The Welfare of Primates in Zoos

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Abstract

One challenge facing zoos is balancing welfare needs with other primary goals, which include conservation, education, research, and entertainment. Managing primates in zoos involves similar welfare challenges faced by primates in other environments, which are covered elsewhere in this volume. In this chapter we identify and discuss welfare challenges that are unique to zoo-housed primates. All captive primates experience the presence of familiar humans (animal care staff), however the presence of unfamiliar humans (visitors) is common in zoo environments. In addition to providing a resource to zoo visitors, zoo primates also have an important conservation role that may involve intensive social management to facilitate captive breeding. We first discuss the influence of both familiar and unfamiliar humans on the welfare of zoo primates. We then examine the impact of different methods of social management on primate welfare.

Keywords

Zoo management · Human–animal interactions · Social management

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1 Introduction

Modern zoological collections have five main responsibilities: animal welfare, conservation, education, research, and entertainment (Godinez and Fernandez 2019). When considering zoo primate welfare, it is important to be aware of these goals because there is a need to evaluate different welfare challenges for different species within a collection. For example, if the primary role of an individual animal is to act as an ambassador for their wild counterparts—an educational role—then one welfare challenge they would face would relate to the effects of exposure to large visitor numbers. On the other hand, if the main role of a species is to maintain a genetically diverse population for captive breeding purposes—a conservation role—then welfare challenges may include the animals' movement to another zoo or the introduction of animals for breeding purposes. With careful enclosure design and planning these goals need not clash. For example, research can occur in front of the public and provide entertainment and conservation education opportunities as well (Farmer et al. 2022).

Zoo design has recently moved toward larger and more naturalistic enclosures (Coe 2003; Hosey 2022). This has brought about improvements in meeting welfare needs as well as providing better educational experiences for visitors. The welfare impacts of enclosure design and management practices are discussed elsewhere in this volume (Coleman et al. 2022; Farmer et al. 2022; Kemp 2022), therefore this chapter focuses on three welfare challenges that we believe are pertinent to zoo-housed primates. The first relates to regular contact with familiar humans. This challenge is not unique to zoo-housed primates (Buchanan-Smith et al. 2022), but the interactions may be different in zoo environments. The second challenge is the presence of large numbers of visitors, which is common in zoos (Hosey 2005). The third challenge is that of social management, which is the manipulation of social groupings based on breeding requirements and/or housing and husbandry constraints. While this third challenge is not unique to zoos, its end goal, that is, maintaining self-sustaining genetically diverse (i.e., breeding) populations, may be different to the end goal of other captive facilities, such as laboratories and sanctuaries for which reproduction may not be a primary goal.

2 Presence of Familiar Humans

The welfare implications of human–animal interactions in zoos resemble those in laboratories and other captive environments (Buchanan-Smith et al. 2022). When human–animal interactions are consistent, human-animal relationships and human-animal bonds may develop (Hosey and Melfi 2012). Positive human-animal relationships develop when humans talk calmly and stroke/groom the animals, for example; negative human-animal relationships develop when humans shout at and roughly handle the animals, for example (Ward and Melfi 2015). The development of positive human-animal relationships can occur after even only small positive interventions. For instance, laboratory chimpanzees (*Pan troglodytes*) that spend

10 min per day engaging in positive interactions with their caregivers show an increase in play and grooming behaviors and a decrease in abnormal behaviors (Baker 2004).

Some evidence indicates that human-animal relationships may be further enhanced if caregivers use species-specific communication, such as gestures based on the species' natural mode of communication. Jensvold (2008) carried out a study on three male chimpanzees housed at Zoo Northwest Florida (now Gulf Breeze Zoo), in which caregivers communicated with chimpanzees using either chimpanzee or human means. For example, when grooming chimpanzees, the human caregiver would either lip-smack and make grooming noises or just examine the chimpanzee's hair without lip-smacking. The three chimpanzees differed in how they responded to the two types of caregiver communication style. For example, two chimpanzees spent more time grooming when caregivers used chimpanzee communication while the other chimpanzee spent more time grooming when the caregivers used human communication. This finding highlights the importance of considering species' natural mode of communication and individual differences in the effect that these interventions have on the human-animal relationship.

Human-animal bonds involve a relationship between a human and an animal that is reciprocal and persistent and that promotes a perceived increase in well-being for both parties (Hosey and Melfi 2012). These bonds are often reported by pet owners. Research on zoo-housed nonhuman primates has only recently examined these bonds. For instance, Hosey and Melfi (2012) explored the prevalence of human-animal bonds by surveying 130 zoo professionals at industry conferences. Irrespective of age, gender, or job role, 78 of the respondents reported that they had formed a bond with a zoo animal. Moreover, a quarter of respondents reported that they had formed a bond with a species of primate and, for over a half of these respondents, the primate was one of the apes. The respondents reported that the benefits that they themselves incurred included a sense of enjoyment and emotional attachment while they perceived benefits to animals as being related to improved husbandry and welfare. Other studies have found that human–animal interactions, such as positive reinforcement training, also enhance husbandry and welfare by making routine management situations, such as isolation (Spiezio et al. 2015) and medication administration (Melfi and Thomas 2005), less stressful for the animals.

It is important to add the caveat that some human–animal interactions may have adverse effects on animals. For example, two groups of chimpanzees and western lowland gorillas (*Gorilla gorilla gorilla*) at Lincoln Park Zoo, USA, were observed for 4 years as part of a continuous behavioral monitoring study. During this study, all occurrences of interactions with caretakers were recorded (provision of food, drink, enrichment, tactile contact, and friendly gestures). Both species showed higher levels of agonistic behaviors and lower levels of pro-social behaviors during observations when caretaker interactions occurred compared to sessions without caretaker interaction (Chelluri et al. 2013). Although the authors considered all interactions to be positive, the behaviors exhibited during the animals' interactions with caretakers suggest that the animals may compete for attention, and that this leads to stress-related behaviors.

Stockmanship may also play a part in human–animal interactions. Developed in the domestic and agriculture industry, good stockmanship refers to the extent to which animals are managed safely, effectively, and in a manner that is low stress for the animal and keeper (Ward and Melfi 2015). Ward and Melfi (2015) evaluated stockmanship of Sulawesi macaques (*Macaca nigra*), black rhinoceroses (*Diceros bicornis*), and Chapman's zebra (*Equus quagga chapman*) in a zoo context by evaluating animal responses to different keepers that delivered different cues when moving animals from one area of the exhibit to another. Ward and Melfi found that these species reacted differently to the different cues and that some keepers were able to initiate a quicker response than others. Based on these and other findings (Ward and Melfi 2013, 2015), the authors suggest that social species, such as macaques, respond more rapidly to general keeper cues and that solitary species, such as rhino, are more influenced by individual human–animal interactions and are more likely to form specific human-animal bonds due to their solitary nature.

Clearly, the human-animal relationships that develop between caregivers and primates can vary depending on many factors. To aid our understanding in the techniques used to evaluate the impact of these relationships, we can consult principles from the domestic, agriculture, and laboratory industries. In the next section, we evaluate the impact of unfamiliar humans on zoo primate welfare.

3 Presence of Unfamiliar Humans

Zoo primates are managed by a small team of familiar humans and exposed to a daily influx of unfamiliar humans: zoo visitors (Hosey and Melfi 2014). Without attracting and engaging visitors, zoos cannot pursue the other goals that are central to the mission of zoos. The presence of zoo visitors, however, may conflict with the goal of maintaining good welfare (Fernandez et al. 2009). Visitor effects can be negative, positive, or neutral (Hosey 2005), but studies on zoo primates overwhelmingly conclude that visitors have a negative impact on welfare (Hosey 2005). Aggression and abnormal behaviors, such as fur plucking, are the most commonly reported negative behaviors associated with increased visitor numbers. For example, Mallapur et al. (2005) observed lion-tailed macaques (*Macaca silenus*) at eight Indian zoos during days when visitors were present and days when visitors were absent. They found that the macaques engaged in more abnormal behaviors on days when visitors were present. The authors of this study highlighted that the level of disturbance by visitors in Indian zoos is relatively high due to the lack of well-established conservation and animal welfare awareness programs; behaviors such as shouting, teasing, feeding, and even physically harming animals are commonplace. If this is the case, it is reasonable to assume that, in some cases, it is the behavior, proximity, and/or type of contact that visitors have with the animals that adversely affect welfare and not simply the presence of visitors. Altering visitor behavior has been shown to reduce their adverse impact. In one study, Chamove et al. (1988) found that encouraging zoo visitors to behave submissively by crouching in front of primate exhibits resulted in less aggressive behavior from the primates.

It is difficult to assess which aspect of visitor interactions primates find most stressful. Is it visual contact with humans, the noise that human visitors make, or something else? One attempt to assess visitor-related disturbances involved imposing one-way screens at a black capped capuchin (*Cebus apella*) enclosure at Melbourne Zoo, Australia. These screens allowed visitors to view the capuchins, but from the capuchin side, the viewing window looked like a white screen. The experimenters watched the animals and took biological samples during the control (no modification to viewing windows) and the reduced visual contact condition. The reduced visual contact condition resulted in a reduction in group aggression and abnormal behaviors. In addition, fecal steroid metabolites, a measure of stress response (Capitanio et al. 2022), were lower in the reduced visual contact condition than in the control condition. The screens reduced the number of visitors present at the enclosures but not visitor behavior (e.g., banging on the viewing window) and noise levels. As the screens were not soundproof, the auditory stimuli were the same in each condition. The study therefore affirmed that it was visual signals such as direct eye contact with visitors that were the fear-eliciting stimuli (Sherwen et al. 2015).

Animal–visitor interactions are potentially enriching (Claxton 2011), but there is limited empirical evidence that visitors have a positive effect on the welfare of zoo-housed primates (Hosey 2005). Also, where positive effects of interactions are described, there are confounds, such as the presence of food rewards. For example, a study of visitor–chimpanzee interactions at Chester Zoo, UK, found that the longer chimpanzees interacted with humans, the more likely they were to receive food from visitors (Cook and Hosey 1995). Receiving this food in addition to their normal diet may pose a welfare issue if it results in nutritional imbalances and/or obesity.

The relationships that zoo animals have with familiar and unfamiliar humans are likely related. Hosey (2008) proposes a model where, if interactions with familiar and unfamiliar humans are positive, animals may learn to not fear humans, and this could lead to a greater likelihood that the animal will be enriched by humans and other environmental stimuli (Fig. 1). Therefore, future studies of human-animal relationships in zoo primates should consider the relationships that primates have with familiar and unfamiliar humans.

3.1 Assessing Human-Animal Relationships

It is difficult to draw firm conclusions about the impact of human-animal relationships on the welfare of zoo-housed primates due to the sheer variety of published studies. There is no standardized method for assessing the “visitor effect” across zoological collections.

One issue comes down to enclosure design. There are many ways that primate species are exhibited. For example, lemurs can be housed in traditional cages, island exhibits, and walk through (free-ranging) exhibits (Farmer et al. 2022). Enclosure design has a large influence on visitor pressure; visitors can get very close to animals

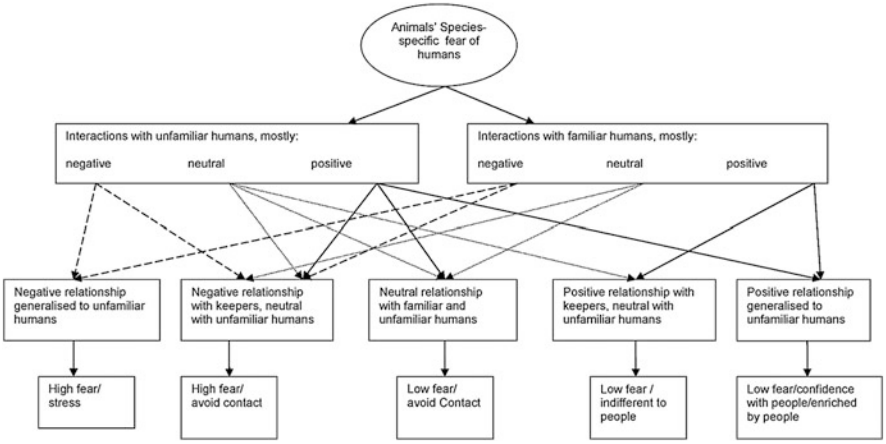

Fig. 1 A model of human–animal interactions and their consequences for human-animal relationships in zoo animals (from Hosey 2008)

in free-ranging exhibits but not when viewing animals in island enclosures or in traditional cages.

When evaluating visitor effects, one problem is how to quantify visitors. For example, researchers may count the number of visitors to an enclosure at a particular time and use these values or, as is more common, researchers may record the number of visitors as being "low" or "high." How these categories are quantified vary. For example, in their study of Diana monkey (*Cercopithecus diana*) behavior, Todd et al. (2007) coded density as being "low" if there were one to five visitors and as being "high" if there were more than five visitors. Bonnie et al.'s (2016) observations of gorilla behavior had similar category labels but different accompanying definitions: they considered 1–30 visitors "low" and more than 30 visitors "high." A different approach is to record total visitors to the zoo rather than at the species enclosure. For example, for her study of gorillas, Wells (2005) compared behavior on days of high visitor density, which they defined as weekends during the summer months (mean of 1288 visitors per day), with days of low visitor density, defined as weekdays during winter months (mean 6 visitors per day).

For most zoo research, cortisol is not used as a welfare indicator due to its cost and the inability to conduct the relevant analyses, there is also the added issue that cortisol could indicate excitement or arousal rather than stress. However, facilities that have collected cortisol data have demonstrated its potential utility in studying the visitor effect. At Chester Zoo, for example, Davis et al. (2005) collected urine samples from four female and three male spider monkeys (*Ateles geoffroyi rufiventris*) three to four times per week during opening hours and when the zoo was closed. They found that urinary cortisol was positively associated with visitor number, although this relationship was not strong and it was possibly nonlinear, and from this, concluded that other factors may have influenced the relationship.

Ultimately, the biggest issue when assessing the impact of human-animal relationships is the fact that welfare is an individual outcome: a stimulus perceived as stressful by one animal may be perceived as neutral or pleasant by another. As such, factors such as personality (Robinson and Weiss 2022) may contribute to these differences. For example, squirrel monkeys (*Saimiri sciureus*) housed at the Living Links Research Centre at the Edinburgh Zoo that were rated as being more playful and less cautious, depressed, and solitary were more likely to approach the viewing window when visitors were present (Polgár et al. 2017).

3.2 Reducing the Impact of Visitors on Welfare

Management practices have been developed to "dilute" the visitor effect. One practice is to reduce visual or auditory contact with visitors. A popular method involves the use of camouflage netting to reduce visual contact. For example, six gorillas at Belfast Zoo, Northern Ireland, UK, displayed significantly less aggression and abnormal behavior when camouflage netting was introduced (Blaney and Wells 2004). The authors noted that the barrier also encouraged quieter, more relaxed behavior on the part of visitors. Thus, the effect of the netting could be attributable to reduced visual contact, noise reduction, the change in visitor behavior, or a combination of these factors.

These techniques can introduce a conflict between visitor engagement and animal welfare. In short, although welfare may be improved by this buffering, visitor engagement may be negatively affected. For example, when screens were used to reduce visual contact between black capped capuchins and zoo visitors, the welfare of the animals was improved, but zoo visitors did not stay at the enclosure for as long as they did before the screens were introduced, potentially impacting on the opportunity to engage and/or educate visitors (Sherwen et al. 2015). However, in the study of camouflage netting in gorilla exhibits, when questioned by researchers, the public considered the animals to be more exciting and less aggressive when netting was present (Blaney and Wells 2004).

3.3 Direct Human-Animal Contact

All of the above examples deal with visitors having indirect contact with primates. However, visitor experiences, such as "keeper for a day" or "feed the animals," are becoming increasingly popular. These experiences offer the chance for visitors to get much closer to the animals—there may even be a chance for direct physical contact—and often take place at "off-show" areas that are normally only accessible by zoo staff. There have been few studies of these programs' impact on welfare.

Within the Wild Planet Trust (Paignton Zoo and Newquay Zoo) the authors of this chapter have been evaluating the implications of visitor experiences. Lemur species are a popular animal for feeding experiences due to their calm temperament. From November 2013 to February 2014, visitor feeding experiences with crowned

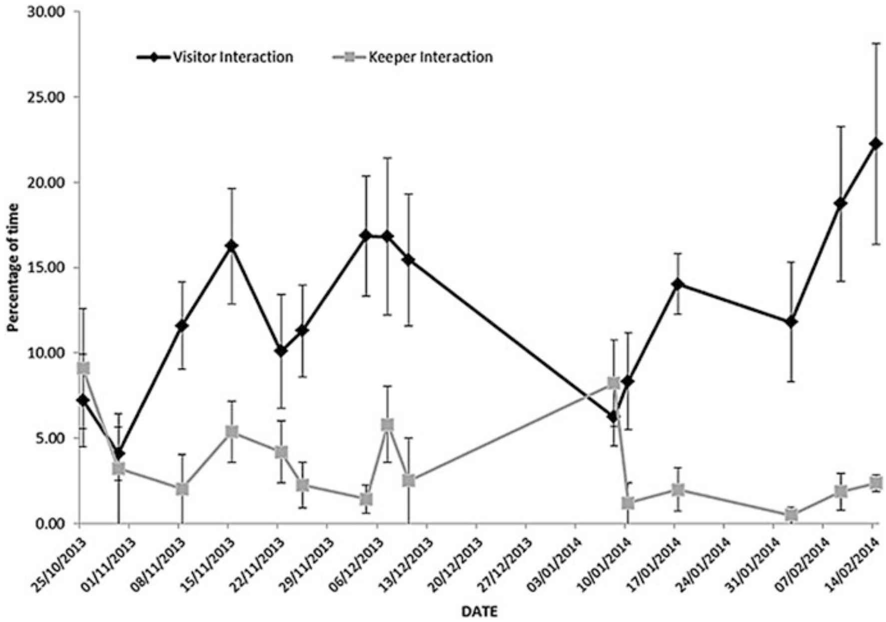

Fig. 2 Mean (± SE) percentage of time crowned lemurs ($N = 4$) spent interacting with keepers or visitors during visitor feed experiences at Newquay Zoo, UK (From Jones et al. 2016)

lemurs (*Eulemur coronatus*) at Newquay Zoo, UK were evaluated by means of behavioral observations during and immediately following either visitor feeds or keeper feeds (Jones et al. 2016). There were minor behavioral changes: during visitor feeds, lemurs spent more time interacting with keepers and less time engaged in aggressive behavior. The reduced aggression may indicate a positive effect of visitor feeds on welfare, but it should be noted that levels of aggression in all conditions were extremely low. The increased interaction with keepers during visitor feeds is probably an artifact of the feed condition, that is, during visitor feeds, keepers may have encouraged interactions for the benefit of visitors. This study also examined changes in the animal–keeper and animal–visitor interactions as the feeding experiences continued. Interestingly we found an increase in animal–visitor interaction and a decrease in animal–keeper interaction as feeding experiences progressed; however, when feeding experiences resumed after a 28-day break, interactions with keepers and visitors returned to levels seen during the first visitor feed experience (Fig. 2). This finding is interesting from two perspectives. First, it shows that the lemurs found the visitors enriching. Second, it suggests that making these events predictable, and thus allowing lemurs to habituate, enhances their well-being.

Regardless of whether visitors have direct or indirect interactions with zoo primates, it is important that the zoo industry continues to develop and standardize ways to evaluate the effects of visitors. Results of these studies, such as ours, can then be used to design programs that engage zoo visitors in such a way as to minimize any negative effects of these visitors.

4 Social Management

Many species housed in zoos are involved in captive breeding programs. These animals are bred and transferred between collections to maintain stable demographics and the genetic health of a population. The IUCN (International Union for Conservation of Nature) endorse captive breeding as an essential component in species conservation (IUCN 1987). Ex-situ species can be managed on both regional and global levels and the type of management varies (Hosey 2022; Prescott 2022).

According to the IUCN Guidelines on the Use of Ex situ Management for Species Conservation (2014), there are a number of roles for species managed through captive breeding programs. These roles are to function as an insurance population, temporary rescue, long-term *ex situ* population, demographic manipulation, source for population restoration, source for ecological replacement, source for assisted colonization, research, and/or training or for an education and awareness program (see Prescott 2022). Population restoration has only been realized for a small number of species and for primates, the main success story being the golden-lion tamarin *Leontopithecus rosalia* (see Ferreira et al. 2022). For similar projects to be successful, we need to maintain self-sustaining and genetically diverse captive populations. Therefore, there are coordinated efforts in the management of many zoo-housed primate species, which are based on genetics and demography.

In some cases, primates managed as part of captive breeding programs are housed in unnatural social groups. For species in which individuals emigrate from their natal group when they reach maturity, zoos may manipulate breeding opportunities or maintain animals in nonbreeding or in small groups, which can affect primate welfare.

Knowledge of social group composition and behavioral repertoires of wild members of a species are thus important for promoting positive welfare in zoo-housed primates. However, this information is limited for some species, because of a lack of research, the elusive nature of the species, or political and social conditions in range countries. Given the limited data on wild individuals, comparisons between zoos can be hugely beneficial. For example, following a series of male–male aggression incidents in a troop of spider monkeys, Chester Zoo, UK began an investigation into the social systems of captive groups. It is known that the social systems of wild *Ateles* involve a fission–fusion dynamic with groups comprising a variety of sex-age classes (Shimooka et al. 2010). To gather information on and to contextualize aggressive behavior in spider monkeys within zoos, Chester Zoo sent a survey to zoos that held the genus. The survey revealed that most zoo-housed spider monkeys were housed in small social groups and that, of the aggressive interactions that resulted in severe or fatal injuries, most were initiated by adult males. The results of the survey also led to several recommendations for ways to allow something like a fission–fusion system to operate, including providing larger, more complex enclosures and creating areas in which individuals can separate themselves from the group (Davis et al. 2009).

The Bornean orangutans (*Pongo pygmaeus*) at Apenheul Primate Park in Apeldoorn, Netherlands, are managed in a fission–fusion social system designed to mimic the social system of this species in the wild where male orangutans are semi-solitary and come together with females to breed (van Schaik et al. 2009). A study compared stress responses of orangutans housed in Apenheul to orangutans housed in permanent captive groups in other European zoos. The study did not find a significant difference in fecal glucocorticoid metabolites between these groups. However, individuals housed in Apenheul were more stressed by high visitor numbers. These findings suggest that, although providing a more naturalistic environment may reduce the influence of group size on social stress, there may be unanticipated welfare costs associated with these environments (Amrein et al. 2014).

Researchers often have access to studbook data for species that are managed in captivity. Studbook data allows researchers to assess the influence of social management practices on breeding success. Studbook data can also enable researchers to investigate the influence of species-specific behaviors and their effect on breeding or welfare. For example, howler monkeys (*Alouatta* spp.) are characterized by their vocalizations (Whitehead 1987, 1995), which in the wild serve many functions, including the regulation of the use of space, allowing neighbors to avoid one another, the demarcation of territory, opponent assessment, predator avoidance, and mate defense (see review by Da Cunha and Byrne 2006). In the wild, groups of black and gold howler monkey (*Alouatta caraya*) range to up to 19 animals and these groups contain adult males and females (for review see Antonio 2007). Analysis of European studbook data by Farmer et al. (2011) found that significantly more offspring were born (and survived to one year of age) to females and males housed in a family group than to pair-housed males and females. The same study found that males who had high rates of vocalizations had greater reproductive success than males who had low rates or males who did not vocalize; females housed with males who vocalized regularly also had higher rates of reproductive success. Four of the 12 males did not perform vocalizations. Based on these results, the authors recommended that zoos conduct playbacks of these vocalizations to encourage successful breeding in this species.

The performance of behaviors that may be deemed undesirable by zoo visitors, such as aggression and infanticide, are also important for maintaining social dynamics in many primate species. For example, in wild Sulawesi macaques (*Macaca nigra*), social aggression is a common and important behavior (Reed et al. 1997). The multi-male social system of macaque species leads to competition for access to receptive females. Males of similar rank engage in more aggressive interactions than those that differ in rank (Reed and O'Brien 1997). This suggests that aggressive behaviors should not be prevented in this species as these behaviors are used to maintain the social hierarchy. Moreover, by permitting these behaviors, the injuries that occur are less likely to be severe and animals can be monitored and treated quickly by veterinary staff.

4.1 Single-Sex Groups

In response to space limitations, zoos often need to manage the surplus of one sex or prevent breeding. The formation of single-sex groups is a common practice used to maintain or reduce population numbers.

The formation of single-sex groups can be difficult if such a social grouping is not common in the wild (Hosey, et al. 2009). A few primate species are reported to form bachelor groups in the wild (western lowland gorillas, Stoinski et al. 2001; chimpanzees, Fritz and Howell 1997; proboscis monkeys *Nasalis larvatus*, Sha et al. 2013; Murai 2004). With the increased success of captive breeding programs, the number of surplus animals is increasing. Consequently, single-sex groups are becoming an important management tool (Neier et al. 2013).

In zoos, western lowland gorilla bachelor groups are formed to manage the surplus of males and to socialize young males (Leeds et al. 2015) as these groups provide an environment where they can learn "appropriate" behaviors before being moved to a breeding situation. Comparable data on wild bachelor groups are mainly drawn from mountain gorillas (*Gorilla beringei beringei*) (Yamagiwa 1987; Stoinski et al. 2001; Robbins 1996). Members of wild mountain gorilla bachelor groups engage in relatively high levels of affiliative behaviors and the groups exhibit a high degree of social cohesion (Yamagiwa 1987; Robbins 1996). All captive bachelor gorilla groups are western gorillas, which, with respect to behavior, are distinct from mountain gorillas (Tutin 1996 as cited in Stoinski et al. 2001). Therefore, care must be taken in when comparing the social behaviors of the two subspecies.

Pullen (2005) compared social behaviors performed by bachelor-housed western gorillas at Paignton Zoo to males of the same species that were part of a breeding group at Belfast Zoo. Despite the small sample size ($n = 8$), the study showed that the two groups used different methods to manage social interactions and that these differences were influenced by the presence of females. Silverback males in both groups performed more aggressive behaviors than lower-ranking males. However, non-escalated aggression (chest beating with no contact) was performed more frequently by the silverback male in the breeding group. These findings suggest that the behavior of individuals in bachelor groups may differ to males in a breeding situation. More recently, Leeds et al. (2015) surveyed wounding in bachelor and mixed-sex groups of western lowland gorillas in 28 North American zoos. The study reported no differences between wounding rates in bachelor and mixed-sex groups when no young silverback males were present, but bachelor groups that contained a young silverback experienced higher rates than those without.

Because of difficulties in introducing unrelated young males into existing family groups (Johnstone-Scott 1988), Species Survival Plans (Association of Zoos and Aquariums, America) and EAZA (European Association of Zoos and Aquaria) ex situ programs for western lowland gorillas involve the formation of bachelor groups

(Pullen 2005). In North America, 23 zoos house at least one bachelor group (Neier et al. 2013) and of the 74 European zoos housing the species, 19 house one bachelor group and one houses two bachelor groups (Bemment 2016). As of 2015, half of the 22 male gorillas which had been moved from a bachelor group to a breeding situation had sired offspring (Bemment 2016). Guidelines for the successful formation and maintenance of bachelor groups includes a diversity in rearing history and a maximum group size of 3 or 4 animals, helping to ensure that bachelor groups may function as a long-term solution in managing surplus males (Stoinski et al. 2004). As it has only been commonplace to form bachelor groups over the last decade, only now are the animals involved in the initial formation of bachelor groups starting to mature. Therefore, the welfare of gorillas kept in permanent bachelor groups requires ongoing monitoring.

The white-faced saki monkey (*Pithecia pithecia*) is managed through an EAZA ex situ program. In response to a surplus of males, EAZA's management strategy involves forming bachelor groups (Webb 2017, personal communication). A study on male interactions in this species carried out in five European zoos compared social interactions between animals housed in breeding and bachelor groups. A bachelor group is considered socially compatible when low levels of aggressive interactions are observed (Fàbregas and Guillén-Salazar 2007). No significant differences in the performance of aggressive behaviors between the two saki monkey social groupings were reported. However, when the study separated aggression into physical and non-physical aggression, compared to males housed in breeding groups, males housed in bachelor groups spent more time engaged in non-physical aggression. The study suggests that bachelor group formation in white-faced saki monkeys is an effective management strategy as the males appear to have ways to avoid conflict (Prins 2015, unpublished data).

Successful bachelor group formation has been reported in other captive primate species. For instance, the formation of an all-male group of proboscis monkeys (*Nasalis larvatus*) at the Singapore Zoo resulted in less contact aggression compared to non-contact aggression, and by the sixth week of the introduction, almost all aggression had stopped (Sha et al. 2013). In wild proboscis monkeys, peripheral males form all male groups (Yeager 1990), thus this research suggests that the formation of bachelor groups may be a solution to managing surplus males in this species. Similarly, for white crowned mangabeys (*Cercocebus atys lunulatus*) housed at the Valencia Zoo, Spain, although non-contact aggression (facial threats) was performed at high rates, physical aggression was rare and mostly between animals in the same age-sex class. In addition, all animals were groomed by at least one other member, which suggests that the males were socially compatible (Fàbregas and Guillén-Salazar 2007). Similar findings have been reported in lion-tailed macaques (*Macaca silenus*; Stahl et al. 2001) and ruffed lemurs (*Varecia* spp.; Romano and Vermeer 2003). Even with the small sample sizes of these studies (most examined only one group), these findings suggest that bachelor groups can be an appropriate social grouping for many primate species. However, comparisons of multiple groups would provide stronger support for managing surplus males in this way; continued monitoring on the impact of non-contact aggression and the lack of reproductive opportunity, on the psychological welfare of these animals, is also essential.

4.2 Contraceptive Methods

Contraception is another means to manage surplus animals and to limit population growth. There is limited research into the long-term effects of contraception on the physiology and behavior of zoo-housed primates. Guidance on the implementation of contraception is available to EAZA member zoos through the EAZA Reproductive Management Group. For AZA institutions, the Reproductive Management Center has expanded to work toward improving reproductive management. Both organizations maintain databases containing over 30,000 records for the use of contraception for a range of species. Their aims are to provide zoos guidance on the use of contraceptives and to collate evidence on the effectiveness and reversibility of different types of contraceptives.

A range of contraceptive methods is available. However, most of the literature on contraception comes from laboratory studies with small sample sizes (see Wallace et al. 2016 for review).

Castration involves removing the testes and thus prevents testosterone production. There is limited work on the effects of castration in zoo-housed primates. In Javan langurs (*Trachypithecus auratus*), castration was used to maintain surplus males in social groups at two UK zoos (Port Lympne and Howletts Wild Animal Parks). The langurs were housed in seven groups: three bachelor pairs and four mixed-sex groups. All groups contained one intact male, with the remaining males being castrated, except for one pair of intact males and one mixed-sex group where all of the males were castrated. Bachelor pair males spent more time engaged in affiliative behaviors compared to males in mixed-sex groups. Moreover, the presence of females did not affect male–male interactions in the mixed-sex groups; all males showed a preference for females as social partners over males. Castrated males were more submissive than intact males, which suggested that castration may have influenced these males' social status (Dröscher and Waitt 2012).

Unlike castration, vasectomy involves blocking the vas deferens. This prevents the passage of sperm out of the penis. Vasectomy should not disrupt testosterone production and so is preferable to castration (Asa and Porton 2010). There is no published data concerning the impact of vasectomy on captive primate behavior. However, anecdotal evidence has been collected from two UK zoos (Paignton Zoo and Shaldon Wildlife Trust) on the use of vasectomy and contraceptive implants to prevent breeding in the white-faced saki monkey population. At Paignton Zoo, the adult male was vasectomized and no effect on behavior was reported initially (Silcocks 2014, unpublished data). However, over the first seven months after surgery, there was a decrease in the amount of social grooming this individual received from group members with grooming returning to original levels one year after the vasectomy (Thornton 2015, unpublished data). At Shaldon, the adult male of the pair was treated with a contraceptive implant Deslorelin. Social grooming rates after implantation increased over the year-long study period. The author concluded that, although both methods were effective for management and did not cause long-lasting changes in behavior, Deslorelin implants were less effective in preventing pregnancies (Thornton 2015, unpublished data).

The success of hormonal implants has been documented for a range of zoo-housed primate species, including chimpanzees (Bettinger et al. 1997; Bourry et al. 2005), western lowland gorillas (Sarfaty et al. 2012), hamadryas baboons (*Papio hamadryas*; Portugal and Asa 1995), white-faced saki monkeys (Savage et al. 2002), white-faced marmosets (*Callithrix geoffroyi*; Mustoe et al. 2012), and golden-headed lion tamarins (*Leontopithecus chrysomelas*; De Vleeschouwer et al. 2000). The contraceptive implant Norplant did not affect the duration of estrus cycles in female chimpanzees, but the duration of their sexual swellings and full-swelling phases were shorter than before implantation (Bettinger et al. 1997). Norplant was also used as a contraceptive in a troop of hamadryas baboons at Paignton Zoo. A study of this troop found no differences in self-directed behaviors or social interactions between implanted and non-implanted females (Plowman et al. 2005), although, later, many females removed their implants (Plowman, personal communication).

The long-term effect of keeping primates in a nonbreeding situation can impact their social competence and/or future breeding success, and ultimately their welfare. Preventing animals from breeding or delaying reproduction has led to reduced fertility in several mammalian and fish species (see Penfold et al. 2014 for a review), but there is only limited evidence that this occurs in nonhuman primates. A survey of zoo-raised chimpanzees that assessed the effect of rearing, age at which the animal was removed from the mother, sex, and participation in shows, revealed that there was no single aspect of rearing that influenced sexual competence; however, individuals that were reared alone with no exposure to conspecifics and individuals removed from their mother at less than 12 months were less likely to reproduce (King and Mellen 1994). By documenting the use of preventative methods in zoos (thought the AZA and EAZA reproductive management centers), we can monitor the long-term impact of captive management techniques and evaluate their success.

5 Conclusions

Primates in zoos are subject to many of the welfare challenges experienced by individuals in other captive situations, as covered elsewhere in this volume. However, zoo-housed primates face unique welfare challenges; being exposed to both familiar and unfamiliar humans on a regular basis and intensive social management to ensure self-sustaining captive populations. The modification of enclosures and management practices have been shown to mitigate the effects of visitor–primate interactions and should be considered in future enclosure designs. The welfare implications of social and genetic management of primates require ongoing monitoring in order to make future decisions evidence-based and to promote positive welfare.

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