought some species in the wild, for example, the Bolivian squirrel monkey (*Saimiri boliviensis boliviensis*) (Williams & Abee 2005) and Talapoin species (*Miopithecus* spp) (Casares *et al* 2011) naturally become sexually segregated *outside* of the breeding season and therefore implementing this in captivity, by separating the sexes *during* the breeding season, would go some way towards allowing them to perform natural behaviours, albeit in reverse. Increased aggression has been seen in Bolivian squirrel monkeys when reintroducing animals after a period of separation, particularly from females directing behaviours towards novel adult males (Williams & Abee 2005). Therefore, if this method were used in captivity, reintroductions would have to be managed closely as there is lack of space for 'escape' from aggressive individuals in captive populations. Husbandry methods to reduce the risk to welfare include controlled reintroductions, whereby the individuals are introduced through a barrier and have visual and/or auditory access to each other prior to being placed together in an enclosure. Keepers and caregivers should have a thorough understanding of the species' behaviour in general and, importantly, an understanding of the particular population's group dynamics and hierarchy. It is very important that behaviours are monitored during these reintroductions and intervention is made where necessary, if an individual's welfare is being compromised.

Separating the sexes during the breeding season is only effective if the keepers are sure of when the season is. Obviously this method should only be implemented in primate species which naturally have a specific breeding season, for example, the Malagasy strepsirrhines (Wright 1997); however, it should be noted that in some species (the cotton-top tamarin), although seasonal breeding is seen in the wild, it has never been exhibited in captivity (Wheaton *et al* 2011). Sexual behaviour and visual signs (eg sexual swellings) would need to be monitored regularly to ensure that the sexes were separated before breeding could take place, while it should be noted that if this method were being used with another contraceptive method, eg hormonal implants, signs of sexual readiness may be reduced or not be apparent at all (Plowman *et al* 2004).

In gregarious species that do not naturally segregate, there are negative social welfare implications of splitting the sexes. The potential for aggression in primates, used as a coping mechanism for stress, increases when unnatural social restrictions are placed upon them (Gustison *et al* 2012). It can be argued that by not allowing an animal to be housed with a natural grouping (eg mixed groups for gregarious species) the collection would not be meeting one of the Five Animal Needs: "…any need it has to be housed with, or apart from, other animals" (Animal Welfare Act 2006 [England and Wales]). This method can also impact negatively upon any social enrichment that the primates would have otherwise had (Hosey *et al* 2009) and is advised against by some so as to prevent undesirable behavioural patterns (Mallapur & Choudhury 2003). Financial constraints can also be a limiting factor when utilising this method, as splitting up sexes will require more enclosures to be built, maintained and managed, which can add pressure to already struggling collections (Glatston 1998).

A benefit of separating the sexes is that a group of males, if managed well, can act as a reservoir for the species gene pool for future use (Glatston 1998). Records have to be kept very efficiently for this to work to prevent inbreeding. In the situation where natal groups are kept together, interbreeding can occur between fathers and sexually mature daughters where reproduction is not suppressed (*Presbytis* spp; Glatston 1998). Inbreeding has been positively correlated to high infant mortality and therefore splitting the sexes or removing offspring all together from the group at the species-appropriate time would prevent this possible welfare issue (Ralls & Ballou 1982). Other issues of not separating the sexes, or at least removing adolescent males from a natal group include them becoming subjected to severe aggression from the dominant male, reinforcing the fact that male animals are far more likely to become surplus than females due to social structure. This has been documented in captive Javan langurs (*Trachypithecus auratus*), where young males reaching sexual maturity were found to be involved in aggressive interactions with the dominant male (Waters *et al* 2001).

Hormonal management

Since culling of surplus animals and surgical sterilisation are controversial methods of population control (Plowman *et al* 2004), hormonal management is a popular alternative. The hormonal methods include synthetic steroids (progestagen or progestaten plus oestrogen) or GnRH (gonadotropin releasing hormone) agonists.

Progestagen contraception

For female primates, synthetic progestins are the most commonly used contraceptive approach. These include melengestrol acetate (MGA) implants, medroxyprogesterone

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acetate injections (Depo-Provera®), and Implanon® implants containing etonorgestrel, which replaced the previously available Norplant® implants (levonorgestrel). MGA implants, by far the most commonly used method in primates in US zoos, are not available outside the US. However, Implanon® implants are available in Europe and other regions.

Levonorgestrel (LNG) also has been administered as a gel matrix by subcutaneous injection, resulting in slow-release of LNG from the injection site. Results from a study with cotton-top tamarins, compared to effectiveness of MGA implants and Depo-Provera® injection, showed the LNG gel to be a successful and possibly more reliable alternative method of contraception (Wheaton *et al* 2011). However, this product is not commercially available.

The only dose-response study conducted for Depo-Provera® for non-human application was conducted with black lemurs (*Eulemur macaco macaco*; Asa *et al* 2007). Results suggested that a range of 2.5 to 5.0 mg kg^{-1} bodyweight should be effective. An interesting and potentially important finding was that treated females began showing male-type colouration. That is, the pelage of the normally brown females began turning black. This outcome is probably attributable to the ability of medroxyprogesterone acetate to bind androgen receptors (Labrie *et al* 1987). It is recommended that further data be gathered on this observation to ensure that welfare is not negatively impacted due to the colouration changes in females.

New World primates, especially callitrichids, present additional challenges. Presumably because these species secrete much higher amounts of oestrogen and progesterone than do Old World primates and prosimians (Coe *et al* 1992), considerably higher doses of synthetic progestatgens are required to achieve negative feedback for effective contraception (Porton & DeMatteo 2005). Because MGA implants are produced as 20% MGA per volume silastic matrix, the resulting implant size for New World primates is quite large, increasing the risk of implant loss.

The post-partum oestrus of many callitrichid species is also problematic. The WCC recommendation for these females in 2000 was injection of Depo-Provera® followed at 14 weeks by insertion of an MGA implant. This regimen was designed to minimise interference with mother and infant interactions, while still preventing post-partum oestrus. However, failures reported to the WCC by 2005 (Porton & DeMatteo 2005) showed that Depo-Provera® duration of efficacy was less than 14 weeks in some females. The recommendation was then revised to either re-injection with Depo-Provera® or insertion of an MGA implant at 35–40 days (Porton & DeMatteo 2005).

MGA implants require a small incision for insertion, necessitating anaesthesia. However, smaller implants, such as Norplant® and Implanon® are inserted with a large-bore needle, which can sometimes be accomplished safely with just physical restraint (eg chimpanzees by Bourry *et al* 2005) and others not (hamadryas baboons; *Papio hamadryas*) by Plowman *et al* 2004). Avoiding anaesthesia allows females to rejoin the social group more quickly, causing less stress and maintaining welfare within the group.

These smaller implants also reduce the problem of loss sometimes encountered with the larger MGA implants that leave a subcutaneous bump that social partners may groom and either remove or cause local infection followed by implant loss. Successful approaches developed by the WCC (see www.stlzoo.org/contraception) include sterilisation of the implants prior to insertion, use of aseptic insertion techniques to reduce incidence of infection, implant placement between the scapulae to prevent self-grooming of the implant, and/or separation of the female from the social group for several days to allow healing to be well underway. If separation is considered too stressful, placing small stainless steel sutures at additional locations to divert attention from the implant site can be successful. Although separation and/or additional sutures may be undesirable, an advantage to MGA implants is their long duration of efficacy (minimum two years), that reduces the number of handling events. However, temporary separation may be necessary to prevent conception while the contraceptive takes effect, usually about one week but sometimes up to two weeks, which should be ample time for healing.

In general, progestagen contraception is highly effective in primates. The primary side-effect of these products across species, including primates, is weight gain (eg hamadryas baboons; Portugal & Asa 1995), which should be controlled with diet and opportunity for exercise. In species with a genetic tendency to develop diabetes mellitus (eg black macaques [*Macaca nigra*], and mangabeys [*Cercocebus* spp]; Munson *et al* 2005), progestagens may exacerbate subclinical diabetes (Straub *et al* 2001) and therefore advice should be sought before implementing the contraception programme.

The uterine endometrium of prosimians and New World primates may react differently to progestagen contraception than that of apes and Old World species (Munson *et al* 2005). Some lemurs and callitrichids develop endometrial hyperplasia spontaneously as they age, a condition that may be made worse by progestagens. In particular, MGA implants in Goeldii's monkeys (*Callimico goeldii*) and squirrel monkeys (*Saimiri sciureus*) have been associated with an aggressive decidual response and secondary endometritis, so progestagens are not recommended in Goeldii's monkeys and should be used with caution in squirrel monkeys (Munson *et al* 2005).

A benefit of using implants is that only one treatment can last one or more years. Although the minimum duration of efficacy of MGA implants is two years, they may in fact continue to suppress the reproductive system for up to five years in some individuals (WCC Database). Thus, when breeding is recommended, the chances of success are higher if the implant is removed (eg golden-lion tamarins [*Leontopithecus rosalia*]; Wood *et al* 2001; golden-headed lion tamarins [*Leontopithecus chrysomelas*]; De Vleeschouwer *et al* 2000; DeMatteo *et al* 2002). A systematic analysis of MGA implant reversibility in golden lion tamarins (Wood *et al* 2001) found that 75% of treated females conceived within two years of removal, which was not different from the conception rate of non-contracepted females. However, a higher rate of stillbirths and infant mortality was seen if implants were left in place, suggesting residual amounts of circulating MGA affected gestation in some way. A similar analysis is underway for hamadryas baboons and colobus monkeys (*Colobus* spp) (WCC). As the study by Wood and colleagues showed, many factors should be considered when analysing reversal, eg the female's age, previous parity, general health, plus fertility of and compatibility with her male partner(s), in addition to contraceptive treatment.

Combination birth control pills

Birth-control pills typically contain a synthetic oestrogen component in addition to a progestagen. The addition of oestrogen makes them more effective while not significantly increasing the risk of side-effects. As the pills were tested and are marketed for humans, they are an obvious option for apes. One drawback is that they have to be given daily, but this can usually be accomplished easily by crushing the pill in a juice or yoghurt treat. The treatment regimen of birth-control pills can be adjusted to provide either continuous suppression of oestrous behaviour (no placebo week) or to allow periodic expression of oestrus by incorporating a week of placebo pills. In some social groups, allowing regular periods of courtship and mating (as might occur during the placebo week) may be beneficial, but in others may lead to increased aggression among males competing for access to oestrous females. An example of where allowing mating behaviours to be exhibited in captivity may be beneficial is seen in bonobos (*Pan paniscus*). Bonobos have a complex social system and mating is important in establishing the hierarchy of the group and regulating social tensions (deWaal 1987). Further evidence is seen in a study by Ryu *et al* (2015), who state that perineal skin swelling in relation to menstrual cycle may increase a female bonobo's attractiveness to other females in the group, allowing them to benefit from increased grooming instances and enhancing affiliative relationships. Instances where mating may impact negatively on the welfare of a species include ring-tailed lemurs (*Lemur catta*), which are group-living, seasonally breeding prosimians. In a study by Cavigelli and Pereira (2000) it was found that male testosterone levels and aggressive interactions increased significantly during the breeding season. In captivity, where there may not be an opportunity for males to escape from this aggression, and where breeding is not required for conservation purposes, it may be better for welfare to reduce breeding opportunities to prevent injury and stress. It was also noted by Cavigelli and Pereira that the increase in testosterone could waste physiological resources and compromise immune function, something that should also be considered by collections when deciding upon a management strategy.

Although combination pills are most commonly used in apes, they are occasionally used for smaller species. In these cases, the pill can be broken to achieve a smaller, more appropriate dose. Great apes receive a full pill, whereas lesser apes usually are given a half pill. This method is safe and effective when the correct dose is used, and it reverses well after treatment ends. It is recommended that the WCC or EGZAC be consulted about dosages for smaller primates.

Social effects of steroid hormone contraception

Social impacts upon groups of hamadryas baboons seemed minimal or non-existent when females were treated with Norplant® (Plowman *et al* 2004) or MGA implants (Portugal & Asa 1995), although treated females did seem to experience more consecutive oestrous cycles. This could be negative, as it was noted that females in oestrus were involved in a higher number of antagonistic encounters with the dominant male and other females (Plowman *et al* 2004). Although this result may suggest that the animals might spend more time in antagonistic interactions, the results of this particular study did not show this to be the case. The effects of MGA implants on social interactions, such as grooming and aggression in hamadryas baboons, have also been reported to be minimal; however, a decrease in the exhibition of sexual behaviours was observed (Guy *et al* 2008).

Depo-Provera® injections have been tested in stump-tailed macaques (*Macaca arctoides*) for possible effects on sexual behaviour. Results showed that males expressed a preference for untreated females in both a semi-free-range setting and a laboratory environment. In the lab, untreated females directed more grooming to males; whereas, grooming behaviour in the semi-free-ranging females was not affected (Steklis *et al* 1982). A subsequent study focusing purely on the semi-free-ranging island population showed that female attractiveness but not female proceptive sexual behaviour was reduced following Depo-Provera® treatment. Dominance relationships were not altered in the population, but treated females showed increased agonistic behaviour (eg low-level threat, bite and fear-grimace) (Linn & Steklis 1990). These results are consistent with the somewhat androgenic nature of medroxyprogesterone acetate.

Welfare implications of implants in primates include the loss of the implants themselves through allo-grooming or abscesses and infection (Wheaton *et al* 2011), the invasive nature of inserting the implant, and in some cases with chimpanzees, the social isolation after insertion to prevent cage-mates interfering with the wound site (Bourry *et al* 2005). Separation from cage-mates can cause stress while the wound heals. The possibility of infection and removal is relatively high in species where grooming and allo-grooming is an important social behaviour to relieve tensions within the group (Terry 1970; Barrett *et al* 2002).

Depo-Provera® injection use in primates can be stressful if the individual has to be caught for the injection to be administered. As smaller primates, such as tamarins, are not often caught, this adds to the stress of the individual.

Gonadotropin-releasing hormone (GnRH) agonists

Since GnRH controls the reproductive axis in both males and females, GnRH agonists, such as Suprelorin® (deslorelin) implants or Lupron® (leuprolide acetate) injections, can be used in either gender. As hormone agonists, they first stimulate the reproductive system, which can result in oestrus and ovulation in females or temporary enhancement of testosterone and semen production in males. The stimulatory phase can be prevented in females

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by administering an oral progestin or birth-control pills for seven days prior to and seven days after injection or insertion of implants. GnRH agonists suppress reproduction by subsequently down-regulating pituitary gonadotrophs, so production of gonadal oestradiol and progesterone in females and testosterone in males is prevented. Observed effects are similar to those following ovariectomy in females or castration in males, but can be reversible.

There is profound individual variation in time to reversal with these products. As GnRH agonists have not yet been used extensively in primates, no systematic analyses of reversal dynamics have been conducted. Due to its high cost, Lupron® injections are seldom used, and there are limited results to date for Suprelorin®. Results from other taxa, though, (eg felids) have shown reversal to be delayed up to five or even six years after treatment in some individuals, although two to three years is more common. As with measures of reversibility in general, there are many other factors that affect fertility, even in never-contracepted individuals. Recent results showing shorter reversal times if implants are removed are promising (WCC, unpublished data).

Immunocontraception

Immunocontraceptives have been developed to act either on ova, sperm or gonadotrophins. They use the individual's immune system which creates antibodies which affect the reproductive process. An example is the porcine zona pellucida (PZP) vaccine, which prevents sperm binding to zona pellucida sperm receptors on the outside of maturing ova, preventing fertilisation (Paterson & Aitken 1990). Using this method females continue to cycle, but cannot conceive (Gray & Cameron 2010). Side-effects in primates from this method include oophoritis in macaques, reduced follicular development and in baboons, long-term use led to increased follicular atresia (Munson *et al* 2005). It is also thought that the vaccination will only work in fit individuals and in immunosuppressed individuals (which can be caused by environmental and other stressors, which primates in collections are subjected to regularly [Morgan & Tromborg 2007]) the effectiveness may be impaired. The methods effectiveness in captive primates may therefore depend on the individual health of the primate concerned (Munson *et al* 2005).

Mechanical procedures

The use of mechanical inter-uterine devices (IUD) generally requires anaesthetic for insertion, and is used widely in apes and other primates with similar reproductive anatomy as humans (Asa 2005). In one study IUDs were used in chimpanzees (*Pan troglodytes*), after insertion under general anaesthesia, the presence of the IUD was checked every 3–6 months, and whenever the animal was anaesthetised for other procedures. It was found that a number of IUDs were ejected (25.6% of those inserted), with the highest expulsion rate in females that had not yet given birth (Bourry *et al* 2005).

The success rate of the IUD is variable and the method may not be as reliable as other contraceptive methods due to the ease with which some individuals seem to be able to remove them. In the study by Bourry *et al* (2005), ten out of 24 chimpanzees conceived after the IUD was implanted (seven still had the device in place, but three did not and may have expelled them prior to conception). IUDs have also been used successfully in gorillas and orangutans (*Pongo* spp), and in one documented case, an orangutan conceived four months after it was removed. Due to their dextrous abilities, the strings have to be shortened to prevent the individuals removing them, but this can make removal by staff difficult (Porton & DeMatteo 2005). From a husbandry and welfare point of view, prevention of removal of the device by the primate takes precedence over the ease of removal for keepers and veterinary staff; therefore it is recommended that the animal be anesthetised (as stated previously) during check-ups and removal to aid staff who may find locating the device challenging. When examining the use of IUDs from a welfare perspective, the nature of the administration and subsequent checking of the IUD is 'hands on' and invasive.

Permanent surgical methods

Permanent contraceptive methods include vasectomy and castration in males, and ovariectomy and ovariohysterectomy in females. All of these methods require surgery, so are invasive. The amount of literature available on these methods in primates is low when compared to other methods of population control. Castration is currently being considered for baboon species that are perceived as nuisance animals in South Africa, and is already in use in some rehabilitation centres to control behavioural issues (Scott, personal communication 2012). The decision to use one of these methods should not be taken lightly, as they are non-reversible (with the possible exception of vasectomy), and in the cases where the complete gonad (ovary or testicle) is removed, it is hypothesised that the behavioural effects on the individual can be changed and in some cases, lead to social imbalances within a population.

Vasectomy prevents the sperm from being released during copulation, but leaves the rest of the male reproductive anatomy intact. There is no change in natural testosterone levels, so the male's behaviour and secondary sexual characteristics are not altered. This method meets most of the guidelines set down by Kirkpatrick and Turner (1991) as the male can continue living in a social group, but it is not easily reversible. Examples of vasectomies include use in wild and semi-wild populations, specifically the Colobus Trust and Kenya Wildlife Service at Diani Beach in wild baboons and in drill monkeys (*Mandrillus leucophaeus*) at the Drill Rehabilitation and Breeding Centre, Nigeria (Egbetade *et al* 2014). In drills, none of the treated males lost their existing place in the group hierarchy, including the dominant males, and all were seen copulating or attempting to copulate with females after the procedure was carried out. It should be noted sperm may persist and can cause pregnancy for a number of ejaculations post treatment, and this should be taken into account when returning treated males to mixed groups.

Although it has not been used widely in non-human primates, reversible vasectomy in humans has become quite successful over the years (eg Silber & Grotjan 2004), especially if the original vasectomy is performed with later possible reversal in mind. The method could be applied at least to larger non-human primate species, and in primates that live in multi-male social groups, the method could assist keepers to control reproduction without ruling an individual out of a future breeding programme. There have been reports of some open-ended vasectomies resulting in recanalisation in humans, but this has not been documented in primates (Temmerman *et al* 1986). Nevertheless, the proper surgical technique can be both effective in blocking sperm while still preserving tissue integrity for possible future reversal (Silber 1977, 1978).

Castration is thought to affect the welfare of the individual through a loss of male secondary sexual characteristics. From observations in different taxa, castration of a male before he reaches sexual maturity may prevent behavioural problems, but it also stunts the appearance of secondary sexual characteristics, which can lead to him becoming subjected to aggressive behaviours by the social group. The effect of castration on behaviour has been observed in talapoin monkeys (*Miopithecus talapoin*), where levels of sexual behaviour are reduced post castration, however, depending on the rank of the male, these behaviours can be restored via the administration of testosterone (Dixon & Herbert 1977). The successful use of castration as a management technique has been documented in Javan langurs where Dröscher and Waitt (2012) found that castrated males displayed more behaviours linked to subordination compared to intact males, which in turn exhibited more dominant behaviours, allowing them to be housed together as there was less competition. It was found that castration can allow for bachelor groups to be formed for surplus males, as the procedure can prevent aggression that would normally be seen in intact males. This can reduce the need to house surplus males in isolation, which can be a welfare issue for gregarious species (Dröscher & Waitt 2012). It should be noted however, that after castration, especially in males which were sexually mature prior to the procedure, libido may drop but learnt behaviours may persist (Asa 2005).

Ovariectomy and ovariohysterectomies are complex operations which involve removing either the ovaries, or the entire female reproductive organs, respectively. Removal of the ovaries prevents reproductive hormones being released and stops cycling. Loss of ovarian function may be associated with osteoporosis in long-lived species, which is something that should be considered when choosing a contraception method (Balena *et al* 1993). These operations are permanent and will affect female behaviour due to the lack of reproductive hormones. It has been seen that in female long-tailed macaques (*Macaca fascicularis*) which have undergone ovariectomy, inter-female affiliations were reduced, and male-female agonistic behaviours were increased (Shively *et al* 1986). If these methods are to be used in captive primate collections more research is required to allow managers a full and thorough understanding of the implications to welfare and behaviour.

Surplus animals

When reproduction is not restricted, the number of animals not needed for programmes or that surpass carrying capacity will increase. Breeding may be unintentional: contraception may have failed, or it may not have been possible to remove individuals from the group before the breeding season or before sexual maturity. Alternatively, unrestricted reproduction may be intentional. Some managers believe that animals should be allowed to breed naturally, so they can exhibit natural behaviours. In any case, the management of surplus animals can be handled in three main ways; culling or rehoming within a zoo or private collection, or moving onto a testing laboratory. These methods are discussed briefly below.

Culling/Management euthanasia

The culling of surplus animals is a very sensitive and emotive issue, especially where primates are involved, seemingly because they are so similar to humans. A strong viewpoint voiced by Lacy (1995) states that the argument regarding culling is not *whether* we should be doing it or not, rather *which* animals should be culled. He states that it is a 'given' that animals in our care will have to be culled so as not to impact on the welfare of other animals (due to lack of space, resources and social constraints). He points out that personal feelings may prevent the required individual being culled, with another animal, which would have been better for the gene pool, being euthanised in its place. An argument for euthanasia is made in the case of hybrid orangutans. These individuals reportedly occupy over one-third of the spaces in zoos for the species, and are thought by some to be of no benefit to the population. Lacy argues that this space could be given over to the purebred individuals, for the good of the species.

Glatston (1998) counters cases made for euthanising non-breeding animals within a social group. He observes that non-reproductive females often have an 'aunt' role within the social system, and removing them from the group may infringe on the group's welfare. Adding to this, the removal of older females may impact negatively on the younger individual's welfare where dominance is passed down from older female family members (Glatston 1998). As mentioned previously, a lack of experienced older females may also impact upon the infant mortality rate of the group as younger females may not have the parenting skills required to successfully raise offspring.

It has recently been reported that management euthanasia does not reduce the welfare of individuals if procedures are carried out humanely. Rather, it could be said that it actually meets the Animal Need linked to behaviour, as it allows animals to exhibit a greater range of natural behaviours than those animals which are not allowed to breed in captivity (Animal Welfare Act 2006 [England and Wales]). These include, courtship, mating and raising of offspring (Penfold *et al* 2014). Penfold *et al* also state that a shortened lifespan does not impact upon the welfare of

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the animal, as welfare is not a cumulative characteristic. The loss of animals through the group, whether an individual is euthanised as an infant, young adult or older group member, is a natural process, and although this can clearly have an effect on some species, the experience can be said to reflect natural behaviours. From a conservation perspective this method may also be preferable, as it has been reported that animals which are kept from breeding for long periods of time are more likely to have issues with fertility, than those which have been allowed to breed at regular intervals (Penfold *et al* 2014).

Relocating surplus animals

Surplus animals are often relocated to other zoos or collections (Graham 1996). A possible issue with this is that the receiving collection may not have as stringent welfare guidelines as the original collection. Although many zoos now can only transfer within their organisation (eg AZA or WAZA), it is thought that some collections within these may still fall short of the welfare requirements. To ensure that welfare is not impacted upon, checks and site visits could be made prior to rehoming, and good communication should be paramount between the two collections. Veterinary records and keeper notes on individual's behaviour should be shared to ensure the animal's needs are met, and to minimise any stress when they are added to a new group. When the animals reach the new collection, introductions should be carefully managed and monitored to ensure that welfare is not impacted upon, as discussed in *Separating the sexes*, previously. The benefits of relocating surplus animals to another collection include the increase in genetic diversity, as well as allowing reproduction, which in turn allows animals to exhibit natural behaviours such as courtship, copulation and raising of offspring. If offspring are to be relocated, then in some species this can mirror them leaving the natal group in the wild, therefore making it a more natural management strategy for some species. It has also been known for surplus primates to be donated or sold to research facilities. This practice is not normally publicised as it is frowned upon by the majority of the general public. In one account an author discusses the rehoming of a troop of macaques (*Macaca* spp) into a laboratory, after first ensuring that the testing they would be subjected to was terminal. This prevented them from being 'recycled' in the laboratory setting; however, it is commented on that this was short-sighted as at no time did they discuss the future of any offspring born within the laboratory (Hosey *et al* 2009). If primates are to be rehomed into laboratory settings, collections should ensure that an agreement is in place that protects both the individuals being rehomed at the time, as well as any offspring that may be produced in the laboratory.

Discussion

Through a thorough search of the available literature and by reviewing data collated by the WCC, it has been found that records of contraceptive techniques focus mainly upon hormonal methods. This could be because hormonal population control methods are the most frequent form of population control used in primates, due to the longevity of the treatment and success rates in preventing pregnancy. Although types of hormonal contraceptives are still being tested in certain species with regards to dosages and administration techniques, overall they allow a greater range of flexibility and reversibility than other methods. From a behavioural view, groups often remain together when hormonal methods are utilised, saving the expense of creating new enclosures for certain individuals, and also preventing possible welfare implications when it comes to splitting up the sexes. The most common hormonal method used is the MGA implant, which is effective in all primate species, but the prevalence of side-effects varies among species. The primary side-effect is weight gain, but in prosimians and some New World monkeys effects on the uterine endometrium may compromise future fertility. These progestagen-based implants do not seem to affect primate behaviour as much as other methods that suppress or eliminate gonadal hormones.

Separating the sexes is a good alternative in species which naturally segregate in the wild, as long as the collection has the facilities to house two or more groups during the breeding season. The process would have to be well-managed to ensure that breeding did not occur prior to the individuals being separated. The method is sound and reversible, and goes some way to allowing the animals to perform natural behaviours, by taking advantage of the natural social grouping, although it is splitting them at the time when they would naturally come together. The negative point is that this reverses what is normally observed in the wild, whereby separation would not occur during the breeding season.

There are fewer published reports and data on surgical methods of contraception in primates, with the majority of information available through key textbooks rather than peer-reviewed journals. Due to authorities in habitat countries considering the use of castration on wild populations, more research should be conducted and published before key decisions are made. A general recommendation would be to seek advice from either the AZA Wildlife Contraception Center (www.stlzoo.org/contraception) or the European Group on Zoo Animal Contraception (www.egzac.org).

Animal welfare implications and conclusion

Contraception is a necessity if we are to continue keeping primates and other wild animals in captivity. Reproduction is a sign of an individual's fitness, and some believe that because animals can breed in captivity, their welfare needs are being met. However, it is not feasible to allow primates uncontrolled breeding in collections. Although an infant often attracts the public, it is not ethical to continue breeding if there is nowhere to place the offspring once they become sexually mature. Contraceptive options should be compared against the Five Animal Needs (Animal Welfare Act 2006 [England

and Wales]), in relation to the species being considered prior to anything being implemented, and the method which meets the most Needs, from a physiological and behavioural point of view, should be short-listed for use. The efficiency of population control methods, along with side-effects and other welfare and behavioural implications, are species-specific, and therefore should be thoroughly researched prior to implementation of any plan. Financial considerations may also be a limiting factor when selecting a population control method. However, this should not be an excuse for tolerating poor welfare. When collections consider obtaining a species, they should first thoroughly investigate the costs involved in maintaining a healthy population. That is, fertility control should be considered a basic cost of good animal management. In collections where species are already being kept, if there is the potential for financial difficulties, they should contact either the WCC or EGZAC, who may be able to advise on which methods are most affordable for their specific situation.

In an ideal world, the only reason that collections would have surplus animals would be if their management strategy was management euthanasia. This is far from possible, however, as unplanned births do occur sometimes because not enough is known about the contraceptive methods being used (eg dosages). It is the animal manager's responsibility to ensure that best methods of fertility control are implemented. The WCC or EGZAC should be consulted for the most up-to-date information, as the field of wildlife contraception is constantly evolving.

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