Evaluating the impacts of chemical contraception in male Colombian Black-faced spider monkeys (*Ateles fusciceps rufiventris*)

Kate Brice

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Introduction

Historically, zoos maintained their animal populations by taking animals from the wild (Melfi, et al., 2013). However, during the 1970s, the Convention on International Trade in Endangered Species (CITES) was agreed and enacted upon with the idea that the trade of endangered wildlife would be limited (CITES, 1973). This meant that the legal trade of wild animals was now regulated more strictly (Nijman, et al., 2011), which made it more difficult for zoos to acquire animals from the wild and resulted in zoos needing to have self-sustaining animal populations. As a result, organised captive breeding programmes were developed which have since become an important conservation tool to help prevent the extinction of threatened species and halt the decline of populations in the wild. The objective of captive breeding programmes is to build demographically secure and genetically viable populations through organised breeding (Ballou et al., 2010; Ebenhard, 1995; Purohit et al., 2021). Zoos were early pioneers in developing *ex-situ* conservation breeding programmes, with several success stories, notably golden lion tamarins (Leontopithecus rosalia) (Stolwijk, 2013; Tribe and Booth, 2003), American bison (Bison *bison*) (Brodie, 2008; Rabb, 2004), California condor (*Gymnogyps* californianus) (Snyder and Snyder, 2000; Moran et al., 2021; Beissinger, 2001), Mauritian kestrel (Falco punctatus), and the Mauritian pink pigeon (Nesoenas mayeri) (Mallinson, 2003; Solitaire, 2015). Zoo led programmes such as these show the importance of captive breeding programmes and the role that zoos play in the potential revival of nearly extinct species (Tribe and Booth, 2003). Critically, of the 520 primate species, 86% have declining population trends (IUCN, 2023), making primates a taxon that might significantly benefit from effective captive breeding efforts.

For years zoos have used genetic and demographic management to manage captive breeding populations. Captive conservation breeding programmes are managed by regional associations such as the European Association of Zoos and Aquaria (EAZA), with recognised committees (Taxon Advisory Groups, or TAGs) to oversee the programmes. In Europe, species are intensively managed in EAZA Ex-Situ Programmes (EEPs), which were founded in 1985. Each EEP has a coordinator who manages the studbook – a comprehensive history of each individual's history – and analyses an individual's parentage to make recommendations of pairings based on reducing inbreeding to zoos (Leus et al., 2001). A studbook keeper's priority is to maintain future populations that are genetically viable and healthy, by using various tools, such as contraception, castration, separation, transferring animals to other zoos, single sex groups and management euthanasia.

Despite their successes, there are also challenges with captive breeding programmes as many lack genetic diversity. In addition, very little is known about the basic biology and behaviour of many species, thus captive populations may not be self-sustaining (Lueders and Allen, 2020; Powell et al., 2019). To compound this, captive animals now often have a longer lifespan compared to wild counterparts due to improved animal welfare and husbandry, resulting in the need for surplus animal management in zoos that are limited in both resources and space (Asa 1997; Sainsbury 1997; Plowman et al., 2004; Bourry et al., 2005; Wallace et al., 2016). In zoos, the phrase 'surplus animal' implies that a zoos captive population has reached its space and resource limit (Carter and Kagan, 2010). The lack of space is especially complicated and concerning for zoos when it comes to species where offspring are unable to stay in their natal groups (Glatston 1998; Wallace et al., 2016).

As welfare standards have risen, zoos find it increasingly difficult to hold surplus animals due to limited space (Bartos and Kelly, 1998; Seal, 1991; Tribe and Booth, 2003; Conway, 1999) and the logistical challenges of moving animals to other collections. The choice to reintroduce surplus captive-bred animals back into the wild is no easy task as animals must be able to thrive and behave as wild animals (McPhee, 2004). Reintroduction is also expensive, as resources are needed to monitor and evaluate the impact reintroductions have on conservation (Mallinson, 1995; Tribe and Booth, 2003; Barbosa and Tella, 2019; Wilson et al., 2014) and the available suitable habitat can be lacking (Tribe and Booth, 2003). While the cost of keeping an animal in captivity may exceed the cost of protecting enough suitable natural environment to maintain it – for example, Alibhai and Jewell (1994) have estimated that it can cost more than 16 times as much to keep a black rhino in captivity than it would be to protect the necessary suitable habitat (Tribe and Booth, 2003) - expectations for successful reintroduction programmes are quite low mostly due to ecological, economic, political and social situations which are not taken into consideration (reviewed in Keulartz, 2015). A review of reintroduction projects suggested that out of 145 reintroduction projects, only 16 were successful using captive-born animals (reviewed in Keulartz, 2015).

Zoos are in a prime position to support ground-breaking research, contribute to, and develop conservation programmes, as they are both involved in captive breeding and *in-situ* programmes (Conde et al., 2013; Lueders and Allen, 2020) and promote the importance of a 'One Plan Approach' in their projects, where captive breeding populations are connected to the conservation of wild populations and their environment (Melfi, et al., 2013; Durrell and Mallinson, 1998; Ellis and Seal, 1995; Hutchins and Conway, 1995; WAZA, 2015).

EAZA institutions have over time expressed concern to the studbook keeper related to management of their groups, and in particular about the management of the males in their groups, owing to excessive male-male aggression. To try to address these issues, it was decided that a survey would be the best way to collect a lot of data from multiple EAZA institutions. Similar research questionnaires have been used successfully in collecting data from multiple sources on patterns of aggression for captive species such as spider monkeys (Davis et al., 2009) and lion tamarins (Inglett et al., 1989). While direct observation remains a primary method for studying non-human primate behaviour, surveys can provide valuable insights into human attitudes, perceptions, and management strategies related to aggression across a large population. Behaviour observations were discussed, even though, this data would have helped to build a better picture on the issues institutions have, it would have been too time costly for keeping staff to carry out alongside their normal work duties. Whereas completing the survey would only take a few minutes to complete.

The aims of this project are to investigate the effects of social cohesion and male aggression in zoo housed Columbian black-faced spider monkeys and to build on and improve the current knowledge on the use of chemical castration as a management tool for primates in captivity. Using survey data collected from zookeepers, I will look for a relationship between age at, and length of, contraception and behavioural impacts of chemical contraception in Colombian black-faced spider monkeys by comparing rates of aggression between contracepted & non-contracepted males.

1. Non-human primates in captivity

One taxonomic group for which captive breeding and husbandry concerns is a particular challenge is primates. There are many reasons as to why primates are kept in captivity including education, supporting of conservation through captive breeding, research and gaining a better insight into their behaviour, biology, and social structure (Wallace, et al., 2016). Zoos have become an important resource for researchers interested in primate biology which has resulted in improved primate husbandry (Hosey, 2023). Due to improved husbandry, medical care, and successful breeding, birth rates often exceed death rates in captive primate populations (Wallace et al., 2016). As a result, zoos find themselves with additional difficulties to resolve, such as 'surplus' animals, which may lead to unnatural social groups and an excess of individuals. This may cause a group conflict and unrest, especially for some species, where individuals would leave their natal group when they reach sexual maturity (Baker and Farmer, 2023).

There could be a range of reasons why animals are classed as being surplus, such as males and females that are unpaired due to lack of breeding opportunities, animals who are non-reproductive due to old age or medical reasons, however, for most group-living species, it commonly refers to an excess of male offspring (Lewandowski, 2003). The formation of all-male groups in captive primates is used as a management tool to deal with surplus males (Koot et al., 2016) but there have been few attempts to assess the feasibility of this management technique across primate species (Fàbregas and Guillén-Salazar, 2007). All-male groups are not favoured by zoos due to the potential difficulties in managing these groups, as multi male groups can be prone to infighting and injury, often meaning that males are isolated for their own safety (Lewandowski, 2003). However, if managed correctly, by understanding species behaviour and by giving animals enough enclosure space to have their own territories, there is evidence of success of managing multi-male groups of ring-tailed lemurs (Lemur catta) (Law et al., 2021) and Western lowland gorillas (Gorilla gorilla gorilla) (Stoinski et al., 2001). However, this may not be the case for all bachelor groups, as not all animals of the same species behave in the same way (Hosey et al., 2009).

2. Impacts of successful breeding in captivity

Captive breeding in zoos is considered to be the last hope in preventing extinction of some species (Alroy, 2015). Successful breeding of captive

primates can benefit captive groups, by not only allowing maternal and paternal behaviours to be demonstrated, but infants also help bond groups through being a form of enrichment (Wallace et al., 2016), and younger animals learn how to rear infants by watching others (Dunayer and Berman, 2018). However, successful captive breeding also presents challenges including inbreeding, overpopulation and space limitations, unnatural mismanagement of groups and social groupings, rehoming difficulties, and injuries.

The formation of single-sexed groups is a common and important management tool in zoos to help alleviate breeding pressures. Although, this can be problematic if this is not a natural social structure for a species, as unnatural bachelor groups can disrupt natural social structures, increase aggression, and compromise animal welfare (Hosey et al., 2009; White et al., 2023). Western lowland gorilla, chimpanzees (*Pan troglodytes*) and proboscis monkeys (*Nasalis larvatus*) all form natural bachelor groups in the wild and successfully in captivity (Baker and Farmer, 2023). However, issues with multiple males tend to arise once the male reaches sexual maturity when testosterone production increases (Kovacs-Balint, et al., 2023), as testosterone is related to aggression and mating behaviour (Anestis, 2006).

In multi-male groups, dominance struggles can occur resulting in overt aggression, potential injury, or death of breeding animals (Penfold et al., 2021). If single-sexed groups are not an option due to space limitation, rehoming or transferring surplus animals to another collection is another method used by zoos. Although transferring animals which are part of a breeding programme, such as an EEP, provide its own issues. Some examples are that the standard of care is not always known, especially if the receiving zoo is not an accredited zoo, or the animal could be transferred to another collection without approval, as they are not part of the association and there is no real penalty for not adhering to the rules of transferring animals to another collection (Porton, 2005).

3. Aggression

Primate societies are complex (Thierry, 2007; Koenig, et al., 2013), and while initially considered as peaceful and democratic (de Waal, 2002), they can often be aggressive and hostile (Jones, 1987; Goodall, 1986). In many primate species, aggression, described as any behaviour directed towards another individual with the intent to cause harm (Anderson and Bushman, 2002), and is integral to dominance and mating (Bernstein and Gordon, 1974; Deag, 1977; Hall, 1964; reviewed in Honess and Marin, 2006b). Due to the high cost of sustainably aggressive behaviour, most animal aggression often occurs in extremely ritualised situations with the intention for maximum effect and minimum risk (Bernstein and Gordan, 1974; de Waal, 1989; Tinbergen, 1968; reviewed in Honess and Marin, 2006b).

Social aggression is a common and important behaviour in multi-male macaque social systems (Baker and Farmer, 2023), and aggressive behaviours have been argued to be necessary to maintain social hierarchies (Baker and Farmer, 2023) and to help defend and obtain resources (Bernstein and Gordon, 1974; De Almeida, et al., 2015). The relationship between dominance and aggressive behaviour is, however, unclear (Dixson, 1980; reviewed in Honess and Marin, 2006b), for example, different types of aggression which are distinguished by different situations, neural, and hormonal activity (reviewed in Honess and Marin, 2006). For example, defensive aggression and threatening behaviour, is often linked with elevated testosterone and offensive aggression and, or spontaneous attacks which is linked to high levels of plasma cortisol and increased frontal lobe activity in the brain (Kalin, 1999). In addition, aggressive behavioural characteristics are influenced by internal and external factors (Thierry 2007) such as: group size, intermale competition for reproductive females, and social instability. Moreover, aggression can increase during specific situations. For example, fear-induced aggression can arise due to a lack of escape routes from potential threats and irritable aggression due to pain from injury or illness (Volavka, 2008; Cowl and Shultz, 2017). In captivity, these aggression drivers are present, but there are also the added stressors of social instability due to unnatural social groups, visitor directed aggression (Fa, 1992), shift in group composition, fluctuation in reproductive – which also occurs in the wild, and social status within the group, and a lack of control over their social and physical environment (Davies et al., 2009).

The way in which some zoos manage their primate groups, such as spider monkeys, does not always mimic the natural structure and group dynamics, which might further promote excessive aggression in individuals (Aureli and Schaffner, 2007; Davis et al., unpublished, in Campbell 2008). Spider monkeys for example, have a fission-fusion social society. The term 'fission-fusion' was first mentioned by Hans Kummer (1971) to describe a social structure, whereby the group size can temporarily change as animals move throughout their environment; animals mix into a group (fusion), e.g., group members sleep in one place, or split up (fission), e.g., group members split up and forage in smaller groups during the day (Aureli and Schaffner, 2008). Fissionfusion dynamics are considered to have evolved to decrease intragroup competition for fruit that is scattered both spatially and temporally (Symington, 1987, 1988, 1990; Chapman et al., 1989). Fissioning is utilised to prevent the escalation of aggression in wild spider monkeys (Davis, et al., 2009). Social group management of captive primates with fission-fusion dynamics, such as chimpanzees, spider monkeys and lemur species, can be a particular challenge, as there is a lack of opportunities for group members to fluidly mix with other group members or split up and forage, which could lead to increased aggression in an already confined captive environment.

An animal in captivity may be more capable of coping with a potentially negative stimuli, such as zoo visitors, if the animal is allowed to respond with active avoidance or escape opportunities (Carlstead, 1996; Hosey, 2005). Evidence shows that factors, such as environmental stressors, the lack of escape routes, and a higher possibility of guarding resources, contribute to captive primates developing higher levels of aggression than in wild populations and increases in behavioural abnormalities such as self-harming (Honess and Marin, 2006). Due to the increased risk of severe trauma, stress, and heightened aggression, this will have notable impacts on animal health and welfare (Broom and Kirkden, 2004; MacCowan et al., 2008; Ross et al., 2009), which in turn may result in euthanasia (Glatston, 1998; Lacy, 1995; Asa and Porton 2005) and managers of captive primates may use chemical means, such as contraception, to reduce aggression rather instilling environmental changes (Wallace, et al., 2016).

4. Hormones

Historical research on the effects that hormones have on aggression has mainly focused on testosterone, and other steroid hormones, and the role that they have on neural pathways (Kling, 1975). Whilst this body of work has proved beneficial in expanding the field, we still do not fully understand the causal links between endogenous testosterone and aggressive behaviour.

Testosterone is one of the primary androgens produced by the body which develops and maintains secondary masculine characteristics in males (Mazur and Booth, 1998). It stimulates male genitalia development and sperm production and regulates the onset and maintenance of behavioural characteristics relating to mating, such as sex drive and aggression (Muller, 2017). Testosterone is mainly produced by the Leydig cells of the testes, but the adrenal cortex also secretes it in both males and females (Mazur and Booth, 1998; Eisenegger et al., 2011) and is the hormone most linked with aggression (Makhanova, 2023; Honess and Marin, 2006). The production of testosterone in both males and females begins in the hypothalamus, where the gonadotropin-releasing hormone is produced (GnRH), which is also known as luteinizing hormone-releasing hormone (LHRH; Figure 1). This controls the release of the gonadotropins, follicle-stimulating hormone (FSH) and luteinizing hormone (LH) from the anterior pituitary (Figure 1). The anterior pituitary is a small, pea-sized gland found at the front lobe of the pituitary gland, located at the base of your brain, below the hypothalamus (Bonczar et al., 2023). FSH stimulates follicles in the ovaries and secrete oestradiol and once oestradiol reaches its peak, it first signals release in GnRH and then in LH, which is then followed by ovulation in females (Asa, 2005; Figure 1). FSH and LH in males are the pituitary hormones that support testosterone production and spermatogenesis in males (Figure 1). In the testes, FSH is significant, as it sets spermatogenesis in motion, at puberty and at the beginning of each breeding season in species that do not produce sperm continuously. Testosterone has various intended tissue locations outside of the testes, including those responsible for the species-specific secondary sex characteristics such as secondary sexual colouration in male mandrills (Setchell, et al., 2008) and muscle development, as well as the areas of the brain which mediate aggression, territoriality, and mating behaviours (Wingfield, et al., 2001).

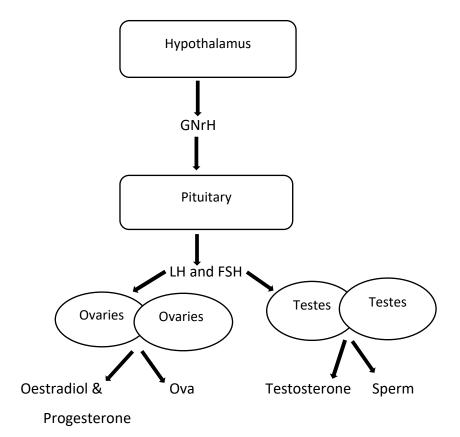


Figure 1. A brief outline of the starting point and the intended destination of reproductive hormones. GnRH – gonadotropin-releasing hormone, LH – luteinizing hormone, FSH – follicle-stimulating hormone (Source: [adapted from] Asa, 2005:31).

The role of hormones in creating or accelerating aggressive behaviour has been studied across a range of animal species (Leshner, 1975). Testosterone is considered the hormone most associated with aggressive behaviour and dominance, although the relationship is complex (Mazur, 1983; Starzyk and Quinsey, 2001; reviewed in Honess and Marin, 2006b). There is evidence that aggressive behaviour is not solely related to increased testosterone, but also by conspecific behaviour, as well as status (reviewed in Honess and Marin, 2006b; Buyukmihci, 2021; Epple, 1978; Dixson, 1980; Michael and Zumpe, 1993). For instance, most vertebrate species have breeding seasons, and several species display aggression outside of the breeding season, even though testicles have regressed and circulating levels of gonadal steroids are comparatively low (Soma, et al., 2015). Studies of wild primate populations support the "Challenge Hypothesis", which suggests that change in male testosterone is more than likely associated with aggressive mating conflict, than with reproductive physiology (Muller and Wrangham, 2004). Muller, (2017) suggested that there are three situations where testosterone would increase in males. In both seasonal and non-seasonal breeding male species, testosterone production increases when competing for fertile females. In species where males compete to preserve permanent access to females, testosterone levels increase when males are threatened with losing access to females, instead of during mating periods. And lastly, when status is linked to mating success, and reliant on aggression, more dominant males normally maintain elevated testosterone levels than subordinate males, particularly when dominance hierarchies are volatile.

Moreover, evidence is mixed concerning the role that testosterone has on dominance and aggression. Some studies suggest that testosterone levels and aggression are correlated in male olive baboons (*Papio Anubis*) (Sapolsky, 1982, 1987) but no relationship between aggression and dominance was found in bonobos (*Pan paniscus*) (Sannen et al., 2004), rhesus macaques (*Macaca mulatta*) (Bercovitch, 1993; Gordon et al., 1976; Turner et al.,1989), stump-tailed macaques (*Macaca arctoides*) (Nieuwenhuijsen et al., 1987) or Japanese macaques (*Macaca fuscata*) (Eaton and Resko, 1974). In species such as chimpanzees (*Pan troglodytes*), mandrills (*Papio sphinx*) and rhesus macaques (*Macaca mulatta*), testosterone and aggressive behaviours appear to be more tightly related, especially in reproductive circumstances (Anestis, 2006). The interactions between testosterone, dominance and aggression in male primates is complex.

Cortisol, and related glucocorticoids, have been referred to as being "stress hormones" in the past, however the relationship between stress and corticosteroids is complex (see, MacDougall-Shackleton, et al., 2019). Glucocorticoids are secreted to help an individual cope with certain stimuli, for example, during a stress response, increased glucocorticoid levels aid an energy balance shift to assist coping with a stressor (MacDougall-Shackleton, et al., 2019). Although testosterone is not directly a product of an acute stress response pathway, cortisol, and testosterone are linked in several ways. Cortisol is a product of the hypothalamic–pituitary–adrenal (HPA) axis, while testosterone is produced via a hypothalamic-pituitarygonadal (HPG) axis, with both cascades initiated by neuronal production of targeted releasing hormones in the hypothalamus. The two hormones suppress each other at different levels, creating a complex mechanism that regulates aggressive behaviour in males and females (Book, et al., 2001). Testosterone and glucocorticoids fulfil multiple adaptive roles in males. Testosterone influences multiple aspects of male reproductive anatomy, physiology, and behaviour, and one of its roles is thought to be the stimulation of aggressive behaviours in response to certain stimuli, as an increase in testosterone production often assists a period of heightened aggression (Soma, 2006; Ostner, et al., 2008).

5. <u>Contraception used in captivity</u>

Although the relationship between aggression and testosterone is complex, castration or chemical contraceptives, interventions that decrease or suppress testosterone production, are often used to mediate aggression. Castration or chemical contraception are widely used in captive management of male non-human primates to limit reproduction of genetically overrepresented individuals (Asa and Porton, 2005). Surgical castration refers to the removal of the testicles; a procedure used primarily to permanently limit reproduction, as the principal products of the testes are sperm and testosterone (Knickmeyer and Baron-Cohen, 2006). As testosterone can be associated with dominance and aggressive behaviour in males (Giammanco et al., 2005; Muller & Wrangham, 2004; Muller, 2017; Simpson, 2001), castration is also used to manage testosterone-mediated

aggression (Ferrie et al., 2011; Takeshita et al., 2017; Dröscher and Waitt, 2012), and to manage surplus males in bachelor groups or in mixed-sex groups (Dröscher and Waitt, 2012).

Contraceptives offer a theoretically temporary solution for reproductive management in individuals who should breed in future. The most widely used contraceptive in captivity for aggression management in male primates is the deslorelin acetate implant (Cowl, et al., 2018). Deslorelin acetate is a GnRH agonist (stimulate) and acts as a contraceptive by briefly suppressing the HPG axis (Cowl, et al., 2018), impeding the production of pituitary hormones such as luteinizing hormone as well as gonadal hormones such as testosterone (Bergfeld et al., 1996). Prior to downregulation, deslorelin acetate stimulates the reproductive system, potentially resulting in the temporary enhancement of semen production and testosterone in males, which may lead to a temporary increase in aggression (Junaidi et al., 2003; Munson et al., 2001; Trigg et al., 2001; Asa and Porton 2005). When deslorelin is released, it binds to GnRH receptors on the pituitary, stimulating the release of FSH and LH. These hormones act on the gonads, prompting testosterone production. Deslorelin binds to GnRH receptors in the hypothalamus, which causes GnRH release. This creates a feedback loop, whereby production of GnRH is inhibited, resulting in deceased levels of FSH and LH, and essentially reduces testosterone levels (Asa, 2005). Benefits of these implants are that they are theoretically reversible; important if animals should need to breed in future (Cowl, et al., 2018; Young, 2013; Asa and Boutelle, 2011), the procedure needs only be done every year (although in some individuals, the duration is longer), implants are moderately noninvasive compared to surgical castration and currently there are no adverse side effects (Young, 2013; Asa and Boutelle, 2011). Ultimately, GnRH agonist implants have similar outcomes to castration, but offer a temporary solution, making them an encouraging advance towards both contraception

and aggression reduction by means of reversible testosterone suppression (Penfold et al., 2021).

Having a contraceptive technique that is reversible is especially important to zoos and sanctuaries, as this provides the management team options to find a more suitable, long-term solution to the problem they face. Reversible contraception is also beneficial in social species, as it prevents social group unrest when removing an individual from the group during breeding seasons, it allows offspring to remain in natal groups averting the possibility of inbreeding and reducing the need to find additional enclosures for animals with no breeding recommendations (Porton, 2005; Porton and Dematteo, 2005). However, reversibility could potentially be individual and the time a contraceptive could take to reverse may vary considerably, which can have an unacceptable impact for some breeding programmes (Asa and Poton, 2010). Mismanagement of both aggressive behaviour and of contraception could lead to reduced conservation impact of an endangered species *ex-situ* breeding program.

European zoos have access to a variety of hormonal contraception drugs ranging from long-lasting implants and injections to oral contraceptives which require daily application (Cowl, et al., 2018; Porton., 2005). As contraceptive products are mostly developed for use in humans, domestic animals, or wild and feral animal populations, when used in captive wildlife, it is still regarded as experimental (Cowl, et al., 2018). As a result, there is little empirical evidence on the dosage needed to dampen the aggressive behaviour and little is understood about the effects of chemical contraceptives on the behaviour of male non-human primates (Cowl et al., 2018; Young, 2013; Ferrie et al., 2011).

However, reduced testosterone concentrations can have unintended social, behavioural, and physical consequences. For example, it can create social instability, increasing the likelihood of aggression (Takeshita et al., 2017; Richards et al., 2009), it can impede sexual communication linked to olfactory and acoustic cues (Zimmermann, 1996; Zimmermann and Lerch, 1993), skeletal and oral health may be impaired due to a thinning of cortical bone (Kessler et al., 2016; Wang et al., 2016), and in dichromatic species, colouration may be affected (Barthold et al., 2009). Furthermore, when castration is used in juveniles, there is a risk of male feminisation (Richards et al., 2009; Michael and Zumpe, 1993), the development of abnormal sexual and aggressive behavioural repertoires as well as an abnormal growth of reproductive organs (Epple, 1990; Dixson, 1993).

The impact of surgical castration and contraception on male nonhuman primates is, therefore, substantial, and, when used for aggression management, may not always be effective as aggression is not solely mediated by testosterone, but also by conspecific behaviour, as well as social status (Buyukmihci, 2021; Epple, 1978). Castration or contraception may not always change patterns of behaviour already established (Asa 2005) and, as a result, may not always be appropriate as an aggression management tool for males which are already sexually mature. When used, they may only partially solve issues with aggression and can lead to unintended negative consequences, warranting the consideration of alternative aggression management tools. Due to the permanency of castration, it is not a practical solution for managing reproduction or aggression in genetically important males who are significant for breeding programmes (Ruivo and Stevenson, 2017).

6. Efficacy, side effects and failures of contraception techniques

The search for information on the use of chemical contraception such as deslorelin in modulating aggression in male nonhuman primates, yields little data and discrepant results of efficacy. In lion-tailed macaques (*Macaca silenus*), deslorelin acetate can temporarily reduce testosterone and is successful in reducing aggression which resulted in social group structures to

continue for years despite the resurgence of testosterone in some males (Penfold, et al., 2021). This implies that new social roles can be learnt and be independent of androgen influence (Penfold, et al., 2021). Deslorelin acetate is also not a permanent solution in stopping aggression. As the effects of deslorein acetate wares off, aggressive behaviour can return over a period of time (Penfold et al., 2005). Testosterone levels take time to reduce post contraception, (Asa and Porton, 2005), and as deslorelin works via hormone feedback, there is a spike of testosterone immediately post contraception (Trigg et al., 2001; Asa and Porton 2005), this may be an issue in captivity, as deslorelin is an agonist of GnRH, it triggers the reproductive system, potentially resulting in the temporary increase of testosterone in males (Cowl et al., 2018), which may result in increased aggression (Penfold et al., 2021). Castration is reported to have little effect on aggressive behaviour in many primate species, whether the procedure was done before or after puberty (Hevesi, 2023). For example, studies on brown-mantled tamarin (Saguinus fuscicollis) report no decrease in aggression, scent marking or display behaviours (Epple, 1978). In Javan langurs (Trachypithecus auratus), castrated males were reported to became more submissive, which could suggest that these methods may have influence on males' social group status (Baker and Farmer, 2023). Castration may also delay social developments in castrated individuals and can be linked to chronic changes in bone densities (Hevesi, 2023).

7. Primates in captivity

Currently, there are 848 institutions in 6 regions currently housing 42,530 primates in captivity globally (ZIMS, 2023). An estimated 968(+) primates are currently on a surplus list and 556 are surplus male primates in European zoos (ZIMS, 2023). A 2021 report from the IUCN Species Survival Commission (SSC) Primate specialist group (IUCN SSC, 2021) states that of the 217 Neotropical monkey species found in Mexico and Central and South America, 24% (52) are

Critically Endangered or Endangered and 42% (92) are threated, either being classed as threatened, including Columbian black-faced spider monkeys (Ateles fusciceps rufiventris).

8. Spider monkeys

8.1 Wild Columbian black-faced spider monkeys

Columbian black-faced spider monkeys are a Neotropical monkey which have one of the broadest geographical ranges, sizes varying between 95 and 390 hectares in continuous forests of any Neotropical primate (Collins, 2008; Wallace, 2008). They are classed as Vulnerable under the IUCN Red list with numbers continuing to decline (IUCN, 2022). Spider monkeys are canopydwelling, frugivorous primates (Ramos-Fernandez, 2008) and have a widespread distribution throughout Central and Southern America and live in a social system described as high fission-fusion (Ramos-Fernandez, 2008; Aureli and Schaffner, 2008) and is thought to have evolved to reduce intragroup conflict over space and fruit distribution (Davis et al., 2009). Research on different wild Ateles groups has highlighted how greatly composition and sex ratio amongst different species vary; they can range between 15-50 individuals in a group with 5-15 adult females and 1-15 adult males and the demographics of communities differ significantly across both communities and species (Shimooka et al., 2008). Spider monkeys form a patrilineal social structure, meaning that the number of males in a group is likely to differ depending on the history of the group (Shimooka et al., 2008). Male spider monkeys will travel in all male subgroups and will affiliate with each other more regularly than females and will also defend their territory during intergroup confrontations and will also make joint raids into neighbouring groups. It is also suggested that this is why males need to travel together with other males (Aureli and Schaffner, 2008).

There are mixed reports on male-male interactions in wild Ateles populations highlighting that while intracommunity adult male-male aggression happens very rarely, there are instances of coalitionary lethal aggression taking place, suggesting that aggression amongst males could be more common than first thought (Fedigan and Baxter, 1984; Aureli and Schaffner, 2008; Valero et al., 2006; Campbell, 2006). Despite male Ateles being philopatric, recent findings suggest that male-male relationships may not be as robust as once thought (Aureli et al., 2013). This may explain why it is currently uncommon for zoos to have more than one adult male in a captive group and that having or introducing more than one adult or subadult male into a group can lead to excessive amounts of severe and lethal aggressive behaviour directed to and received by males (Aureli and Schaffner, 2008). Zoo-housed spider monkeys are mainly kept in small social groups, with an adult breeding male, breeding adult females and their offspring (Davis et al., 2009). This is an unnatural social grouping as in the wild, males would remain in their natal group and females would leave to join new groups when reaching sexual maturity (Davis et al., 2009). Spider monkeys are unusual as they do not display a clear dominance hierarchy, but instead form strong bonds and exhibit highly developed coalitionary behaviour (Aureli & Schaffner, 2008).

8.2 Male Spider monkey aggression in captivity

There is little information relating to aggression between zoo housed male spider monkeys, but Davis *et al.*, (2009), highlight important factors to consider, such as housing unrelated and unfamiliar males together, decreased value of male social relationships due to the absence of rival males, equalling a higher level of male intolerance, zoo husbandry management of spider monkey groups and lack of suitable sized enclosures which could be components associated to aggression in male spider monkeys. One factor that could affect male-male aggression is the level of certain hormones, such as testosterone. Chemical contraception and castration are methods used to affect these hormones, which in turn affects fertility. While it is often thought that this could reduce aggression, there is limited research confirming a causal relationship. Deslorelin implants are a safe and successful method for reducing aggression in male baboons (Young 2013), while the efficacy of deslorelin implants for aggression management may be affected by potentially learnt aggressive behaviors (Cowl et al. 2018). More research is needed to determine if chemical or physical castration truly leads to decreased aggression. This project aims to address some of these knowledge gaps by investigating links between contraception or castration and aggression in captive spider monkeys.

The purpose of this research project is to firstly, investigate the effects of contraception and castration on Columbian black-faced spider monkeys' behaviour, especially the effects on social cohesion and male aggression. Secondly, building on the results collected here, I am to improve the current knowledge on the use of chemical castration as a management tool for primates in captivity. The use of contraception and castration is common practice in EAZA zoos as a tool to manage male aggression within a mixed-sex social group due to its testosterone dampening properties. However, it is unclear what effects chemical contraceptives have on reducing aggression in male primates. To address the first aim, I built an in-depth survey to collect information on current management husbandry and welfare practices in EAZA collections that hold Columbian black-faced spider monkeys. Survey results will provide insight into both current husbandry practice, and opinions on the links between and roles of contraceptive techniques and aggression. To address the second aim, faecal samples were collected from sexually mature contracepted and non-contracepted males to establish baseline testosterone concentrations for the species, and relate this to reproductive status (contracepted, castrated, or intact), age-class, and behaviour.

9. Methods

9.1 Study subjects

A survey was prepared using Jisc Online Surveys (Jisc, 2023), a web-based survey software, designed to collect information from EAZA collections currently holding Columbian black-faced spider monkeys.

Survey data was collected from 12 keepers at 12 EAZA institutions. These institutions house groups of 1-15 spider monkeys (96 total). The subjects of this study are 6 contracepted, 1 surgically castrated and 16 noncontracepted male Columbian black-faced spider monkeys (Appendix A). The EEP coordinator for this studbook is responsible for managing the genetic population of 244 animals in 38 EAZA institutions, which hold 82 males and 143 females of various ages, 19 animals classed as unsexed (ZIMS, 2022; Appendix B). My sample size accounts for 9.42% of the total European population.

9.2 Survey

In order to determine whether there are any associations between chemical contraception and testosterone-mediated aggression and to collate as much data as possible from multiple EAZA institutions, it was decided that an indepth survey would be suitable. I chose to survey spider monkey keepers rather than ask them to perform new behavioural observations for several reasons: the first being that a survey allowed me to investigate both current and historical observations and experiences from these keepers, and the second being that a zookeeper's schedule is limited, and requesting them to conduct behavioural observations would impose a larger demand on their time, making it less likely for many keepers to agree to participate, especially given the constraints on institutional resources and staff availability imposed by the global COVID pandemic. Zookeeper surveys have successfully been used in previous studies to address questions about animal behaviour, zookeeper attitudes, knowledge, experience, and animal management (Ward and Melfi, 2015, Bullock et al., 2021, Freeman et al., 2010). In order to validate my survey, a pilot test of the survey would need to be constructed and sent to the EAZA institutions first (Tsang et al., 2017), although it was not be possible to send the survey to all the EAZA institutions as I had a very small and specific audience, and I did not want to burden them by having to complete multiple versions of the survey. However, a pilot was sent out to other Chester Zoo primate keepers prior to sending the survey to other institutions. Moreover, a social scientist at Chester Zoo, Dr. Andrew Moss, reviewed the survey question design and wording before it was sent to participants. The survey was developed using Jisc Online Surveys (Jisc, 2023) to collect information on the current management husbandry and welfare practices in EAZA collections that hold spider monkeys. This survey was sent out to 38 EAZA institutions in March 2022 and ran till the end of December 2022. Each institution was asked to answer all the survey questions for each individual male in their collection, whether each male was chemically contracepted, castrated or was intact. The survey provides a baseline understanding of aggressive behaviour for all adult males (4 years and older) in the EEP and includes questions on the frequency and intensity of aggression, aggression in relation to contraception, the type and dose of contraception used. Behavioural data collected from the survey were split into behaviour prior to contraception and, or castration, post contraception/castration behaviour and institutional opinions on contraceptive use. The full survey can be found in Appendix D. Participant information sheets and consent forms were sent out to the participants who agreed to take part in the project.

9.3 Statistical analyses

Descriptive statistics were used to summarise the data. Chi-square tests were used as the data are categorical. The test was to determine whether common aggressive behaviours, aggression received from and directed towards, the intensity of aggression, consequences of and veterinary intervention due to aggression, situations causing aggression, institutional opinions on male aggression and the use of contraception as a management tool to mitigate male aggression occurred more frequently than by chance prior to contraception/castration. Since the survey data deviates from the assumptions of normality and exhibits skewness, Kruskal-Wallis tests were used to identify whether dominance had a significant effect on trends in aggression and contraception. All tests were done in Jamovi (The Jamovi project, 2021, R Core Team, 2021) using R packages retrieved from https://cran.r-project.org (R packages retrieved from MRAN snapshot 2021-04-01). Significance was determined when $P \le 0.05$.

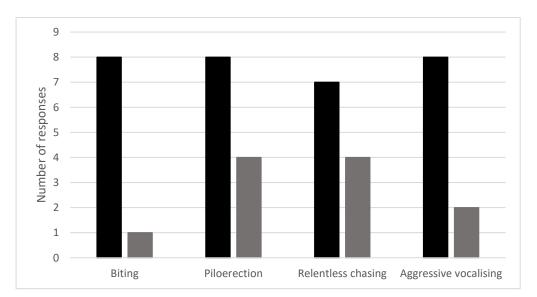
10. Results

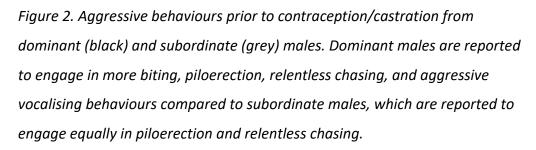
Survey Results

In total, only 12 out of a total of 38 European zoos completed the survey, providing a response rate of 35.2% of zoos which currently hold male Columbian black-faced spider monkeys. This provided data for 34.8% of the European sexually mature male population. Of the 23 males, 13 were classed as dominant and 9 were deemed as being subordinate by zookeepers working with these animals. A third of the males which data has been collected for were either contracepted or castrated. One male was omitted from the results as he lives on his own, is not contracepted/castrated and no behavioural data was provided in the survey.

10.1 Aggressive behaviour

A Chi – squared test was used to calculate the frequencies of all the surveyed males' aggressive behaviours prior to contraception/castration. There was no significant difference in the frequency that aggressive behaviours occurred to prior to contraception (biting – χ^2 = 0.200, df 1, *P* = 0.655; piloerection erection – χ^2 = 0.800, df 1, *P* = 0.371; relentless chasing – χ^2 = 0.200, df 1, *P* = 0.655; aggressive vocalising – χ^2 = 0.000, df 1, *P* = 1.000). A Kruskal-Wallis test was used to analyse whether male dominance status influenced male aggression prior to contraception/castration. Dominant males displayed more aggressive behaviour prior to contraception/castration than subordinate males (Figure 2), however, this was non-significant (χ^2 = 3.74, df 1, *P* = 0.053). One institution commented that aggressive behaviour was not an issue with their males.





10.2 Intensity of aggression

A Chi –square test was used to calculate the intensity of aggression prior to contraception/castration in all surveyed males. There was no significant difference in the frequency that low, mid, and high intensity aggression were reported (χ^2 = 3.65, df 2, *P* = 0.161). A Kruskal-Wallis test was used to determine whether dominance played a role in the intensity of aggression seen. Dominant males were reported to engage more in high (long-term and continuous [54.5%]) to mid (several isolated incidents [45.5%]) intensity of aggression, with no low frequencies of aggression occurring (Figure 3). Subordinate males were reported to engage in more mid (50.0%) to 33.3% low (one isolated incident) frequency of aggression, with one count of high frequency (long-term and continuous) intensity aggression being reported, however, there was no significant effect of dominance status on aggression (χ^2 = 4.34, df 1, *P* = 0.037).

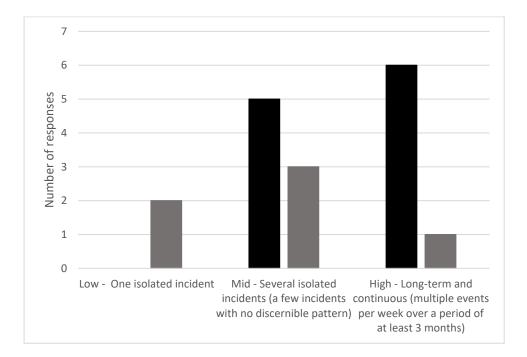


Figure 3. Intensity of aggression reported from dominant (black) and subordinate males (grey).

10.3.1 Consequence of aggression

A Chi – square test was used to calculate the consequences of aggression of all the surveyed males prior to contraception/castration. Respondents were asked whether aggression caused injuries and how severe these injuries were. There was no significant difference in the frequency that different consequences of aggression between males prior to contraception/castration were reported (χ^2 = 2.68, df 3, P = 0.443). A Kruskal Wallis test was used to compare consequence of aggression and dominance. However, as expected, there was a significant difference in the consequences of aggression between dominant and subordinate males (χ^2 = 5.29, df 1, P = 0.021; Figure 4a) in that dominant male aggression resulted in more significant consequences. Half of the respondents said that aggression from dominant males resulted in severe to lethal trauma, while no subordinate males caused severe to lethal outcomes. Aggression from dominant males led mainly to mild to moderate trauma (no veterinary intervention required) (33.3%). Institutions also reported that aggression from 16.7% dominant males resulted in no injury, compared to 57.1% of subordinate male aggression. Subordinate male aggression was only reported to cause mild to moderate injuries in 42.9% of cases (Figure 4a).

10.3.2 Frequency of vet intervention due to male aggression

A Chi – square test was used to calculate the frequency of veterinary intervention due to aggression in all surveyed males prior to contraception/castration while a Kruskal-Wallis test was used to analyse whether dominance had an effect on the frequency of veterinary intervention in all surveyed males. The test indicates how often veterinary intervention was required for aggression caused by either subordinate or dominant males and suggests that the dominance hierarchy was evenly distributed, with no significant differences observed (frequency of aggression: $\chi 2 = 7.05$, df = 4, P = 0.133; dominance: $\chi 2 = 0.632$, df = 1, P = 0.427). Interestingly, 42.9% of dominant male aggression never needed veterinary intervention, compared with 60.0% subordinate males. There were no reports for veterinary intervention occurring on a daily or weekly basis (Figure 4b).

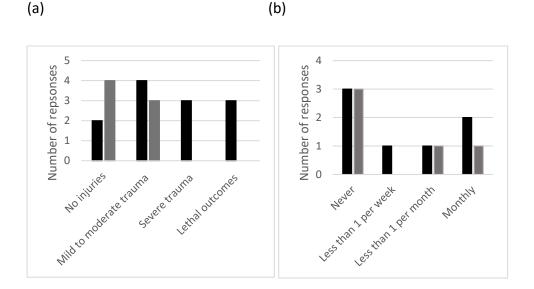


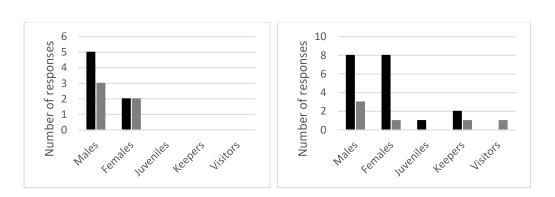
Figure 4. Consequences of dominant male (black) and subordinate male (grey) aggression (a). Frequency of vet intervention between dominant (black) and subordinate (grey) males (b).

10.4 Aggression received from and directed towards

A Chi - square test was used to assess the directionality of aggression prior to contraception/castration, while the Kruskal Wallis test assessed whether dominance influenced the directionality of aggression. Males did not receive aggression from other males, females, or juveniles more than expected prior to contraception or castration, ($\chi^2 = 0.800$, df 1, P = 0.371), irrespective of their dominance status ($\chi^2 = 0.033$, df 1, P = 0.856). However, aggression directed to males from females ($\chi^2 = 7.20$, df 1, P = 0.007; Figure 5a) was significant, but not when comparing across dominance status ($\chi^2 = 0.198$, df 1, P = 0.656). There were no reports of juveniles directing their aggression to

adult males, irrespective of their dominance status. Dominant males were reported to receive 71.4% aggression from other males and 28.5% from females, while subordinate males were reported to receive 60% aggression from other males and 40% from females. No reports of aggression received from juveniles, zookeepers, or visitors for either dominant or subordinate males.

Interestingly, directed aggression from males towards other males and females did not occur significantly more than expected (males: χ^2 = 0.00, df 1, *P* = 1.000; females: χ^2 = 0.00, df 1, *P* = 1.000). There was no significant difference in the proportion of aggression directed towards other males $(\chi^2 = 3.17, df 1, P = 0.075)$ or females $(\chi^2 = 3.17, df 1, P = 0.075)$ between dominant and subordinate males. Significantly less aggression was directed towards juveniles (χ^2 = 16.2, df 1, P = < 0.001), keepers (χ^2 = 9.80, df 1, P = 0.002) and visitors (χ^2 = 16.2, df 1, P = < 0.001) than expected. Dominant males directed aggression towards other males and females equally (42.11% each; Figure 5b), which is expected, compared to 5.3% directed aggression towards juveniles and 10.5% towards keepers. There were no reports of dominant males directing aggression towards visitors. Subordinate males directed half of their aggression towards other males, and 16.7% to females, keepers, and visitors, respectively. No reports of aggression directed towards juveniles was reports. There was no effect of dominance on aggression directed towards juveniles ($\chi^2 = 0.667$, df 1, P = 0.414), keepers $(\chi^2 = 0.0621, df 1, P = 0.803)$ or visitors $(\chi^2 = 1.50, df 1, P = 0.221)$.



(b)

Figure 5. Dominant male (black) and subordinate (grey) male received aggression (a). Dominant (black) and subordinate (grey) directed aggression (b).

10.5 Opinion on male aggression

(a)

A Chi – square test was used to determine zookeepers' perception of dominant and subordinate male aggression within their institutions. Respondents were asked whether males were never aggressive, currently aggressive, or not now, but have been aggressive in the past. Zookeepers reported that 53.84% of dominant males never displayed unmanageable aggression and were equally described as either currently or previously displaying unmanageable aggression (23.08% each). While 100% of subordinate males were described as never displaying unmanageable aggression and 22.22% of zookeepers did not answer this question for subordinate males. There were no reports for subordinate males currently or previously displaying unmanageable aggression. Zookeepers reported that their males never displayed unmanageable aggression significantly more than expected (χ^2 = 11.1, df 3, P = 0.011). However, there was no difference in the frequency that unmanageable aggression was reported across dominance status when using a Kruskal-Wallis test (χ^2 = 6.90, df 3, P = 0.075). Of the 12 institutions taking part in the survey, stated that 53.8% of dominant and all subordinate males never displayed unmanageable aggression (Figure 6), while the remaining 46.2% of dominant males were equally described by zookeepers as either currently or previously displaying unmanageable aggression. Interestingly, of the 12 institutions, 25% did not provide data for this question, which accounts for 13.04% of males for whom we have data for. There were no reports for subordinate males currently or previously displaying unmanageable aggression.

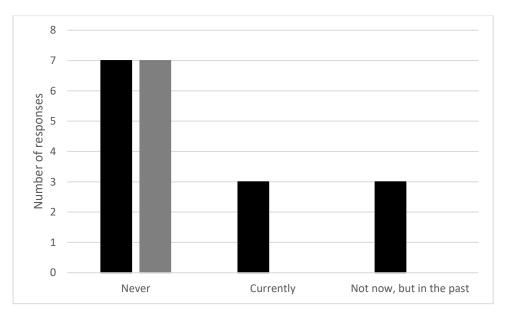


Figure 6. Zookeepers' opinions on dominant (black) and subordinate (grey) male unmanageable aggression.

10.6 Situations causing aggression

A Chi – square test was used to determine which situations caused aggression amongst the sampled males in their groups. Aggression was reported to occur significantly less than expected in response to building work (χ^2 = 12.8, df 1, *P* = <0.001), members of the public (χ^2 = 9.80, df 1, *P* = 0.002), food (χ^2 = 5.00, df 1, *P* = 0.025), public events (χ^2 = 12.8, df 1, *P* = <0.001), females in oestrous and/or mating behaviour (χ^2 = 9.8, df 1, *P* = 0.002), dominance change and/or other male aggression (χ^2 = 5.00, df 1, *P* = 0.025) and keepers (χ^2 = 16.2, df 1, *P* = <0.001) than expected. There was no significant

difference when using Kruskal – Wallis tests across dominance status (building work – χ^2 = 0.088; df 1, *P* = 0.076; members of the public – χ^2 = 0.9935, df 1, *P* = 0.319; food – χ^2 = 1.055, df 1, *P* = 0.304; public events – χ^2 = 0.0880, df 1, *P* = 0.767; females in oestrous and/or mating – χ^2 = 0.062, df 1, *P* = 0.803; dominance change and/or other male aggression – χ^2 = 0.000, df 1, P = 1.00 and keepers – χ^2 = 1.500, df 1, *P* = 0.221). Despite a non-significant finding, interestingly, food caused the most aggression amongst dominant males (33.3%), whereas dominance change and/or other male aggression (25%) and females oestrous and/or mating behaviours were reported less frequently (17%) (Figure 7). Keeper presence did not influence dominant male aggression. Situations reported to cause the least amount of aggression amongst dominant males equally, were building work, members of the public and public event (8.3% each). No reports of keeper presence causing aggressive behaviour in dominant males. Notably, dominance change and/or other male aggression and members of the public caused the most aggression amongst subordinate males (22.3%, respectively). Building work, food, public events, female oestrous and/or mating behaviours, and keepers were reported the least (11.1% each). Interestingly, females oestrous and/or mating behaviours caused very little aggression amongst dominance hierarchies.

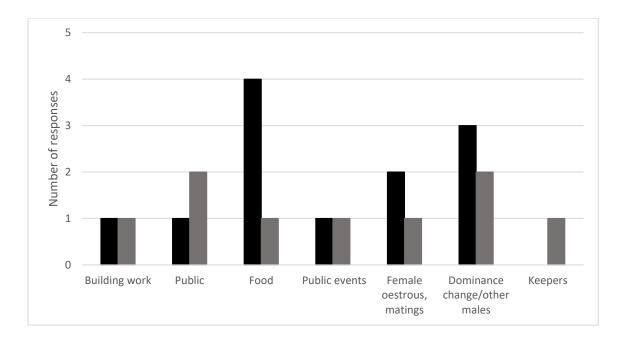


Figure 7. Situations causing dominant (black) and subordinate (grey) male aggression.

10.7 Institutional methods used to mitigate aggression in males

A Chi – square test was used to determine which methods institutions used to mitigate aggression in their groups. Of the 12 institutions that responded to the survey, 8 reported that either contraception and/or castration and enclosure design were their preferred methods to use, followed by 6 institutions preferring transferring of problem animals, 4 choosing separating groups and 3 using fission-fusion management. Training (2 reports), euthanasia (2 reports), and the use of anti-psychotic drugs (1 report) were the least reported methods by institutions. Although, contraception or castration ($\chi^2 = 1.33$, df 1, *P* = 0.248), enclosure access and design ($\chi^2 = 0.333$, df 1, *P* = 0.564), transferring of problem animals ($\chi^2 = 0.00$, df 1, *P* = 1.000), separation of groups ($\chi^2 = 1.33$, df 1, *P* = 0.248) and fission-fusion management ($\chi^2 = 3.00$, df 1, *P* = 0.083) were not reported significantly more than expected, institutions preferred to use these methods to mitigate male aggression than other methods (Figure 8). The least popular methods (training of problem animals – $\chi^2 = 5.33$, df 1, *P* = 0.021; euthanasia –

 χ^2 = 5.33, df 1, *P* = 0.021 and anti-psychotic drugs – χ^2 = 8.33, df 1, *P* = 0.004) were reported significantly less frequently than expected.

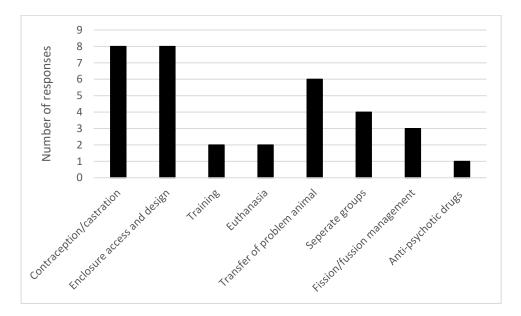


Figure 8. Institutional methods used to mitigate aggression.

10.9 Institution opinion on the use of contraception in mitigating aggression

A Chi – square test was used to determine institutional opinion on the use of contraception in mitigating aggression within their groups. When surveyed about the efficacy of contraception in mitigating aggression, only 8.3% of institutions reported contraception to be "ineffective" ($\chi^2 = 8.33$, df 1, *P* = 0.004), while more than half reported it to be effective ($\chi^2 = 3.00$, df 1, *P* = 0.083) or sometimes effective ($\chi^2 = 1.33$, df 1, *P* = 0.248). A further 17% ($\chi^2 = 5.33$, df 1, *P* = 0.021) responded "I don't know" to the question, and 17% ($\chi^2 = 3.00$, df 1, *P* = 0.083) responded with "other" (Figure 9). The institutions that reported 'other' said that their male was never aggressive and that the group population was controlled, or that they were not using contraception, but may consider using it in the future. No institutions responded that while contraception was useful, they primarily use other methods.

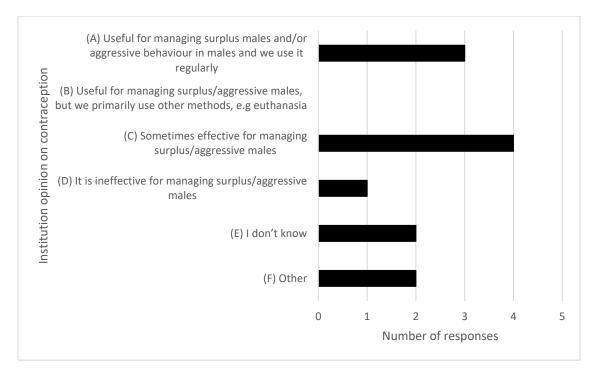


Figure 9. Institutional opinion on the use of contraception to manage male aggression.

11. Contraception

A Chi – square test was used to assess whether there is a disproportionate number of males in each category, i.e. contracepted, castrated, and intact males from the survey. Contraception data collected from the survey for the 23 male spider monkeys indicated that 17.39% were contracepted and/or castrated. There was no significant difference in the number of responses for contraception and/or castrated males and intact males ($\chi^2 = 1.80$, df 1, P = 0.180). While using Kruskal-Wallis test around two-thirds of dominant and subordinate males were left intact, and only a third were contracepted or castrated, there was no significant difference between incidence of treatment and dominance level ($\chi^2 = 0.0348$, df 1, P = 0.852).

The majority of castrated or contracepted males (71.43%) had been contracepted/castrated after the age of sexual maturity, between the age of 4 and 6 years old, while 28.57% were contracepted at the age of 2 years old, when they would still be considered juveniles. All the males which were contracepted, received either 1 x 9.4mg (3 males) or 2 x 9.4mg (3 males) deslorelin implants. One male was reported to be castrated. Institutions were more likely to report that aggression remained the same than that aggression increased post contraception and/or castration (83.33%; $\chi^2 = 13.3$, df 2, *P* = 0.001; Appendix C). No institutions reported a decrease in aggression, while 16.66% reported an increase in male aggressive behaviour.

Discussion

In this thesis, I investigated whether contraception has an effect in modifying aggression in male Columbian black-faced spider monkeys (*Ateles fusciceps rufiventris*). Using an in-depth survey of spider monkey keepers at European zoological institutions, I found that there is no evidence for a mediating role of chemical contraception or castration in aggression levels in adult males of this species. Despite the low sample size, contraception or castration did not appear to decrease aggression, and institutional opinions on the use of contraception to manage male aggression were divided. Further, the survey results show that dominant males received and directed the most aggression and the intensity and consequence of dominant male directed aggression resulted in higher frequencies of severe trauma and lethal outcomes than from subordinate males.

Rates of aggression

While none of the reported aggressive behaviours occurred more than expected, there was a higher frequency of dominant males displaying more types of aggressive behaviours, such as biting, piloerection, relentless chasing, and aggressive vocalising compared to subordinate males, which engaged mostly in piloerection and relentless chasing.

According to Vick, (2008), reports of wild populations explain that while females leave their natal groups, immature males will stay in the group, and they must also join the male hierarchy. This enables the immature males to partner up more with adult males over time, as this partnership with adult males not only provides future training but serves as protection for juveniles within the group. As male spider monkeys cooperate with each other to defend their females, from other groups' males, the collaboration with and the protection of younger males may help to build future coalitions (Vick, 2008). This suggests that captive subordinate male spider monkeys from my study display aggressive behaviours as they try to establish their place in the dominance hierarchy.

Knowing this could suggest the reason why captive subordinate male spider monkeys from my study were reported to display aggressive behaviours in their groups, as they find their place in the dominance hierarchy.

The proportion of aggressive incidents that resulted in severe trauma or lethal outcomes from this study is higher (31.6%) than what was reported by Davis *et al.*, (2009) (26.7%). This proportion is high when comparing data from long-term studies of captive primates in which no severe aggression was reported (Bernstein et al., 1983; Thierry, 1985; Ren et al., 1991; Zucker, 1994; Fuentes et al., 2002, Davis et al., 2009). Interestingly, reported incidents of lethal aggression in captive primates are rare, but have previously been reported in chimpanzees (de Waal, 1986) and golden lion tamarins (Inglett et al., 1989). However, lethal aggression is more frequently reported in wild primates (Itani, 1982 review in) in species such as chimpanzees (Nishida, 1996; Watts et al., 2006), white-faced capuchin monkeys (*Cebus capucinus*) (Gros-Louis et al., 2003) and black-handed spider monkeys (*Ateles geoffroyi*) (Campbell, 2006; Valero et al., 2006). This suggests that higher levels of severe aggression in captive spider monkeys may be a natural behaviour influenced by their social dynamics and environmental conditions.

Dominant males from this survey were reported to engage in higher frequencies of aggression prior to contraception and/or castration than subordinates. Interestingly, dominant male aggression always resulted in trauma, with only two institutions reporting that dominant male aggression resulted in no injuries. Subordinate males caused less severe trauma, ranging from no injuries and mild to moderate trauma. Regular agonistic, noninjurious interactions are typically used to maintain dominance relationships which reduce conflict within a social group (Beisner, et al., 2023). These relationships are used to mitigate conflict among group members by allowing individuals to estimate the outcome of potential contests (Bernstein and Gordon 1974; Rowell, 1974). Dominant and subordinate animals, both use this relationship knowledge to avoid inherent injures from a more serious physical contest. Therefore, a certain level of aggression, and even injury is normal in stable social groups, as seen in macaques and baboons (Beisner, et al., 2023). Although, what can be judged to be normal in terms of frequency and severity of aggression depends on the species (Ruehlmann et al., 1988; Alford et al., 1995; Byrne et al., 1996; McCowan et al., 2008; Beisner et al., 2012).

The severity of dominant male aggression compared with that of subordinates was further evidenced when asking respondents about the frequency of vet intervention due to dominant male aggression. While most zoos reported that very few aggressive events led to the need for veterinary intervention when subordinate males were the instigators, more than half of institutions reported regular interventions when dominant males were involved. These results highlight critical need for better research on ways to effectively mitigate aggressive behaviour within captive primates, particularly in dominant males.

Observations reported by institutions suggest that males received aggression from other males, females, or juveniles, irrespective of their dominance status. Interestingly, there were fewer reports of female directed aggression towards males and as expected, there were no reports of juveniles directing their aggression to adult males. A field study of wild populations of spider monkeys report that injuries or lethal wounds due to intragroup aggression from adult males is more likely to happen to maturing young (Vick, 2008). Ad libitum data from the same field study suggests that subordinate males across all ages are involved in more aggressive behaviours than subordinate females and that males initiate more aggression than females. There was, however, no difference in the frequency of aggression directed by adult males towards or submissive behaviours received from young subordinate males and females at a young age (Vick, 2008). As such, subordinate male aggression appears to be a normal part of a spider monkey society.

Interestingly, dominant males direct the most aggression towards other males and females and caused nearly a guarter of reported lethal outcomes. Dominant males also received aggression mostly from other males, with few accounts from females, while subordinate males were more likely to receive aggression from dominant males and females. This corresponds with the data from Davis *et al.*, 2009 study, which found that captive male spider monkeys were responsible for most of the directed aggression towards other males and some females, while subadult males were more likely to receive aggression from males and females. However, this contradicts reports on wild populations which found that female directed aggression towards males occurs more frequently and reports of aggression between males was virtually absent (Aureli and Schaffner, 2008). This raises the question of whether institutions are wary of "labelling" their males as aggressive and is aggression seen purely as a negative behaviour in the zoo community. Aggression is a natural behaviour and should be talked about and discussed more openly to be able to manage males which are potentially displaying unmanageable aggression. There is little information regarding aggressive behaviour in captive spider monkeys (Davis et al., 2009). Davis et al., (2009), found that even though adult males were responsible for most reported minor aggression and that adult females were more often the targets of minor aggression, it was the subadult males who were more frequently the actors and targets of minor aggression than expected. This result contradicts reports in wild populations, which report that female's direct aggression

towards males more frequently and reports of aggression between males was virtually absent from wild populations, although has been reported (Davis et al., 2009). The frequency of severe and lethal aggression in captive spider monkeys was also investigated by Davis *et al.*, (2009), who highlighted that adult males were more likely to direct aggression and responsible for severe and lethal aggression, while subadult males were more likely to receive aggression. This could be due to the number of males in a group, as the typical aggression pattern in this species, predominantly shown by adult males, starts early. Young males not only participate in more aggressive interactions but also initiate more aggression than young females (Vick, 2008). In previous reports, tension between males was indicated as the cause of aggression, and unrelated males being housed together (because of unnaturally transferring males to other collections) was suggested as another potential cause of tensions and aggression (Davis et al., 2009).

Zookeepers' perception

Respondents' opinions differed, which was not unexpected, however the data gathered from the survey highlighted a few ways in which surveys can be problematic. In this survey, several questions were phrased with many potential answers relating to "negative" information regarding opinion on male aggression, such as the frequencies of vet intervention or severity of consequences of aggression. Institutions may have been wary of labelling males as being "too" aggressive for fear of how aggression is perceived. This could be one reason that some of the institutions chose to not complete these questions at all. If this is the case, then the stigma surrounding aggression and aggressive males need to be removed. Therefore, future surveys should consider using more positive language which may lead to more willingness to engage with certain topics by the respondents.

Keepers also provided more data relating to dominant male aggression, which may suggest that keeping staff are biased towards dominant males. We also found that responses to the survey were discrepant; while keepers did not report that males that displayed long-term and continuous aggression were unmanageable, one male was reported to cause severe trauma, and monthly veterinary intervention was required due to aggression from two males. Interestingly, a quarter of the institutions which completed the survey did not provide data relating to males displaying unmanageable aggression. This gap in the data accounts for 13% of males for whom data was given, even though there were reports of males engaging in several isolated incidents, long term, and continuous bouts of aggression in these males.

Situations causing aggression

Respondents were asked to select which situations caused aggression amongst males in their collection. Food, females in oestrous and/or mating behaviour and dominance change and/or other male aggression caused the most aggression amongst dominant males, which is expected and has been referenced in primate aggression literature, such as Anestis (2006) and Penfold et al. (2021) which discuss the impacts that mating behaviour and dominance have in inducing aggression in males. Contrastingly, subordinate male aggression is sparked by dominance change and/or other male aggression and members of the public, which could suggest redirected aggression towards members of the public. The latter is interesting; Hosey (2005), suggests that captive primate's direct aggression towards targeted visitors, which may suggest that captive primates may view humans as agonistic competitors. Remarkably, fission-fusion management was not a popular method used to mitigate aggression, as potentially zoo enclosures are too small, not equipped and/or built to enable fission-fusion in spider monkey groups which may affect the severity of aggression in captive spider monkey groups.

It is well documented that captive environments have the potential to alter an animal's behaviour when compared to their wild counterparts (Kummer and Kurt, 1965; Hosey, 2005). As previously mentioned, visitors, limited space and animal husbandry practices have the potential to impact animal behaviour in captive primates (Hosey, 2005) and group social behaviours are expected to link with these stimuli (Davis et al., 2009). To try and alleviate this issue from occurring in zoos in the future, the social system of captive primate species, such as spider monkeys and chimpanzees, which live in a high degree of fission-fusion dynamics needs to be taken in to consideration more seriously, as captive situations prevent animals in these sorts of social structures to naturally disperse, where their wild counterparts have the option to leave subgroups to in order to reduce conflict situations (Aureli and Schaffner, 2007, Davis et al., 2009).

Contraception

Institutional opinions were split regarding the effectiveness of contraception as a management tool to mitigate male aggression. This highlights the point that more research needs to be done into the use of chemical contraception in mitigating male aggression. The EAZA Reproductive Management Group, who specialise on contraceptive use in managed wildlife, recommend using 2 x 9.4mg deslorelin implants as a starting dose to reduce testosterone related aggression in male spider monkeys (EAZA RMG, 2023). All the implanted males were reported to either be implanted with 1 x 9.4mg or 2 x 9.4mg deslorelin implants. Interestingly, institutions reported that aggressive behaviour had not changed in most of the male's post contraception, bar one individual, whose aggression was reported to have increased post contraception. Multiple factors could contribute to the lack of efficacy of the implants. Firstly, three of the males that had no change in aggressive behaviour, were described as more subordinate. As the submitting institutions reported that these males never displayed unmanageable aggression, aggression may never have been a significant issue for the institution. Another factor that may explain sustained levels of aggression post-contraception could be the dose, as only 1-2 implants were used in this study (Penfold et al., 2021).

The single instance of increased aggression post-contraception was in a more dominant male who currently displayed unmanageable aggression. This male received his first implant at the age of 9, when he was sexually mature. The lack of contraceptive efficacy in mediating aggression may arise if behavioural patterns of dominance and aggression are already in place by the time an individual reaches sexual maturity (Cowl, et al., 2018; Penfold et al., 2021). Several male spider monkeys in this study had been contracepted/castrated after the age of sexual maturity, while others were contracepted as juveniles. This raises the question of when patterns of aggressive behaviour become established in an individual and potentially resulting in the contraception having no effect in reducing aggression or the contraceptive dose was too low to dampen aggressive behaviour. A recent study by Penfold et al. (2021) points out a variation in response to deslorelin acetate reducing testosterone across individual lion-tailed macaques. One individual was reported to be the most resistant to suppression and was also described as being the most dominant and the most aggressive before treatment. His rank was not a function of his physical size, suggesting that other components may be involved, such as the differences in how each individual absorbs and metabolises the GnRH agonists. Even though aggression had stayed the same in most of the sampled males, and due to the small sample size, this provides a starting point for further investigation into this matter.

Future recommendations

There were four main issues which came out of the survey related to aggression including: further research into chemical contraception as a tool to mitigate aggression in male non-human primates, a reluctance to "label" males as aggressive and generally, what male aggression really is. And lastly, providing appropriate enclosures to species which live in fission-fusion social groups, such as spider monkeys, to enable a more natural flow within the groups.

Further research is needed to better understand whether chemical contraception has an impact on male non-human primate aggression and the use for it in more modern animal management. New or updated best practice guidelines for primates would benefit from having a more detailed section on chemical contraception in aiding mitigating aggression in males, specifically, the recommended age to contracept males, the appropriate dosage needed, the importance and the impact that learnt aggression may have on chemical contraception. This will provide zoos with more information and a better understanding on chemical contraception and the potential benefits of it mitigating aggression in males.

Bacon (2018) discusses the crucial role of zookeepers in managing animal welfare and emphasises the importance of stockmanship skills and knowledge. Stockmanship refers to the skills and practice of managing animals in a safe, effective, and low-stress manner, i.e. a zookeeper needs to posse the knowledge and experience necessary to care for animals under their supervision. Two highlighted aspects of stockmanship include keeper attitude towards animals and their understanding of the animals under their care. This includes understanding the animals' behaviours, needs, and welfare requirements, as well as having a positive attitude towards the animals. Taking a proactive approach to monitor behaviours such as aggression patterns in juvenile and adult males and gaining a deeper understanding of male aggression will facilitate making well-informed decisions regarding the timing of male contraception. A better understanding of male spider monkey aggression in wild and captive populations, including intensity, frequency, and associated agonistic behaviours, as well as potential causes, will equip keeping staff to manage their captive populations more naturally. This is particularly important given the survey's indication that aggression from subordinate males is still perceived negatively. Where in fact, aggression plays a crucial role in shaping social dynamics and ensuring the survival and reproductive success of the group (Bernstein and Gordon, 1974, Holekamp and Strauss, 2016). A quarter of the institutions that took part in the survey did not provide data when asked whether their males displayed unmanageable aggression, which again raises the question of whether keeping staff may have observer bias and are reluctant to describe males as aggressive (Tuyttens, et al., 2014). A better understanding of animal behaviour, circumstances occurring within groups and whether a male is new and its history, are all important factors which should be considered when looking at aggression. Creating a visual aggression management guide for male primates to help zookeepers to assess what is normal and/or unmanageable aggression may help to reduce the stigma surrounding male aggression. This can be done by collecting video footage of these aggressive behaviours, presented at zookeeper workshops, and having open discussions, would be very useful.

Interestingly, only two institutions said that they used euthanasia as a management tool for aggressive males. This highlights another concern: Institutions might hesitate to admit to euthanising healthy animals due to difficulties in managing this sensitive information effectively (Hutchins, 2006). Although euthanasia shouldn't be the primary approach for managing a group, it remains widespread, although often not publicly disclosed (Browning, 2018). Estimates suggest that European zoos affiliated with the European Association of Zoos and Aquaria (EAZA) euthanize between three and five thousand animals annually (Barnes 2014). Institutions should feel more comfortable discussing this issue openly.

Additionally, zoos have a crucial role in public education and engagement. While this aligns with conservation efforts, modern zoos prioritize raising awareness about the challenges faced by endangered species and rallying efforts to protect them, sometimes even more than direct conservation initiatives like breeding programs. Global conservation relies on public involvement and actions, with zoos playing a unique role in promoting environmental responsibility. However, management euthanasia in this context could potentially undermine these objectives.

When housing species which live in a fission-fusion society, such as spider monkeys, institutions must provide more escape routes than are currently available to mitigate aggression (Caws et al., 2008). It's widely acknowledged that animals in captivity can behave differently from their wild counterparts (Kummer and Kurt, 1965; Hosey, 2005). Hosey (2005) emphasised that various factors in zoo environments, such as visitor presence, limited space, and management practices, affect behaviour, often interacting with social dynamics. For instance, the social structure of a species, which varies in terms of group cohesion and mating patterns (van Schaik and van Hooff, 1983), could be altered in captive settings. This might be particularly significant for species with high fission-fusion dynamics, where individuals in the wild can leave subgroups to avoid conflict (Aureli and Schaffner, 2007). Although in this study the relationship between aggression and enclosure design was not investigated, there are reports of lower rates of aggression due to enclosure design enabling fission-fusion, this could be due to coping strategies seen in other primates when confined (Aureli and de Waal, 1997; Judge and de Waal, 1997; Caws and Aureli, 2003). Moreover, small enclosures limit opportunities for subgroup separation, which could affect the intensity of aggression in zoohoused primates (Nieuwenhuijsen and de Waal, 1982). Space is essential for

animals not only because it facilitates access to resources but also serves as a resource itself, providing a physical area for behaviour (Nicol, 2007). Additionally, space plays a crucial role in regulating group social dynamics, with interindividual spacing limits typically enforced through aggression (McBride, 1971). Captive animals exhibit changes in aggression linked to changes in physical environment and resulting effects on social organization (de Waal, 1989). Research extensively explores the effects of changes in available space, particularly regarding spatial restriction in captive environments. Preliminary observations led to the development of a 'densityintensity' model (Nieuwenhuijsen and de Waal, 1982), supported by various studies in primates (Erwin and Erwin, 1976; Nash and Chilton, 1986; Demaria and Thierry, 1989) and non-primates (Blanc and Thériez, 1998; Blanc et al., 1999; Li et al., 2007). However, some primate studies found inconsistent support for this model. For instance, captive chimpanzees showed higher aggression in smaller indoor enclosures, while aggression in socially housed pigtail macaques increased with density but was socially regulated (Nieuwenhuijsen and de Waal, 1982; Anderson et al., 1977). De Waal (1989) proposed a 'coping model,' suggesting that primates modify social interactions to counteract increased aggression risk, employing pre-existing social mechanisms like reconciliation and appeasement behaviours (Judge et al., 2006). Several studies support this coping model (Demaria and Thierry, 1989; Clarke and Mayeaux, 1992; Cordoni and Palagi, 2007), although alternative coping tactics have also been suggested. Designing enclosures which enable and encourage temporary and natural fluctuations in group sizes can be achieved by not only providing more sleeping areas to enable group members to sleep in one place together or on their own and by having bigger enclosures with more areas for dispersion.

In conclusion, this thesis explored the potential effects of contraception on aggression in male Columbian black-faced spider monkeys. Through a comprehensive survey, it was found that chemical contraception and castration did not appear to mediate aggression levels in adult males. Despite the limited sample size, the findings suggest that contraception or castration did not lead to a decrease in aggression, and opinions on the use of contraception to manage male aggression varied among institutions. The survey results revealed that dominant males exhibited higher frequencies of aggression compared to subordinate males, with dominant male aggression resulting in more severe trauma and lethal outcomes. This aligns with reports from both captive and wild primate populations, indicating that dominant males are often the primary instigators and recipients of aggressive behaviours. However, there were discrepancies between captive and wild populations regarding the frequency and targets of aggression, highlighting the complex interplay of factors influencing aggressive behaviour in captive environments. Furthermore, the survey highlighted challenges in managing aggression within captive spider monkey groups, including unnatural groupings, limited understanding of male aggression, and reluctance to address aggression openly. To address these issues, future research should focus on understanding the underlying causes of aggression, evaluating the efficacy of chemical contraception, and implementing better management practices, such as providing appropriate enclosures and promoting natural group dynamics.

References

Alibhai, S. and Jewell, Z. (1994) 'Saving the last rhino: In-situ conservation or captive breeding'. *Unpublished report for the Rhino Foundation*.

Anderson, B., Erwin, N., Flynn, D., Lewis, L. and Erwin, J. (1977) 'Effects of short-term crowding on aggression in captive groups of pigtail monkeys (*Macaca nemestrina*)'. *Aggressive Behaviour*, *3*(1), pp. 33-46.

Anderson, C.A. and Bushman, B.J. (2002) 'Human aggression'. *Annual review of psychology*, 53(1), pp. 27-51.

Anestis, S.F. (2010) 'Hormones and social behaviour in primates'. *Evolutionary Anthropology: Issues, News, and Reviews*, 19(2) pp. 66–78.

Anestis, S.F. (2006) 'Testosterone in juvenile and adolescent male chimpanzees (*Pan troglodytes*): Effects of dominance rank, aggression, and behavioral style'. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, 130(4), pp. 536-545.

Alford, P.L., Bloomsmith, M.A., Keeling, M.E. and Beck, T.F. (1995) 'Wounding aggression during the formation and maintenance of captive, multimale chimpanzee groups'. *Zoo Biology*, *14*(4), pp. 347-359.

Alroy, J. (2015) 'Limits to captive breeding of mammals in zoos'. *Conservation Biology*, 29(3) pp. 926–931.

Ahumada, J.A. (1992) 'Grooming behaviour of spider monkeys (*Ateles geoffroyi*) on Barro Colorado Island, Panama'. *International journal of primatology*, *13*, pp. 33-49.

Asa, C. (1997) 'The development of contraceptive methods for captive wildlife'. *In* Kreeger, T.J. (ed.) *Contraception in Wildlife Management*. Washington DC, United States of America: Technical Bulletin 1853. US Dept of Agriculture, Animal and Plant Health Inspection Service, pp. 235-240.

Asa, C. S. and Porton, I. J. (2005) 'Types of contraception: the choices'. *In* Asa, C.S. and Porton, I. J. (eds.) *Wildlife Contraception, Issues, Methods, and Applications*. Baltimore, Maryland, United States of America: The Johns Hopkins University Press, p. 10, 29-52 and p. 187.

Asa, C.S. (2005) 'Assessing efficacy and reversibility'. *In* Asa, C.S. and Porton, I.J. (eds.) *Wildlife Contraception, Issues, Methods, and Application*. Baltimore, Maryland, United States of America: The Johns Hopkins University Press, pp. 53-65.

Asa, C.S. and Poton, I.J. (2010) 'Contraception as a management tool for controlling surplus animals.' *In* Kleiman, D.G., Thompson, K.V. and Baer, C.K. (eds). *Wild mammals in captivity: principles and techniques for zoo management*. 2nd ed., Chicago: University of Chicago Press, p. 477.

Asa, C.S. and Boutelle, S. (2011) 'Contraception'. *In* Miller, E. and Fowler, M.E. (eds.) *Fowler's Zoo and Wild Animal Medicine Current Therapy*. Vol
7. London, United Kingdom: Elsevier Health Sciences, pp. 8-14.

Asa, C.S (2016) 'Weighing the options for limiting surplus animals'. *Zoo Biology*, 35(3) pp. 183-186.

Aureli, F. and De Waal, F.B. (1997) 'Inhibition of social behavior in chimpanzees under high-density conditions'. *American Journal of Primatology*, *41*(3), pp. 213-228.

Aureli, F., Cords, M. and Van Schaik, C.P. (2002) 'Conflict resolution following aggression in gregarious animals: a predictive framework'. *Animal behaviour*, 64(3), pp. 325-343.

Aureli, F., Schaffner, C.M., Verpooten, J., Slater, K. and Ramos-Fernandez, G. (2006) 'Raiding parties of male spider monkeys: insights into human warfare?'. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, 131(4), pp. 486-497.

Aureli, F. and Schaffner, C.M. (2007) 'Aggression and conflict management at fusion in spider monkeys'. *Biology Letters*, 3(2), pp. 147-149.

Aureli, F and Schaffner, C.M. (2008) 'Social interactions, social relationships and the social system of spider monkeys'. *In* Campbell, C.J. (ed) *Spider Monkeys: Behaviour, Ecology and Evolution of the Genus Ateles*. England: Cambridge University Press, pp. 236 - 265.

Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Fiore, A.D., Dunbar, R.I., Henzi, S.P. and Holekamp, K. (2008) 'Fission-fusion dynamics: new research frameworks'. *Current Anthropology*, *49*(4), pp. 627-654.

Aureli, F., Di Fiore, A., Murillo-Chacon, E., Kawamura, S. and Schaffner, C.M. (2013) 'Male philopatry in spider monkeys revisited'. *American Journal of Physical Anthropology*, *152*(1), pp. 86-95.

Bacon, H., 2018 'Behaviour-based husbandry—A holistic approach to the management of abnormal repetitive behaviours'. *Animals*, *8*(7), p. 103.

Baker, K.R. and Farmer, H.L. (2023) 'The Welfare of Primates in Zoos – Social management'. *In* Robinson, L.M. and Weiss A. (eds.) *Nonhuman Primate Welfare – From History, Science and Ethics to Practice*. Switzerland: Springer, pp. 87-92.

Baratay, E. and Hardouin-Fugier, E. (2004) '*Zoo: A history of zoological gardens in the West*'. London, United Kingdom: Reaktion Books, p. 17.

Barthold, J., Fichtel, C. and Kappeler, P. (2009) 'What is it going to be? Pattern and potential function of natal coat change in sexually dichromatic redfronted lemurs (*Eulemur fulvus rufus*)'. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, 138(1), pp. 1-10.

Beck, B. (1995) 'Reintroduction, zoos, conservation, and animal welfare'. *In* Norton, B., Hutchins, M., Stevens, E. and Maple, T. (eds.) *Ethics on the Ark*.

Washington, United States of America: Smithsonian Institution Press, pp. 155–163.

Becker, J.B., Breedlove, S.M., Crews, D. and McCarthy, M.M. (2002) 'Behavioural Endocrinology'. *In* Becker, J.B., Breedlove, S.M., McCarthy, M.M and Crews, D. (eds.) *Behavioural Endocrinology*. Cambridge, Massachusetts, United states of America: MIT Press, pp. 219-260.

Beisner, B.A., Jackson, M.E., Cameron, A. and McCowan, B. (2012) 'Sex ratio, conflict dynamics, and wounding in rhesus macaques (*Macaca mulatta*)'. *Applied Animal Behaviour Science*, *137*(3-4), pp. 137-147.

Beisner, B.A., Hannibal, D.L., Vandeleest, J.J. and McCowan, B. (2023) 'Sociality, health, and welfare in nonhuman primates'. *In* Robinson, L.M. and Weiss A. (eds.) *Nonhuman Primate Welfare – From History, Science and Ethics to Practice*. Switzerland: Springer, pp. 413-443.

Beissinger, S.R. (2001) 'The California Condor: A Flagship Adrift' [Review of The California Condor: A Saga of Natural History and Conservation, by N. Snyder & H. Snyder]. Conservation Biology, 15(4), pp. 1197–1199.

Bergfeld, E.G.M., D'occhio, M.J. and Kinder., J.E. (1996) 'Pituitary function, ovarian follicular growth, and plasma concentrations of 17p-estradiol and progesterone in prepubertal heifers during and after treatment with the luteinizing hormone-releasing hormone agonist deslorelin'. *Biology of Reproduction*, 54(4), pp. 776–782.

Bernstein, I.S. and Gordon, T.P. (1974) 'The function of aggression in primate societies: Uncontrolled aggression may threaten human survival, but aggression may be vital to the establishment and regulation of primate societies and sociality'. *American Scientist*, 62(3), pp. 304-311.

Bernstein, I., Williams, L. and Ramsay, M. (1983) 'The expression of aggression in Old World monkeys'. *International Journal of Primatology*, *4*, pp. 113-125. Blanc, F. and Thériez, M. (1998) 'Effects of stocking density on the behaviour and growth of farmed red deer hinds'. *Applied Animal Behaviour Science*, *56*(2-4), pp. 297-307.

Blanc, F., Thériez, M. and Brelurut, A. (1999) 'Effects of mixed-species stocking and space allowance on the behaviour and growth of red deer hinds and ewes at pasture'. *Applied Animal Behaviour Science*, *63*(1), pp. 41-53.

Brodie, J.F. (2008) 'A review of American bison (*Bos bison*) demography and population dynamics'. Wildlife Conservation Society & Pennsylvania State University. [Online] [Accessed on 14th September 2022].

Bonczar, M., Wysiadecki, G., Ostrowski, P., Michalczak, M., Plutecki, D., Wilk, J., Michalik, W., Walocha, J., Balawender, K., Iskra, T., Lusina, D., Koziej, M., Radek, M. and Żytkowski, A. (2023) 'The Morphology of the Pituitary Gland: A Meta-Analysis with Implications for Diagnostic Imaging'. *Brain Sciences*, 13(1) p. 89.

Book, A.S., Starzyk, K.B. and Quinsey, V.L. (2001) 'The relationship between testosterone and aggression: A meta-analysis'. *Aggression and Violent Behaviour*, 6(6), pp. 579-599.

Bourry, O., Peignot, P. and Rouquet, P. (2005) 'Contraception in the chimpanzee: 12-year experience at the CIRMF Primate Centre, Gabon'. *Journal of Medical Primatology*, 34(1), pp. 25-34.

Broom, D.M. and Kirkden, R.D. (2004) 'Welfare, stress, behaviour and pathophysiology'. *Veterinary pathophysiology*, pp. 337-369.

Brown, J., Wasser, S., Wildt, D., and Graham, L. (1994) 'Comparative aspects of steroid hormone metabolism and ovarian activity in felids, measured noninvasively in feces'. *Biol. Repr.* 51(4), pp. 776-786. Browning, H. (2018) 'No room at the zoo: Management euthanasia and animal welfare'. *Journal of Agricultural and Environmental Ethics*, *31*(4), pp. 483-498.

Brück, K. (1983) 'Functions of the Endocrine System'. *In* Schmidt, R.F. and Thews, G. (eds.) *Human Physiology*. Heidelberg, Berlin: Springer, pp. 658–687.

Bullock, N., James, C. and Williams, E. (2021) 'Using keeper questionnaires to capture zoo-housed tiger (*Panthera tigris*) personality: considerations for animal management'. *Journal of Zoological and Botanical Gardens*, *2*(4), pp. 650-663.

Buyukmihci, N.C. (2021) 'Castration for Population Control of Macaques in a Sanctuary Setting'.

Byrne, G., Abbott, K.M. and Suomi, S.J. (1996) 'Reorganization of dominance rank among adult males in a captive group of tufted capuchins (*Cebus apella*)'. *Laboratory Primate Newsletter*, *35*, pp. 1-4.

Campbell, C.J. (2006) 'Lethal intragroup aggression by adult male spider monkeys (*Ateles geoffroyi*)'. *American Journal of Primatology: Official Journal of the American Society of Primatologists, 68*(12), pp. 1197-1201.

Chapman, C.A., Fedigan, L.M., Fedigan, L. and Chapman, L.J. (1989) '*Post-weaning resource competition and sex ratios in spider monkeys*'. *Oikos*, pp. 315-319.

Chapman, C.A. and Peres, C.A. (2021) 'Primate conservation: Lessons learned in the last 20 years can guide future efforts'. *Evolutionary Anthropology: Issues, News, and Reviews*, 30(5), pp. 345–361.

Carlstead, K. (1996) 'Effects of captivity on behaviour'. *In* Kleiman, D.G., Allen, M.E., Thompson, K.V. and Lumpkin, S. (eds.) *Wild Animals in Captivity:*

Principles and techniques for zoo management. Chicago, United States of America: University of Chicago Press, pp. 317-333.

Carter, S. and Kagan, R. (2010) 'Management of "surplus" animals'. *In* Kleiman, D.G., Allen, M.E., Thompson, K.V. and Lumpkin, S. (eds.) *Wild mammals in Captivity: Principles and techniques for zoo management*. Chicago, United States of America: University of Chicago Press, pp. 263-267.

Caws, C. and Aureli, F. (2003) 'Chimpanzees cope with temporary reduction of escape opportunities'. *International Journal of Primatology, 24*, pp. 1077-1091.

Caws, C.E., Wehnelt, S. and Aureli, F. (2008) 'The effect of a new vertical structure in mitigating aggressive behaviour in a large group of chimpanzees (Pan troglodytes)'. *Animal Welfare*, *17*(2), pp. 149-154.

CITIES! (n.d.) What is CITIES?. [Online] [Accessed on 23rd October 2022]. <u>https://cites.org/eng/disc/what.php#:~:text=CITES%20(the%20Convention%200n%20International,the%20survival%20of%20the%20species</u>

Clarke, M.R. and Mayeaux, D.J. (1992) 'Aggressive and affiliative behaviour in green monkeys with differing housing complexity'. *Aggressive Behaviour*, *18*(3), pp. 231-239.

Collins, A.C. (2008) 'The taxonomic status of spider monkeys in the twentyfirst century'. *In* Campbell, C.J. (ed). *Spider Monkeys: Behaviour, Ecology and Evolution of the Genus Ateles*. England: Cambridge University Press, p. 51.

Conde, D.A., Colchero, F., Gusset, M., Pearce-Kelly, P., Byers, O., Flesness, N., Browne, R.K. and Jones, O.R. (2013) 'Zoos through the lens of the IUCN red list: a global metapopulation approach to support conservation breeding programs'. *PloS One*, 8(12) pp. e80311.

Conway, W. (1999) 'Linking Zoo and field, and keeping promises to dodos'. *In Proceedings of the 7th World Conference on Breeding Endangered Species*.

Cincinnati, Ohio, United States of America: Cincinnati Zoo and Botanical Garden, pp. 5-11.

Cordoni, G. and Palagi, E. (2007) 'Response of captive lowland gorillas (*Gorilla gorilla gorilla*) to different housing conditions: testing the aggression-density and coping models'. *Journal of Comparative Psychology*, *121*(2), p.171.

Cowl, V.B. and Shultz, S. (2017) 'Large brains and groups associated with high rates of agonism in primates'. *Behavioural Ecology*, *28*(3), pp. 803-810.

Cowl, V.B., Walker, S.L., and Rambaud, Y.F. (2018) 'Assessing the efficacy of deslorelin acetate implants (Suprelorin) in alternative placement sites'. *Journal of Zoo and Wildlife Medicine*, 49(1), pp. 1-8.

Cowl, V. B., Walker, S. L. and Shultz, S. (2021) 'Reproductive males are effective at managing conflict in captive Sulawesi crested macaques (*Macaca nigra*)'. *American Journal of Primatology*, 83(7).

Davis, N., Schaffner, C.M. and Smith, T.E. (2005) 'Evidence that zoo visitors influence HPA activity in spider monkeys (*Ateles geoffroyii rufiventris*)'. *Applied Animal Behaviour Science*, 90, pp. 131-141.

Davis, N., Schaffner, C.M. and Wehnelt, S. (2009) 'Patterns of injury in zoohoused spider monkeys: A problem with males?'. *Applied Animal Behaviour Science*, 116(2-4), pp. 250-259.

De Almeida, R.M.M., Cabral, J.C.C. and Narvaes, R. (2015) 'Behavioural, hormonal and neurobiological mechanisms of aggressive behaviour in human and nonhuman primates'. *Physiology & behaviour*, 143, pp. 121-135.

Deag, J.M. (1977) 'Aggression and submission in monkey societies'. *Animal Behaviour*, 25(2), pp. 465-474.

Demaria, C. and Thierry, B. (1989) 'Lack of effects of environmental changes on agonistic behaviour patterns in a stabilizing group of stumptailed macaques (*Macaca arctoides*)'. *Aggressive behaviour*, *15*(5), pp. 353-360. Dettmer, A.M., Heckman, J.J., Pantano, J., Ronda, V. and Suomi, S.J. (2020) 'Intergenerational effects of early-life advantage: lessons from a primate study'. *National Bureau of Economic Research*, No. w27737.

de Waal, F.B. (1989) 'The myth of a simple relation between space and aggression in captive primates'. *Zoo biology*, *8*(S1), pp. 141-148.

de Waal, F.B. (1986) 'The brutal elimination of a rival among captive male chimpanzees'. *Ethology and Sociobiology*, *7*(3-4), pp. 237-251.

de Waal, F. B. M. (1989). 'Dominance 'style' and primate social organization'. *In* Standen, V. and Foley, R. A. (eds.) *Comparative Socioecology*, Oxford, United Kingdom: Blackwell, pp. 243–263.

de Waal, F. B. (2002) 'Codevelopment of dominance relations and affiliative bonds in rhesus monkeys'. *In* Fairbanks, L.A. and Pereira, M.E. (eds.) *Juvenile primates: Life history, development and behaviour.* Chicago, United States of America: University of Chicago Press, pp. 259-270.

Dixson, A.F. (1980) 'Androgens and aggressive behaviour in primates: A review'. *Aggressive Behaviour*, 6(1), pp. 37-67.

Dixson, A.F. (1993) 'Sexual and aggressive behaviour of adult male marmosets (*Callithrix jacchus*) castrated neonatally, prepubertally, or in adulthood'. *Physiology & behaviour*, 54(2), pp. 301-307.

Dröscher, I. and Waitt, C.D. (2012) 'Social housing of surplus males of Javan langurs (*Trachypithecus auratus*): Compatibility of intact and castrated males in different social settings'. *Applied Animal Behaviour Science*, 141(3-4), pp. 184-190.

Dunayer, E.S. and Berman, C.M. (2018) 'Infant Handling Among Primates'. International Journal of Comparative Psychology, 31.

Egbedate, A.O., Gadsby, E.L., Idoiga, A. and Jenkins, P.D. (2014) 'Vasectomy in Drill Monkeys (*Mandrillus leucophaeus*)-A Population Management Tool'. *World Journal of Zoology*, 9(2), pp. 107-110. Eisenegger, C., Haushofer, J. and Fehr, E. (2011) 'The role of testosterone in social interaction'. *Trends in Cognitive Sciences*, 15(6) pp. 263–271.

Ekanayake-Alper, D.K., Wilson, S.R. and Scholz, J.A. (2018) 'Retrospective Review of Surgical Outcomes and Pair-housing Success in Vasectomized Rhesus Macaques (*Macaca mulatta*)'. *Comparative Medicine* 68(2), pp. 168-176.

Epple, G. (1978) 'Lack of effects of castration on scent marking, displays, and aggression in a South American primate (*Saguinus fuscicollis*)'. *Hormones and behaviour*, 11(2), pp. 139-150.

Epple, G., Alveario, M.C. and Belcher, A.M. (1990) 'Copulatory behaviour of adult tamarins (*Saguinus fuscicollis*) castrated as neonates or juveniles: effect of testosterone treatment'. *Hormones and behaviour*, 24(4), pp. 470-483.

Erwin, N. and Erwin, J. (1976) 'Social density and aggression in captive groups of pigtail monkeys (*Macaca nemestrina*)'. *Applied Animal Ethology*, *2*(3), pp. 265-269.

European Association of Zoos and Aquaria (EAZA RMG). (2023) *Brown spider monkey contraception factsheet* [Online] [Accessed on 24th January 2023]. https://eazarmg.org/home/viewdocument?filename=EGZAC%20Brown%20sp ider%20monkey%20contraceptive%20guideline%202016.pdf

Fa, J. E. (1992) 'Visitor-directed aggression among the Gibraltar macaques'. *Zoo Biology*, *11*(1), pp. 43-52.

Fàbregas, M. and Guillén-Salazar, F. (2007) 'Social compatibility in a newly formed all-male group of white crowned mangabeys (*Cercocebus atys lunulatus*)'. *Zoo Biology*, 26(1) pp. 63–69.

Farmer, H.L., Baker, K.R. and Cabana, F. (2023) 'Housing and husbandry for primates in zoos.' *In* Robinson, L.M. and Weiss, A. (eds.) *Nonhuman primate welfare: from history, science, and ethics to practice*. Cham, Switzerland: Springer International Publishing pp. 355-374. Faust, L.J., Long, S.T., Perišin, K. and Simonis, J.L. (2019) 'Uncovering challenges to sustainability of AZA Animal Programs by evaluating the outcomes of breeding and transfer recommendations with PMCTrack'. *Zoo biology*, 38(1), pp. 24-35.

Fedigan, L.M. and Baxter, M.J. (1984) 'Sex differences and social organization in free-ranging spider monkeys (*Ateles geoffroyi*)'. *Primates*, *25*(3), pp. 279-294.

Ferrie, G.M., Becker, K.K., Wheaton, C.J., Fontenot, D. and Bettinger, T. (2011) 'Chemical and surgical interventions to alleviate intraspecific aggression in male collared lemurs (*Eulemur collaris*)'. *Journal of Zoo and Wildlife Medicine*, 42(2), pp. 214-221.

Freeman, E.W., Schulte, B.A. and Brown, J.L. (2010)' Using behavioural observations and keeper questionnaires to assess social relationships among captive female African elephants'. *Zoo Biology*, *29*(2), pp. 140-153.

Fuentes, A., Malone, N., Sanz, C., Matheson, M. and Vaughan, L. (2002) 'Conflict and post-conflict behaviour in a small group of chimpanzees'. *Primates*, *43*, pp. 223-235.

Fultz, A. (2017) 'A guide for modern sanctuaries with examples from a captive chimpanzee sanctuary'. *Animal Studies Journal*, 6(2), pp. 9-29.

Giammanco, M., Tabacchi, G., Giammanco, S., Di Majo, D. and La Guardia, M. (2005) 'Testosterone and aggressiveness'. *Med Sci Monit*, 11(4), pp. 136-145.

Gibson, K.N. (2010) 'Male mating tactics in spider monkeys: sneaking to compete'. *American journal of primatology*, *72*(9), pp. 794-804.

Glaeser, S., Edwards, K., Paris, S., Scarlata, C., Lee, B., Wielebnowski, N., Finnell, S., Somgird, C., and Brown, J. (2022) 'Characterization of longitudinal testosterone, cortisol, and musth in male Asian elephants (*Elephas maximus*), effects of Aging, and adrenal responses to social changes and health events'. *Animals*, 12(10): 1332. Goodall, J. (1977) 'Infant killing and cannibalism in free-living chimpanzees'. *Folia primatologica*, 28(4), pp. 259-282.

Greenwell, P. J., Riley, L. M., Lemos De Figueiredo, R., Brereton, J. E., Mooney, A. and Rose, P. E. (2023) 'The societal value of the modern zoo: A commentary on how zoos can positively impact on human populations locally and globally'. *Journal of Zoological and Botanical Gardens*, 4(1) pp. 53–69.

Gros-Louis, J., Perry, S. and Manson, J.H. (2003) 'Violent coalitionary attacks and intraspecific killing in wild white-faced capuchin monkeys (*Cebus capucinus*)'. *Primates*, *44*, pp. 341-346.

Ha, J. C. and Sussman, A. F (2023) 'Primate Breeding Colonies: Colony management and Welfare. 4.3 Genetic Management'. *In* Robinson, L.M. and Weiss A. (eds.) *Nonhuman Primate Welfare – From History, Science and Ethics to Practice*. Switzerland: Springer, p 317.

Hall, K. R. L. (1964) 'Aggression in monkey and ape societies'. *In* Carthy, J.D. and Ebling, F.J. (eds.) *The natural history of aggression*. London, United Kingdom and New York, United States of America: Academic Press, pp. 51-64.

Hevesi, R. (2023) 'The Welfare of Primates Kept as Pets and Entertainers -'Undesirable' Behaviours and Interventions'. *In* Robinson, L.M. and Weiss A. (eds.) (2023) *Nonhuman Primate Welfare – From History, Science and Ethics to Practice*. Switzerland: Springer, pp. 134-135.

Higginbottom, K., Tribe, A. and Booth, R. (2003) 'Contributions of nonconsumptive wildlife tourism to conservation'. *Nature-based tourism, environment and land management*, pp. 181-195.

Hiller-Sturmhöfel, S. and Bartke, A. (1998) 'The endocrine system: an overview'. *Alcohol health and research world*, 22(3), p. 153.

Holekamp, K.E. and Strauss, E.D. (2016) 'Aggression and dominance: an interdisciplinary overview'. *Current Opinion in Behavioural Sciences*, *12*, pp. 44-51.

Homer, T. (2006). *The Book of Origins*. London, United Kingdom: Portrait, Piatkus Books Limited, p. 334 and p. 336.

Honess, P.E. and Marin, C.M. (2006a) 'Enrichment and aggression in primates'. *Neuroscience & Biobehavioural Reviews*, 30(3), pp. 413-436.

Honess, P.E. and Marin, C.M. (2006b) 'Behavioural and physiological aspects of stress and aggression in nonhuman primates'. *Neuroscience & Biobehavioural Reviews*, 30(3), pp. 390-412.

Hosey, G.R. (2005) 'How does the zoo environment affect the behaviour of captive primates?' *Applied Animal Behaviour Science*,90(2), pp. 107–129.

Hosey, G., Melfi, V.A. and Pankhurst, S. (2009) 'Captive breeding'. *In* Hosey, G., Melfi, V.A. and Pankhurst, S. (eds.) *Zoo animals: behaviour, management and welfare*. New York, United States of America: Oxford University Press, pp. 292–345.

Hosey, G. (2023) 'The History of Primates in Zoos'. *In* Robinson, L.M. and Weiss A. (eds.) *Nonhuman Primate Welfare – From History, Science and Ethics to Practice*. Switzerland: Springer, pp. 3-29.

Hutchins, M. (2006) 'Death at the zoo: The media, science, and reality'. *Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association*, *25*(2), pp. 101-115.

Inglett, B.J., French, J.A., Simmons, L.G. and Vires, K.W. (1989) 'Dynamics of intrafamily aggression and social reintegration in lion tamarins'. *Zoo Biology*, *8*(1), pp. 67-78.

Itani, J. (1982) 'Intraspecific killing among non-human primates'. *Journal of Social and Biological Structures*, *5*(4), pp. 361-368.

Jamieson, D. (1986) 'Against zoos'. *In* Armstrong, S.J. and Botzler, R.G (eds.) (2017) *The animal ethics reader*. 3rd ed., New York, United States of America: Routledge, pp. 606-611. The jamovi project. (2021). *jamovi*. Version 2.2 [Software]. Sydney: Australia. [Accessed on 1st April 2023) <u>https://www.jamovi.org</u>

Jisc Online surveys (formerly BOS). (2023). *Jisc Online surveys*. Version 3 [Software]. Bristol: United Kingdom. [Accessed on 31st December 2022] <u>https://admin.onlinesurveys.ac.uk</u>

Jones, C. (1987) 'Goodall, J. The Chimpanzees of Gombe, Patterns of Behaviour'. *Journal of Mammalogy*, 68(1), pp. 201-202

Jones, C.G. (2015) 'The limits of the Ark: What are the constraints on maintaining populations of endangered species in captivity?' *Durrell Solitaire*, 26, pp. 3-8. [Online].

Judge, P.G. and De Waal, F.B. (1997) 'Rhesus monkey behaviour under diverse population densities: coping with long-term crowding'. *Animal behaviour*, *54*(3), pp. 643-662.

Judge, P.G., Griffaton, N.S. and Fincke, A.M. (2006) 'Conflict management by hamadryas baboons (*Papio hamadryas hamadryas*) during crowding: A tension-reduction strategy'. *American Journal of Primatology: Official Journal of the American Society of Primatologists, 68*(10), pp. 993-1006.

Junaidi, A., Williamson, P.E., Cummins, J.M., Martin, G.B., Blackberry, M.A. and Trigg, T.E. (2003) 'Use of a new drug delivery formulation of the gonadotrophin-releasing hormone analogue deslorelin for reversible longterm contraception in male dogs'. *Reproduction, Fertility and Development*, 15(6), pp. 317-322.

Kalin, N.H. (1999) 'Primate models to understand human aggression'. *Journal* of Clinical Psychiatry, 60(15), pp. 29-32.

Kemppainen, R.J. (2022) *Professional Version. The Endocrine System of Animals.* MSD Manual. Veterinary Manual [Online] [Accessed on 24th October 2022] <u>https://www.msdvetmanual.com/endocrine-system/endocrine-systemintroduction/the-endocrine-system-of-animals</u> Kessler, M.J., Wang, Q., Cerroni, A.M., Grynpas, M.D., Gonzalez Velez, O.D., Rawlins, R.G., Ethun, K.F., Wimsatt, J.H., Kensler, T.B. and Pritzker, K.P. (2016) 'Long-term effects of castration on the skeleton of male rhesus monkeys (*Macaca mulatta*)'. *American journal of primatology*, 78(1), pp. 152-166. <u>https://doi.org/10.1002/ajp.22399</u>

Keulartz, J. (2015) 'Captivity for Conservation? Zoos at a Crossroads'. *Journal of Agricultural and Environmental Ethics*, 28(2) pp. 335-351.

Klein, L. and Klein, D. (1971) 'Aspects of social behaviour in a colony of spider monkeys at San Francisco Zoo'. *International Zoo Yearbook*, *11*(1), pp. 175-181.

Kling, A. (1975) 'Testosterone and aggressive behaviour in man and nonhuman primates'. *Hormonal correlates of behavior*, *1*, pp. 305-326.

Knickmeyer, R.C. and Baron-Cohen, S. (2006) 'Foetal testosterone and sex differences'. *Early human development*, 82(12), pp. 755-760.

Koenig, A., Scarry, C.J., Wheeler, B.C. and Borries, C. (2013) 'Variation in grouping patterns, mating systems and social structure: what socio-ecological models attempt to explain'. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1618), p.20120348.

Koot, S., Kapteijn, C.M., Huiskes, R.H. and Kranendonk, G. (2016) 'A note on the social compatibility of an all-male group of hamadryas baboons (*Papio hamadryas*)'. *Journal of Zoo and Aquarium Research*, 4(1), pp. 7-13.

Kovacs-Balint, Z.A., Raper, J., Richardson, R., Gopakumar, A., Kettimuthu, K.P., Higgins, M., Feczko, E., Earl, E., Ethun, K.F., Li, L. and Styner, M. (2023) 'The role of puberty on physical and brain development: A longitudinal study in male Rhesus Macaques'. *Developmental Cognitive Neuroscience*, 60, p.101237.

Kummer, H. (1971) *Primate Societies: Group Techniques of Ecological Adaptation*. Arlington Heights, IL: AHM Publishing Corporation. Kummer, H. (1965) 'A comparison of social behaviour in captive and wild hamadryas baboons'. *The baboon in medical research*, pp. 1-46.

Law, S., Prankel, S., Schwitzer, C. and Dutton, J. (2021) 'Inter-specific interactions involving *Lemur catta* housed in mixed-species exhibits in UK zoos'. *Journal of Zoo and Aquarium Research*, 9(4), pp. 247-258.

Lemmens, C. (2018) *Contraception techniques in non-human primates in the context of shelter and rehabilitation.* Ph.D. Ghent University. [Online] [Accessed 9th June 2022]

https://libstore.ugent.be/fulltxt/RUG01/002/481/242/RUG01-002481242 2018 0001 AC.pdf

Leshner, A.I. (1975) 'A model of hormones and agonistic behaviour'. *Physiology & Behaviour*, 15(2), pp. 225-235.

Leus, K., Traylor-Holzer, K. and Lacy, R.C. (2011) 'Genetic and demographic population management in zoos and aquariums: Recent developments, future challenges and opportunities for scientific research'. *International Zoo Yearbook*, *45*(1), pp. 213-225.

Lewandowski, A.H. (2003) 'Surplus animals: the price of success'. *Journal of the American Veterinary Medical Association*, 223(7), pp. 973-983.

Li, C., Jiang, Z., Tang, S. and Zeng, Y. (2007) 'Influence of enclosure size and animal density on faecal cortisol concentration and aggression in Pere David's deer stags'. *General and Comparative Endocrinology*, *151*(2), pp. 202-209.

Lueders, I. and Allen, W.T. (2020) 'Managed wildlife breeding - An undervalued conservation tool?'. *Theriogenology*, 150, pp. 48-54.

McCowan, B., Anderson, K., Heagarty, A. and Cameron, A. (2008) 'Utility of social network analysis for primate behavioural management and wellbeing'. *Applied Animal Behaviour Science*, *109*(2-4), pp. 396-405. MacDougall-Shackleton, S.A., Bonier, F., Romero, L.M. and Moore, I.T. (2019) 'Glucocorticoids and "stress" are not synonymous'. *Integrative Organismal Biology*, 1(1), p.obz017.

Makhanova, A. (2023) 'Hormonal Mechanisms of Partnership Formation'. *In* Shackelford, T.K. (ed.) *The Oxford Handbook of Evolutionary Psychology and Romantic Relationships*. New York, United States of America: Oxford University Press, Incorporated, p. 132.

Mallinson, J.J. (2003) 'A sustainable future for zoos and their role in wildlife conservation'. *Human Dimensions of Wildlife*, 8(1), pp. 59-63.

Mazur, A. (1983) 'Hormones, aggression, and dominance in humans'. *In* Svare, B. (ed.) *Hormones and aggressive behavior*. New York, United States of America: Plenum, pp. 563-576.

Mazur, A. (1976) 'Effects of testosterone on status in primate groups'. *Folia Primatologica*, *26*(3), pp. 214-226.

Mazur, A. and Booth, A. (1998) 'Testosterone and dominance in men'. *Behavioural and Brain Sciences*, 21(3), pp. 353-363.

McBride, G. (1971) 'Theories of animal spacing: the role of flight, fight and social distance'. In *Behaviour and environment: The use of space by animals and men*. Boston, MA: Springer US, pp. 53-68.

Ha, J. C. and Sussman, A. F (2023) 'Primate Breeding Colonies: Colony management and Welfare. 4.3 Genetic Management'. *In* Robinson, L.M. and Weiss A. (eds.) *Nonhuman Primate Welfare – From History, Science and Ethics to Practice*. Switzerland: Springer, p 317.

McPhee, M.E. (2004) 'Generations in captivity increases behavioural variance: considerations for captive breeding and reintroduction programs'. *Biological conservation*, 115(1), pp. 71-77.

Melfi, V., Pankhurst, S. and Hosey, G. (2013). *Zoo Animals: Behaviour, Management, and Welfare*. 2nd ed., Oxford, United Kingdom: OUP Oxford, pp. 16-21.

Michael, R.P. and Zumpe, D. (1993) 'A review of hormonal factors influencing the sexual and aggressive behaviour of macaques'. *American Journal of Primatology*, 30(3), pp. 213-241.

Montoya, E.R., Terburg, D., Bos, P.A. and Van Honk, J. (2012) 'Testosterone, cortisol, and serotonin as key regulators of social aggression: A review and theoretical perspective'. *Motivation and Emotion*, 36(1) pp. 65-73.

Moran, B.M., Thomas, S.M., Judson, J.M., Navarro, A., Davis, H., Sidak-Loftis, L., Korody, M., Mace, M., Ralls, K., Callicrate, T. and Ryder, O.A. (2021) 'Correcting parentage relationships in the endangered California Condor: Improving mean kinship estimates for conservation management'. *Ornithological Applications*, 123(3), p.duab017.

Morgan, K.N. and Tromborg, C.T. (2007) 'Sources of stress in captivity'. *Applied animal behaviour science*, *102*(3-4), pp. 262-302.

Muller, M.N. and Wrangham, R.W. (2004) 'Dominance, aggression and testosterone in wild chimpanzees: a test of the 'challenge hypothesis'. *Animal Behaviour*, 67(1), pp. 113-123.

Muller, M.N. (2017) 'Testosterone and reproductive effort in male primates'. *Hormones and Behaviour*, 91, pp. 36-51.

Munson, L., Bauman, J.E., Asa, C.S., Jöchle, W. and Trigg, T.E. (2001) 'Efficacy of the GnRH analogue deslorelin for suppression of oestrous cycles in cats'. *Journal of reproduction and fertility. Supplement*, 57, pp. 269-273.

Nash, L.T. and Chilton, S.M. (1986) 'Space or novelty?: Effects of altered cage size on Galago behaviour'. *American journal of primatology*, *10*(1), pp. 37-49.

Nicol, C. (2007) 'Space, time, and unassuming animals'. *Journal of Veterinary Behaviour*, 2(6), pp. 188-192.

Nieuwenhuijsen, K. and de Waal, F.B. (1982) 'Effects of spatial crowding on social behaviour in a chimpanzee colony'. *Zoo biology*, 1(1), pp. 5-28.

Nijman, V., Nekaris, K., Donati, G., Bruford, M. and Fa, J. (2011) 'Primate conservation: measuring and mitigating trade in primates'. *Endangered Species Research*, 13(2) pp. 159-161.

Nishida, T. (1996) 'Reports from the field: Mahale, Tanzania: the death of Ntologi, the unparalleled leader of M group [4]'. *Pan Africa News*, *3*(1), pp. 3-4.

Norconk, M.A., Atsalis, S., Tully, G., Santillán, A.M., Waters, S., Knott, C.D., Ross, S.R., Shanee, S. and Stiles, D. (2020) 'Reducing the primate pet trade: Actions for primatologists'. *American Journal of Primatology*, 82(1).

Oates, J.F., Koné, I., McGraw, S. and Osei, D. (2020) *Piliocolobus waldroni. IUCN Red List* (amended version of 2019 assessment). The IUCN Red List of Threatened Species 2020: *e.T18248A166620835*. [Online] [Accessed on 7th April 2022] <u>https://www.researchgate.net/profile/John-Oates-</u> <u>8/publication/341272310 Piliocolobus waldroni IUCN Red List/links/62c33f</u> <u>d63f38b17066d3b94c/Piliocolobus-waldroni-IUCN-Red-List.pdf</u>

Ostner, J., Kappeler, P. and Heistermann, M. (2008) 'Androgen and glucocorticoid levels reflect seasonally occurring social challenges in male red-fronted lemurs (*Eulemur fulvus rufus*)'. *Behavioral Ecology and Sociobiology*, 62(4) pp. 627-638.

Penfold, L.M., Norton, T. and Asa, C.S. (2021) 'Effects of GnRH agonists on testosterone and testosterone-stimulated parameters for contraception and aggression reduction in male lion-tailed Macaques (*Macaca silenus*)'. *Zoo Biology*, 40(6), pp. 541-550.

<u>Penfold, L.M.,</u> Patton, M.L. and Wolfgang, J. (2005) 'Contraception agents in aggression control'. *In* Asa, C.S. and Porton, I.J. (eds.) *Wildlife Contraception,*

Issues, Methods, and Applications. Baltimore, Maryland, United States of America: The Johns Hopkins University Press, p. 188.

Porton, I.J. (2005) 'The ethics of wildlife contraception.' *In* Asa, C.S. and Porton, I.J. (eds.) *Wildlife Contraception, Issues, Methods, and Applications*. Baltimore, Maryland, United States of America: The Johns Hopkins University Press, pp. 3-16.

Porton, I.J. and Dematteo, K.E. (2005) 'Contraception in nonhuman primates'. *In* Asa, C.S. and Porton, I.J. (eds.) *Wildlife Contraception, Issues, Methods, and Applications*. Baltimore, Maryland, United States of America: The Johns Hopkins University Press, p. 119.

Plowman, A., Jordan, N.R., Anderson, N., Condon, E. and Fraser, O. (2004)
'Welfare implications of captive primate population management:
behavioural and psycho-social effects of female-based contraception, oestrus
and male removal in hamadryas baboons (*Papio hamadryas*)'. *Applied Animal Behaviour Science*, 90(2), pp. 155-165.

Powell, D.M., Dorsey, C.L. and Faust, L.J. (2019) 'Advancing the science behind animal program sustainability: An overview of the special issue'. *Zoo Biology*, 38(1), pp. 5-11.

Purohit, D., Manu, S., Ram, M.S., Sharma, S., Patnaik, H.C., Deka, P.J., Narayan, G. and Umapathy, G. (2021) 'Genetic effects of long-term captive breeding on the endangered pygmy hog'. *PeerJ*, 9, p.e12212.

R Core Team (2021) *R: A Language and environment for statistical computing*. Version 4.0. [Software] America: Posit, PBC [Accessed on 1st April 2023] <u>https://cran.r-project.org</u>

Rabb, G.B. (2004) 'The evolution of zoos from menageries to centres of conservation and caring'. *Curator: The Museum Journal*, 47(3), pp. 237-246.
[Online] [Accessed on 28th September 2022].

Ramos-Fernandez, G. (2008) 'Communication in spider monkeys: the function and mechanisms underlying the use of the whinny'. *In* Campbell, C.J. (ed). *Spider Monkeys: Behaviour, Ecology and Evolution of the Genus Ateles*. England: Cambridge University Press, pp. 220-232.

Reed, C., O'Brien, T.G. and Kinnaird, M.F. (1997) 'Male Social Behavior and Dominance Hierarchy in the Sulawesi Crested Black Macaque (*Macaca nigra*)'. *International Journal of Primatology* 18, pp. 247-260.

Ren, R., Yan, K., Su, Y., Qi, H., Liang, B., Bao, W. and de Waal, F.B. (1991) 'The reconciliation behaviour of golden monkeys (Rhinopithecus roxellanae roxellanae) in small breeding groups'. *Primates*, *32*, pp. 321-327.

Richards, A.B., Morris, R.W., Ward, S., Schmitz, S., Rothmond, D.A., Noble, P.L., Woodward, R.A., Winslow, J.T. and Weickert, C.S. (2009) 'Gonadectomy negatively impacts social behaviour of adolescent male primates'. *Hormones and behaviour*, 56(1), pp. 140-148.

Roe, K., McConney, A. and Mansfield, C.F. (2014) 'The role of zoos in modern society - A comparison of zoos' reported priorities and what visitors believe they should be'. *Anthrozoös*, *27*(4), pp. 529-541.

Ross, S.R., Bloomsmith, M.A., Bettinger, T.L. and Wagner, K.E. (2009) 'The influence of captive adolescent male chimpanzees on wounding: Management and welfare implications'. *Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association*, *28*(6), pp. 623-634.

Rowell, T.E. (1974) 'The concept of social dominance'. *Behavioural biology*, *11*(2), pp. 131-154.

Ruehlmann, T.E., Bernstein, I.S., Gordon, T.P. and Balcaen, P. (1988) 'Wounding patterns in three species of captive macaques'. *American journal of primatology*, *14*(2), pp. 125-134.

Ruivo, E.B. and Stevenson, M.F. (2017) *EAZA best practice guidelines for Callitrichidae*. 3.1. [Online] [Accessed 7th April 2022].

https://www.eaza.net/assets/Uploads/CCC/2017-Callitrichidae-EAZA-Best-Practice-Guidelines-Approved.pdf

Ryan, C. and Saward, J. (2004) 'The zoo as ecotourism attraction - Visitor reactions, perceptions and management implications: The case of Hamilton Zoo, New Zealand'. *Journal of Sustainable Tourism*, 12(3) pp. 245-266.

Sainsbury A.W. (1997) 'The humane control of captive marmoset and tamarin populations'. *Animal Welfare* 6(3), pp. 231-242.

Sapolsky, R.M. (1982) 'The endocrine stress-response and social status in the wild baboon'. *Hormones and behaviour*, 16(3), pp. 279-292.

Sapolsky, R. M. (1987) 'Stress, social status, and reproductive physiology in free-living baboons'. *In* Crews, D. (ed.) *Psychobiology of reproductive behaviour: An evolutionary perspective*. New Jersey, United States of America: Prentice-Hall, Inc, pp. 291-322.

Schally, A., Kastin, A., and Coy, D. (1979) 'LH-releasing hormone and its analogues: recent basic and clinical investigations'. International Journal of Fertility, 21, pp. 1-30.

Schlaepfer, M.A., Hoover, C., Dodd, C.K. (2005) 'Challenges in Evaluating the Impact of the Trade in Amphibians and Reptiles on Wild Populations'. *BioScience*, 55(3), pp. 256-264.

Seppan, P. and Krishnaswamy, K. (2014) 'Long-term study of vasectomy in Macaca radiata—histological and ultrasonographic analysis of testis and duct system'. *Systems biology in reproductive medicine*, 60(3), pp. 151-160.

Setchell, J.M., Smith, T., Wickings, E.J. and Knapp, L.A. (2008) 'Social correlates of testosterone and ornamentation in male mandrills'. *Hormones and Behaviour*, 54(3) pp. 365-372.

Silber, S.J., Barbey, N., Lenahan, K. and Silber, D.Z. (2013) 'Applying clinically proven human techniques for contraception and fertility to endangered

species and zoo animals: a review'. *Journal of Zoo and Wildlife Medicine*, 44(4s).

Simpson, K. (2001) 'The role of testosterone in aggression'. *McGill Journal of Medicine*, 6(1), pp. 32-40.

Simon, N.G., McKenna, S.E., Lu, S.F. and Cologer-Clifford, A. (1996) 'Development and expression of hormonal systems regulating aggression'. *In* Ferris, C.F. and Grisso, T. (eds.) *Understanding aggressive behaviour in children*. New York Academy of Sciences. Annals of the New York Academy of Sciences 794, pp. 8-17.

Snyder, N.F.R. and Snyder, H. (2000). *The California Condor: A Saga of Natural History and Conservation*. San Diego, California, United States of America: Academic Press, p. 410.

Soma K. K. (2006). 'Testosterone and aggression: Berthold, birds and beyond'. *Journal of Neuroendocrinology*, 18(7), pp. 543-551.

Soma, K.K., Rendon, N.M., Boonstra, R., Albers, H.E. and Demas, G.E. (2015) 'DHEA effects on brain and behavior: insights from comparative studies of aggression'. *The Journal of steroid biochemistry and molecular biology*, 145, pp. 261-272.

Stoinski, T.S., Hoff, M.P., Lukas, K.E. and Maple, T.L. (2001) 'A preliminary behavioural comparison of two captive all-male gorilla groups'. Zoo Biology, 20, pp. 27-40.

Shimooka, Y., Campbell, C.J., Di Fiore, A., Felton, A.M., Izawa, K., Link, A., Nishimura, A., Ramos-Fernandez, G. and Wallace, R.B. (2008) 'Demography and group composition of Ateles'. *In* Campbell, C.J. (ed). *Spider Monkeys: Behaviour, Ecology and Evolution of the Genus Ateles*. Cambridge, England: Cambridge University Press, pp. 332-334.

Stolwijk, R.C. (2013) *The golden lion tamarin (Leontopithecus rosalia): A flagship species for the Atlantic Forest of Brazil*. M.Sc. Utrecht University.

[Online] [Accessed on 8th February 2023].

https://studenttheses.uu.nl/handle/20.500.12932/14009

Symington, M.M. (1987) 'Sex ratio and maternal rank in wild spider monkeys: when daughters disperse'. *Behavioural Ecology and Sociobiology, 20*, pp. 421-425.

Symington, M.M. (1988) 'Demography, ranging patterns, and activity budgets of black spider monkeys (Ateles paniscus chamek) in the Manu National Park, Peru'. *American Journal of Primatology*, *15*(1), pp. 45-67.

Symington, M.M. (1990) 'Fission-fusion social organization in Ateles and Pan'. *International Journal of Primatology*, *11*, pp. 47-61.

Takeshita, R.S., Huffman, M.A., Kinoshita, K. and Bercovitch, F.B. (2017) 'Effect of castration on social behaviour and hormones in male Japanese macaques (*Macaca fuscata*)'. *Physiology & behaviour*, 181, pp. 43-50.

The International Union for Conservation of nature Primate specialist group. (2021) An Assessment of Endangered Primates - The IUCN Red List of Threatened Species. [Online] [Accessed on 15th July 2022]. http://www.primate-sg.org/red_list_threat_status/

The International Union for Conservation of Nature Red List. (2023) [Online] [Accessed on 9th February 2023].

Thierry, B. (1985) 'Patterns of agonistic interactions in three species of macaque (Macaca mulatta, M fascicularis, M tonkeana)'. *Aggressive Behavior*, *11*(3), pp. 223-233.

Thierry, B. (2007) 'Unity in diversity: lessons from macaque societies'. *Evolutionary Anthropology: Issues, News, and Reviews, 16*(6), pp. 224-238.

Tinbergen, N. (1968) 'On War and Peace in Animals and Man: An ethologist's approach to the biology of aggression'. *Science*, 160(3835), pp. 1411-1418.

Toone, W.D. and Wallace, M.P. (1994) 'The extinction in the wild and reintroduction of the California condor (*Gymnogyps californianus*)'. *In* Olney, P.J.S., Mace, G.M. and Feistner, A.T.C. (eds) *Creative Conservation*. Dordrecht, Germany: Springer, pp. 411-419.

Tribe, A. and Booth, R. (2003) 'Assessing the role of zoos in wildlife conservation'. *Human dimensions of wildlife*, 8(1), pp. 65-74.

Tsang, S., Royse, C.F. and Terkawi, A.S. (2017) 'Guidelines for developing, translating, and validating a questionnaire in perioperative and pain medicine'. *Saudi journal of anaesthesia*, *11*(Suppl 1), pp. S80-S89.

Valero, A., Schaffner, C.M., Vick, L.G., Aureli, F. and Ramos-Fernandez, G. (2006) 'Intragroup lethal aggression in wild spider monkeys'. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *68*(7), pp. 732-737.

Van Roosmalen, M.G.M. (1988) 'The spider monkeys, genus Ateles'. *Ecology* and behaviour of neotropical primates, 2, pp. 455-537.

Van Schaik, C.P. and Van Hooff, J.A.R.A.M. (1983) 'On the ultimate causes of primate social systems'. *Behaviour*, *85*(1-2), pp. 91-117.

Vick, L.G. (2008) 'Immaturity in spider monkeys: a risky business'. *In* Campbell,
C.J. (ed). *Spider Monkeys: Behaviour, Ecology and Evolution of the Genus Ateles*. England: Cambridge University Press, pp. 308-309, 314-319.

Volavka, J. (1995) *Neurobiology of violence*. Washington, DC, United States of America: American Psychiatric Press, pp. 19-21.

Wallace, P.Y., Asa, C.S., Agnew, M. and Cheyne, S.M. (2016) 'A review of population control methods in captive-housed primates'. *Animal Welfare*, 25(1), pp. 7-20.

Wallace, R.B. (2008) 'Factors influencing spider monkey habitat use and ranging patterns'. In Campbell, C.J. (ed). Spider Monkeys: Behaviour, Ecology

and Evolution of the Genus Ateles. England: Cambridge University Press, p. 138.

Wang, Q., Kessler, M.J., Kensler, T.B. and Dechow, P.C. (2016) 'The mandibles of castrated male rhesus macaques (*Macaca mulatta*): The effects of orchidectomy on bone and teeth'. *American journal of physical anthropology*, 159(1), pp. 31-51.

Ward, S.J. and Melfi, V. (2015)' Keeper-animal interactions: Differences between the behaviour of zoo animals affect stockmanship'. *PloS one*, *10*(10), p.e0140237.

Watts, D.P., Muller, M., Amsler, S.J., Mbabazi, G. and Mitani, J.C. (2006) 'Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda'. *American Journal of Primatology: Official Journal of the American Society of Primatologists, 68*(2), pp. 161-180.

WAZA Animal Welfare strategy (2015) *Chapter 5: Breeding Programmes and Collection Planning* [Online] [Accessed on 15th July 2022]. <u>https://www.waza.org/wp-content/uploads/2019/03/WAZA-Animal-Welfare-</u> <u>Strategy-2015 Portrait.pdf</u>

White, B.C., Beare, J., Fuller, J.A. and Houser, L.A. (2003) 'Social spacing in a bachelor group of captive woolly monkeys (*Lagothrix lagotricha*)'. *Neotropical primates*, *11*(1), p. 35.

Willoughby, J.R., Fernandez, N.B., Lamb, M.C., Ivy, J.A., Lacy, R.C. and Dewoody, J.A. (2015) 'The impacts of inbreeding, drift and selection on genetic diversity in captive breeding populations'. *Molecular Ecology*, 24(1), pp. 98-110.

Wingfields, J.C., Lynna, S.E. and Somab, K.K. (2001) 'Avoiding the 'Costs' of Testosterone: Ecological Bases of Hormone-Behaviour Interactions'. *Brain, Behaviour and Evolution*, *57*, pp. 239-251.

Young, H. (2013) The use of deslorelin, a GnRH agonist, to reduce aggression in male chacma baboons (Papio ursinus) to improve animal welfare in a captive setting. M.Sc. Oxford Brookes University.

http://www.nocturama.org/wp-content/uploads/2012/03/Young-2013.pdf

Zimmermann, E. and Lerch, C. (1993) 'The complex acoustic design of an advertisement call in male mouse lemurs (*Microcebus murinus, Prosimii,* Primates) and sources of its variation'. *Ethology*, 93(3), pp. 211-224.

Zimmermann, E. (1996) 'Castration affects the emission of an ultrasonic vocalization in a nocturnal primate, the grey mouse lemur (*Microcebus murinus*)'. *Physiology & behaviour*, 60(3), pp. 693-697.

ZIMS. [Online] [Accessed on 26th September 2022, and 09th February 2023].

https://zims.species360.org/Login.aspx?ReturnUrl=%2f

Zordan, M. (2021) 'Progressive Zoos and Aquariums must be part of the world's response to COVID-19'. IUCN. [Online] [Accessed on 30th January 2023].

Zucker, E.L. (1994) 'Severity of agonism of free-ranging patas monkeys differs according to the composition of dyads'. *Aggressive Behavior, 20*(4), pp. 315-323.

Appendices

Appendix A – Study subjects' breakdown.

Institution	Animal	Dominance	Reproduction
	ID		<u>status</u>
Banham	MIG12-	Subordinate	Intact
(1) +	29775441		
Banham	MIG12-	Subordinate	Intact
(1) +	29775345		
Banham	CBC12-	Dominant	<u>Intact</u>
(1) +	00429		
Chester (2)	MIG12-	Dominant	<u>Intact</u>
*+	29430574		
Chester (2)	CFF17-	Subordinate	<u>Castrated</u>
* +	22672		
Colchester	27313596	Dominant	<u>Intact</u>
(3) * +			
Debrecen	24115980	Unknown	Intact
(4) +			
Emmen (5)	MIG12-	Dominant	<u>Contracepted</u>
+	29251885		
Emmen (5)	VTL14-	Subordinate	<u>Contracepted</u>
+	02879		
Emmen (5)	VTL17-	Dominant	<u>Contracepted</u>
+	00619		
Les_Sables	JYH12-	Dominant	<u>Intact</u>
(6) +	00002		
Wuppertal	DVY14-	Dominant	<u>Contracepted</u>
(7) * +	01018		
Antwerp	12022286	Dominant	<u>Intact</u>
(8) +			
Antwerp	QTR15-	Dominant	<u>Intact</u>
(8) +	04169		

Antwerp	QTR16-	Subordinate	<u>Intact</u>
(8) +	05051		
Blackpool	21041993	Dominant	Intact
(9) +			
Blackpool	YGK18-	Subordinate	Intact
(9) +	02709		
Drayton	MIG12-	Dominant	Intact
Manor (10)	28285727		
+			
Drayton	CBT18-	Subordinate	Intact
Manor (10)	00666		
+			
Fontaine	SWC17-	Dominant	<u>Contracepted</u>
(11) +	01242		
Twycross	MIG12-	Subordinate	Contracepted
(12) * +	29927247		
Twycross	wycross SSD15-		<u>Intact</u>
(12) * +	12725		
Twycross	SSD15-	Subordinate	Intact
(12) * +	12747		c) (L Completed su

(* Faecal samples collected from males) (+ Completed survey for males)

Appendix B - Columbian black-faced spider monkey European holdings and

sex structure.

Region: Europe 38 Institutions	Male	Female	Other	Birth (last 12 month)	Total
Aalborg Zoo - Denmark	1	1	0	0	2
Zoo of Antwerp - Belgium	5	3	1	1	10
Apenheul Primate Park -	2	12	1	1	16
Netherlands					
ZSEA Ltd (Banham Zoo) - England	3	4	0	0	7
Zoo Parc de Beauval - France	6	5	1	1	13
Belfast Zoological Gardens - Ireland	0	7	0	0	7
Zoologischer Garten Berlin AG - Germany	1	1	0	0	2
Birmingham Wildlife Conservation Park - England	0	1	0	0	1
Blackpool Zoo - England	2	4	1	0	7
Chessington World of Adventures, Ltd England	5	7	0	0	12
North of England Zoological Society - England	3	7	0	0	10
Colchester Zoo - England	1	5	0	0	6
Nagyerdei Kultúrpark Nonprofit Kft - Hungary	1	0	0	0	1
Dudley Zoological Gardens - England	1	4	0	0	5
Ree Park - Ebeltoft Safari - Denmark	1	3	1	1	6
Wildlands Adventure Zoo Emmen - Netherlands	5	9	0	1	15
Parco Zoo di Falconara - Italy	1	0	0	0	1
BioParc de Doué - France	1	5	0	0	6
Fota Wildlife Park - Ireland	4	5	0	1	10
Kristiansand Dyrepark ASA - Norway	2	0	0	0	2
Parc Zoologique de La Fleche - France	3	3	0	1	7
Zooland-Park - France	4	0	0	0	4
Zoo Landau in der Pfalz – Germany	6	11	0	2	18
Zoo des Sables d'Olonne - France	1	8	0	0	9
Jardim Zoologico / Lisbon Zoo - Portugal	2	3	1	0	6
Parc Zoologique Et Botanique Mulhouse - France	1	2	0	0	3
Münchner Tierpark Hellabrunn - Germany	1	2	0	0	3
Nyíregyházi Állatpark Nonprofit KFT (Sosto Zoo) - Hungary	1	0	0	0	1

Zoo Osnabrück - Germany	1	6	0	0	7
Château et Parc Zoologique de la	4	5	0	1	10
Bourbansais - France					
Les Terres de Nataé - France	2	0	2	0	4
Drayton Manor Park Zoo - England	3	4	0	0	7
Touroparc - France	2	0	0	0	2
Twycross Zoo - England	4	3	0	0	7
Dierenpark Zie-Zoo - Netherlands	0	1	0	0	1
Zoologischer Garten Wuppertal -	1	4	0	0	5
Germany					
Ogrod Zoologiczny im. Stefana	1	2	0	0	3
Milera - Poland					
Dierenpark 'De Vleut' (BestZoo) -	0	6	1	0	7
Netherlands					
Total	82	143	9	10	244

Male	Dominance status	Age first implanted	Deslorelin implant history	Deslorelin formulation	Castration age	Castration history	Contraception reason	Aggression changes post treatment	Consequenc e of aggression	Frequency of aggression
1	Subordinate	2 yrs 10m	1 st -26/08/20 2 nd -23/09/21	2 x 9.4mg	5 yrs 1m	09/11/22	Implanted early to prevent aggression	No change	Mild to moderate	Several isolated incidents
2	Dominant	9 yrs 0m	1 st - 19/03/18 2 nd - 15/06/20 3 rd - 04/06/21 4 th - 27/06/22	1 x 9.4mg	N/A	N/A	Studbook	Increase	Lethal	Long term and continuous
3	Subordinate	5 yrs 9m	1 st - 15/06/20 2 nd - 04/06/21 3 rd - 27/06/22	1 x 9.4mg	N/A	N/A	Studbook	No change	No injuries	No information provided
4	Dominant	2 yrs 7m	1 st - 15/06/20 2 nd - 19/12/22 3 rd - 28/02/23	1 x 9.4mg	N/A	N/A	Studbook	No information given	Lethal	Long term and continuous
5	Dominant	7 yrs 3m	1 st - 25/02/22	2 x 9.4mg	N/A	N/A	Aggression and Studbook	No change	Lethal	Long term and continuous
6	Dominant	N/A	N/A	N/A	4yrs 11m	10/12/21	Studbook	No change	Mild to moderate	Long term and continuous
7	Subordinate	25 yrs 5m	1 st - 09/05/19 2 nd - 21/04/20 3 rd - 17/03/21 4 th - 07/09/21 5 th - 19/08/22	2 x 9.4mg	N/A	N/A	Studbook	No change	No injuries	One isolated incident

Appendix C - Breakdown of contracepted and/or castrated male aggression in relation to contraception history.

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Appendix D - Survey

Evaluating the impacts of chemical contraception in male Colombian black-faced spider monkeys (Ateles fusciceps rufiventris)

Introduction

My name is Kate, and I am a primate keeper at Chester Zoo, with over 13 years' experience working with primates. I am currently undertaking an MPhil at Manchester Metropolitan University and my project title is "Evaluating the impacts of chemical contraception in male Colombian black-faced spider monkeys (*Ateles fusciceps rufiventris*)".

The aim of this research project is to investigate the effectiveness of various contraceptive techniques in the species stated, especially the effects on social cohesion and male aggression. My findings will be used to update social primate management protocols for using hormonal contraception more efficiently for behavioural management, warn against potential issues, and assess aggression management alternatives to contraception. Data generated from this study will be used as a model for similar management issues in other captive primate populations.

All questions should be filled in by an animal keeper and/or team leader or curator.

¹⁰ I hereby give Kate Brice consent to use the data which I am providing in this survey.

C Yes	C No		
Respondent's information			
Respondent's mormation			
^{2.} Name:			
2.a. Email address:			

2.6. Would you be happy for me to contact you if I have any further questions?

Yếs	⊂ No	
3. Name of collection:		
4. How long have you worked wit	h this species?	
4.a. How long have you worked w	ith this species at this institution?	
5. What is your opinion on the use	e of contraception as a managemen	t tool for male primates?
 A) Useful for managing surplus males and/or aggressive 	B) Useful for managing surplus/aggressive males, but	C) Sometimes effective for managing surplus/aggressive males

5.a. If you answered D) It is ineffective for managing surplus/aggressive males, E) I don't know or F) Other, please provide more information below.

C F) Other

we primarily use other

E) I don't know

methods e.g., euthanasia



behaviour in males and we use it

D) It is ineffective for managing surplus/aggressive males

regularly.

C

6.		arc	against aggression in you		ficetion (picase tiek an that app
Γ	 A) Contraception and/or castration 	Г	B) Enclosure access and design	Γ	C) Training
Γ	D) Euthanasia	Γ	E) Anti-psychotic drugs	Γ	F) Transfer of problem animal
Γ	G) Fission-fusion management	Γ	H) Separate groups	Γ	l) Other

6 How do you try to mitigate against aggression in your collection (please tick all that apply)

^{6.a.} If you answered I) Other, please provide more information below.

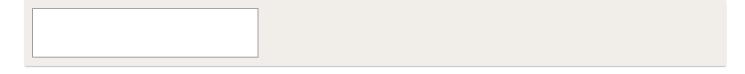
Group composition and Enclosure design

Group composition

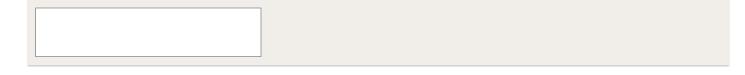
⁷ Please list the local ID of any females who are currently contracepted/permanently sterilized.

8 How many spider monkey groups do you have at your institution?

If you have multiple groups, please list the local IDs of the individuals held together. If you have multiple groups, please number your groups consecutively e.g., Group 1: Local ID, Local ID, Local ID; Group 2: Local ID, Local ID, etc.



g.a. Why do you have multiple groups? Please provide details below. If you have multiple groups, please answer the following question for each group e.g., Group 1 (Insert information), Group 2 (Insert information), etc.



Enclosure design

¹⁰ What is the approximate usable space of the indoor enclosure(s) in cubic meters (HxWxL)?

1. How many areas/compartments are there in the indoor enclosure?

12. How many enclosures do you have for this species?

13. Is the outdoor enclosure:

∩ A) Enclosed (Netted over, meshed over, meshed over, B) Open (No fitted/solid roof or context)

13.a. If the outdoor enclosure is enclosed, what is the height in meters?

14. What is the approximate area of the outdoor enclosure floor area in square meters (LxW)?

Male information

Please fill this page in for all sexually mature males in your collection.

15. Studbook number/GAN/Local ID of males aged 4 years and older.

	Studbook number
Male #1	
Male # 2	
Male # 3	
Male # 4	
Male # 5	
Male # 6	

16. Has this male been hand-reared?

	Yes or No
Male #1	
Male # 2	
Male # 3	
Male # 4	
Male # 5	
Male # 6	

17. Is the male more dominant or more subordinate in the group? (Please answer with an X).

	Studbook number	More dominant	More subordinate
Male			
#1			
Male			
# 2			
Male			
#3			
Male			
#4			

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Male	 	
#5		
Male	 	
#6		

18. What are the most frequent examples of aggressive behaviour observed from this animal? (Please answer all that apply with an X).

	Studbook number	Biting	Piloerection
Male			
#1			
Male			
#2			
Male			
#3			
Male			
#4			
Male			
#5			
Male			
#6			

18.a. If you answered "Other", please provide more information.

	Studbook number	Please provide more information.
Male # 1		
Male # 2		
Male # 3		
Male # 4		
Male # 5		
Male#6		

 $_{\ensuremath{\texttt{19.}}}$ How frequently do these incidents occur? (Please answer with an X).

	Studbook number	One isolated incident	Several isolated incidents (a few incidents with no discernible pattern)
Male			
#1			
Male			
# 2			
Male			
#3			
Male			
#4			
Male			
#5			
Male			
#6			

19.a. If you answered "Other", please provide more information.

	Studbook number	Please provide information.
Male # 1		
Male # 2		
Male # 3		
Male # 4		
Male # 5		
Male # 6		

20. What are the most frequent consequences of the aggressive behaviour from this male? (Please answer with an X).

	Studbook number	No injuries	Mild to moderate trauma (no veterinary intervention required)
Male			
#1			
Male			
# 2			
Male			
#3			
Male			
#4			
Male			
#5			
Male			
#6			

	Studbook number	Please provide more information.
Male # 1		
Male # 2		
Male # 3		
Male # 4		
Male # 5		
Male # 6		

20.a. If you answered "Other", please provide more information.

21. If veterinary interventions are required due to the aggressive behaviour of this male, how frequently do these interventions occur? (Please answer with an X).

	Studbook number	Daily	Weekly
Male			
#1			
Male			
#2			
Male			
#3			
Male			
#4			
Male			
#5			
Male			
#6			

22. Does the male direct aggression towards others (Please answer all that apply with an **X**):

	Studbook number	Males	Females
Male			
#1			
Male			
# 2			
Male			
#3			
Male			
#4			
Male			
#5			
Male			
#6			

23. Is the male the recipient of aggression from (Please answer all that apply with an X):

	Studbook number	Other males	Females
Male			
#1			
Male			
# 2			

Male # 3		
Male # 4		
Male # 5		
Male # 6		

23.a. In what situations does aggression occur? Please provide details.

	Studbook number	Please provide more information
Male # 1		
Male # 2		
Male # 3		
Male # 4		
Male # 5		
Male # 6		

24. In your opinion, does the male display unmanageable aggression? (Please answer with an X).

	Studbook number	Currently	Not now, but has in the past
Male			
#1			
Male			
# 2			
Male			
#3			
Male			
#4			
Male			
#5			
Male			
#6			

25. Is the male currently contracepted or castrated? (Please answer with an **X**).

Studbook number	Yes	No	

Male # 1		
Male		
# 2 Male		
# 3		
Male # 4		
Male		
# 5 Male		
# 6		

If you answered "Yes" for any of these males, please complete Q26-33 for the contracepted males.

If "No", but the male has previously been contracepted. Please provide more information below and answer Q26a-33.

26. If yes, what is the product name and dosage administered?

	Studbook number	Product name	Dosage
Male			
#1			
Male			
# 2			
Male			
#3			
Male			
#4			
Male			
#5			
Male			
#6			

26.a. Was this the males first contraception? (Please answer with an X). If No, please list the dates/product/dose of prior contraception.

	Studbook number	Yes	No
Male			
#1			
Male			
#2			

Male		
#3		
Male		
#4	 	
Male		
#5		
Male		
#6	 	

27. If he has received contraception multiple times, was the old contraception implant removed when the new implant was inserted? Please detail which implants were left in place and reason why. (Please answer with an **X**).

	Studbook number	Yes	No
Male			
#1			
Male			
# 2			
Male			
#3			
Male			
#4			
Male			
#5			
Male			
#6			

28. What was the reason for contraception/castration? (Please answer with an X).

	Studbook number	Aggression management	Studbook requirement
Male			
#1			
Male			
# 2			
Male			
#3			
Male			
#4			
Male			
#5			
Male			
#6			

29. How does his aggressive behaviour relate to contraception/castration? (Please answer with an X).

		Aggression decreased after contracepted/castration
Male	 	
#1		
Male	 	
#2		
Male	 	
#3		
Male	 	
#4		
Male	 	
#5		
Male	 	
#6		

30. How long after contraception/castration were changes in aggressive behaviour noted?

	Studbook number	Please provide information.
Male # 1		
Male # 2		
Male # 3		
Male # 4		
Male # 5		
Male#6		

31. What behaviours were observed?

	Studbook number	Please provide information.
Male # 1		
Male # 2		
Male # 3		

Male # 4	
Male # 5	
Male # 6	

32. Did his social rank change following contraception? (Please answer with an X).

	Studbook number	Yes, his rank increased	Yes, his rank decreased
Male			
#1			
Male # 2			
Male # 3			
Male # 4			
Male # 5			
Male # 6			

33. Did changes to the male's weight occur following contraception? (Please answer with an X).

	Studbook number	Yes, weight loss	Yes, weight gain
Male			
#1			
Male			
#2			
Male			
#3			
Male			
#4			
Male			
#5			
Male			
#6			

Thank you

I would like to thank you for taking the time to complete this survey, it is very much appreciated.

I hope that the data generated from this questionnaire will help build on current knowledge of contraceptive use in social primates, both as a reproductive management tool and in modulating aggression. This will also support EEP coordinators, keeping staff and curatorial teams' husbandry and management in decision making, as well as provide the EAZA Reproductive Management Group Contraception Database with more high-quality data to improve the accuracy of current EAZA RMG advice. And, ultimately, to understand the physiological and behavioural impacts of chemical contraception in Columbian black-faced spider monkeys.

Kind regards, Kate

Appendix E – Safe operating procedures



FAECAL COLLECTION PROTOCOL

Proper Identification

- The most important requirement for any sample collection protocol is that that you know which animal the sample came from.
- The best approach is to separate animals at night to properly identify faecal samples.
- Otherwise, you must observe the animal defecating and collect the sample as soon as possible.
- It is also possible to mark the faecal samples by feeding a marker (i.e., food colouring)

Frequency of Collection

- The second most important requirement is you are able to collect samples with a frequency that will provide useful and meaningful data.
- The frequency of sample collection is species dependant and is also dependent on the question you would like to answer.
- Please contact us and we can help you determine what frequency you should be collecting samples.

Contamination

Things to be careful of:

- The faeces are not contaminated with urine. (Urine has hormones too and this interferes with measurements of faecal hormone concentrations)
- The faeces are not contaminated with another individual's sample (faeces or urine)
- Try to collect samples as soon as possible. (hormone concentrations in samples left exposed to environment for extended periods will increase the risk of incorrect values)

Collection

- Once you have properly identified the sample, collect sample into zip-lock baggies.
- Do not collect the entire faecal sample. Instead (as 'pockets' of hormone concentrations can be found in the faecal sample) turn bag inside out and collect several (3-4) 'sub' samples from the same faecal sample.
- Try to minimize the amount of debris (hair/bones/hay) you collect, obviously the more faecal material present the better

- Label the bag using a waterproof permanent maker (*i.e. Sharpie[®] pen*) with:
 - Animal's Name Species Date (day/month/y ear) Time Collected

Storage

 Store sample ASAP in freezer at -20°C (Hormones concentrations will degrade if samples are left out too long)

For more information please contact:	Endocrinology
	North of England Zoological Society, Chester Zoo, UK
	Phone: 01244 389747