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Birth Control Behind Bars: An Anthropological Perspective on the Care of Captive Bonobos

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Abstract

Bonobos are one of our closest living primate relatives. They are primarily known for their unique social structure and sexual behavior. In their native setting, the Democratic Republic of the Congo, bonobos are often seen engaging in sexual behaviors not only for reproduction, but for social reasons too. Unfortunately, research in the wild is difficult because of political unrest and rapidly declining population numbers. Since bonobos are endangered, it is crucial that we maintain and properly care for a captive population to ensure the survival of the species. A captive setting provides a safe, controlled environment for researchers to observe bonobos and their normal range of behaviors. While captivity is beneficial to the species, I propose that there are differences between wild and captive populations of bonobos due to the behavioral and biological controls that captivity requires. The behavior of bonobos differs substantially from their own relatives, chimpanzees, yet they are viewed by zoos as biologically similar. This thesis presents the argument for an anthropological perspective in the management and care of captive bonobos.

Bonobos: Background Information

The genus *Pan* is comprised of two species: *Pan troglodytes* (chimpanzees) and *Pan paniscus* (bonobos). Despite being taxonomically similar, the two show distinct differences in temperament and behavior. Bonobos, formerly known as pygmy chimpanzees, are one of our closest living primate relatives and are primarily known for their highly sexual behavior. In 1929, researchers distinguished bonobos as a separate species. Since they were discovered within the last century, relatively little is known about them compared to chimpanzees and other great apes. Additionally, they are on the International Union for Conservation of Nature's (IUCN) Red List as an endangered species whose population numbers in the wild are currently unknown, but are suspected to be low and declining. Research is limited, in part, because they live only in the rainforests of the Democratic Republic of the Congo. Political

conflict and civil war have made it difficult to observe and track bonobos in the wild. Not only are they native to a small geographic area that suffers from deforestation, but people hunt bonobos to sell their meat in the bushmeat trade. Rescuing bonobos from these dangerous environments and keeping them under human care in zoos and sanctuaries has helped researchers learn more about their unique behaviors.

In the wild, bonobos live in multi-male, multi-female communities ranging anywhere between 10 and 100 individuals. Bonobos live up to 40 years in the wild, but in captivity they can live to be 65. Females reach sexual maturity at about 9 years of age and tend to have their first offspring around age 13. They are primarily arboreal, as opposed to terrestrial, meaning they spend most of their time in the trees. Fruit trees are their main food source along with plants, seeds, nuts, and insects. Occasionally, they eat small mammals like flying squirrels (The Bonobo & Congo Biodiversity Initiative). Bonobos play an important ecological role in the rainforest as seed dispersers. As they consume the fruits and plants of over 90 species of grass, trees, and shrubs, the seeds stay in their digestive tract for an entire day which carries them to different locations throughout the forest (Beaune, 2012). The survival of these plant species relies on the existence of frugivorous animals in the wild, like the bonobo, which makes their conservation even more crucial.

Bonobos are often compared to chimpanzees due to their similar morphology, yet they exhibit completely different temperaments and social structures. Chimpanzees are a patriarchal or male-dominated society characterized by aggression and competition. On the other hand, bonobos have a matriarchal or female-dominated society where male aggression is minimal. One commonality between the two societies is that they are both male-philopatric. This means that females migrate out of the community upon sexual maturation while the males remain in their natal groups. Typically, the sex that remains in the natal group forms the strongest bonds because they are the most familiar with each other (de Waal, 1995). Bonobos are the exception to this rule because while the females migrate away from their birthplace and into an unfamiliar community, they manage to form the strongest social bonds amongst themselves. One reason that female bonobos can make this smooth transition into unknown territory is because of the physiological change that they experience in response to ovulation called sexual swelling.

Unlike human females who experience concealed ovulation, non-human female primates exhibit a visible swelling of the genitals which indicates fertility and sexual

receptivity. Sexual swelling refers to the swelling of the perineal skin (the area extending from the genitals to the anus) and occurs on a cyclical basis that aligns with the timing of menstruation and ovulation (Ryu, Hill, and Furuichi, 2015). Approximately 5 days after menstruation, the onset of sexual swelling occurs. The swelling gradually increases in size and firmness for about 9 days until it reaches maximal swelling size, also referred to as maximum tumescence (Heistermann et al., 1996). The timing of ovulation is highly variable, but often occurs toward the end of the maximal swelling period. Ovulation is followed by gradual detumescence, or a gradual reduction of swelling, and then the cycle is repeated. These swellings occur in many species of non-human primates such as baboons, macaques, chimpanzees, and bonobos (Fitzpatrick et al., 2015; Higham et al., 2012; Deschner, Heistermann, Hodges, & Boesch, 2004; and Douglas et al., 2016). The primary sense for primates is vision, therefore sexual swelling is an important visual indicator to males that the female is ovulating and sexually receptive.

In a study on wild West African chimpanzees, maximal sexual swelling lasted between 7 and 19 days (Deschner et al., 2004). Within this maximal swelling phase, researchers observed a further increase in swelling size of about 20% during the periovulatory or follicular phase (Deschner et al., 2004). This phase represents the days preceding and including ovulation and is also known as the window of fertility. In response to these visible changes, the alpha male chimpanzees change their behavior to allow them access to the estrous female, maximizing their reproductive opportunities. One way they do this is by increasing copulation frequency with a female when she is exhibiting the additional increase in swelling during the days leading up to ovulation. The maximal swelling period continues for up to 3 days after ovulation. During this time, males exhibit mate-guarding where they continue to copulate after the fertile window has passed to ensure paternity. The males also prevent other males from copulating with that female. The slight increase in maximal swelling size informs the alpha male about when to copulate, which efficiently maximizes his reproductive efforts. Female chimpanzees appear to have a reliable and precise way to convey ovulation through sexual swelling. In this case, the swelling supports reproduction in chimpanzees. In contrast, the function of sexual swelling is not as straightforward in bonobo society.

Female bonobos prolonged sexual swelling can comprise up to 74% of the total menstrual cycle length (Heistermann et al., 1996). In contrast to female chimpanzees

who have consistent and reliable swelling cycles, female bonobos have a period of maximum swelling that is less discrete. They exhibit prolonged periods of maximal sexual swelling which conceals the actual window of fertility. In 30% of cycles, ovulation occurred outside of the period of maximal sexual swelling (Paoli, Palagi, Tacconi, & Tarli, 2006). This leads us to believe that the state of sexual swelling is not a reliable indicator of ovulation, especially when compared with chimpanzees. Differences in maximal swelling duration may explain the differential impact that swelling has in both societies.

Bonobos, compared to chimpanzees, tend to have prolonged periods of maximal swelling that can last up to 26 days (Ryu, Hill, & Furuichi, 2015; Heistermann et al., 1996). Like human females, menstrual and ovulatory cycle lengths differ between individuals. This may account for some of the variation in swelling duration, along with the general lack of studies conducted on bonobos. Nonetheless, there is a difference in the duration of sexual swelling that may impact its function in bonobo societies. Chimpanzee females may not exhibit as much maximal sexual swelling because it confers risks for her. For example, when she is exhibiting sexual swelling, males are more attracted to her and she may receive unwanted or forced copulation from males in neighboring groups (Heistermann et al., 1996). Chimpanzee males also show more aggression toward each other because they are in competition over a limited number of estrous females. Typically, there are numerous estrous female bonobos in a group at any given time, so mating competition between males is unnecessary. Also, female bonobos do not experience forced copulation or aggression from males. If a male bonobo shows aggression toward a female, other females will usually come to her defense. For female bonobos, prolonged sexual swelling has less risks and provides them with relational benefits when compared to chimpanzees.

When female bonobos first experience sexual swelling, it indicates their sexual maturity. As mentioned previously, females migrate out of their natal group upon reaching maturity. This is a stressful time for the female because she is leaving her established group, joining a community where the social relationships are already in place, and she is starting from the bottom of the dominance hierarchy. Established females are wary of this newcomer, which can be a source of stress for them too. Bonobos need to cope with this stress, and they do so by engaging in sexual behaviors such as copulation and genital-genital rubbing (GG-rubbing). GG-rubbing is when females rub their sexual swellings against each other. When females migrate from

their natal group and transition into a neighboring group of bonobos, they maintain a prolonged period of maximal sexual swelling and show an increased frequency of GG-rubbing (Ryu, Hill, & Furuichi, 2015). The young female will not have her first offspring until about 4 years later, so the swelling is not aimed at immediately attracting males from the new group to facilitate reproduction. Instead, several researchers suggest that sexual swelling does not only function as a reproductive mechanism in bonobos, but as a social mechanism that encourages GG-rubbing among female bonobos (Douglas, Hohmann, Murtagh, Thiessen-Bock, & Deschner, 2016; Ryu, Hill, & Furuichi, 2015; Paoli, Palagi, Tacconi, & Tarli, 2006). Since the swelling lasts for a prolonged period, it helps integrate the new female into the group by reducing tension that arises from being a newcomer in unfamiliar territory. It also helps convey that they are not a threat and can be trusted. This scenario underscores the social role (not just biological function) of sexual swelling in bonobo societies.

Unlike many other non-human primates, bonobos engage in sexual behaviors not only for reproduction, but also for social reasons. They are used as a social mechanism to help reduce tension and strengthen social relationships. Since these behaviors are not purely for reproduction, they will be referred to as socio-sexual behaviors to capture the unique social aspect of sex that is usually not present in other species aside from humans. To illustrate an example of socio-sexual behavior, we look at feeding, a high-stress event for both chimpanzees and bonobos. For both species, if food is not abundant, individuals compete over resources to survive. Reducing tension among chimpanzees involves aggressively fighting over the food, whereas bonobos overcome stressful situations by engaging in a myriad of sexual behaviors. In addition to copulation, bonobos engage in GG-rubbing as mentioned previously. GG-rubbing is not only used when a young female is migrating into a new community, but it is also used continuously within the group to strengthen female social relationships. These strong female-female bonds help to support the matriarchal society and provide protection against unwanted male aggression.

Bonobos in Captivity

Endangered species benefit greatly from living in captivity because it helps ensure that a healthy and genetically diverse population remains if the wild population dies out. Population numbers for bonobos are very low in the wild and are estimated to be as low as 20,000. There are only about 160 bonobos living in captivity in the US

and Europe. Since their population is so small, it is essential that we understand how the captive environment impacts them differently than the wild setting to ensure they are given the best care. I propose that bonobos in captivity differ behaviorally and biologically from wild populations. I also argue that in a captive setting, a biological perspective on bonobo care and management is relied on too heavily. Instead, I propose that zoos utilize an anthropological perspective to ensure the most comprehensive care of bonobos.

One way that zoos and sanctuaries differ from the wild is in terms of space; the amount of space bonobos are given is dependent upon the institution's availability of resources. Individuals are in a fixed setting with limited range under human care. In the wild, bonobos are part of a large community of individuals that break off into smaller, temporary subgroups through fission-fusion. This allows for foraging under different conditions based on the abundance of food available and the distance it is from their community. These small groups fluctuate often and are comprised of a mix of ages, sex, and status. Zoos attempt to mimic the natural fission-fusion system that bonobos display in the wild by alternating the individuals that are housed together for the day, but I believe it cannot be replicated to the same extent.

The Jacksonville Zoo and Gardens (JZG) houses one of seven captive bonobo populations. I spoke with several personnel that work closely with the bonobos and collect behavioral observation data. Through my conversations, I learned about how they manage their group of bonobos. In terms of housing, there are certain individuals at the JZG who are not housed together to avoid behavioral and social problems. Additionally, there is a young female bonobo at the JZG that is beginning to reach sexual maturity and she is housed in female-only groups when she exhibits sexual swelling. These specific situations require human intervention in the form of organizing the sub-groups to prevent unwanted pregnancies or to avoid injury due to relational aggression. This prevents the bonobos from choosing their own groups freely like they would in the wild because there are practical considerations for the zoo to consider. While fission-fusion is simulated at JZG, I would argue that it is not identical to how bonobos live in the wild and is one way that their behavior is regulated in captivity.

Unless new bonobos are born at JZG, brought in from another zoo, or removed from the captive setting, the group members stay the same. These decisions are made by the zoo based on recommendations outlined in the Bonobo Species Survival

Plan (SSP). An SSP is a management program for North American zoos created for all species, not just bonobos, that are classified as endangered. With help from the Zoological Society of Milwaukee, the Milwaukee County Zoo created the Bonobo SSP in 1988 (The Bonobo & Congo Biodiversity Initiative). While membership is not required, all zoos housing bonobos in North America operate in compliance with the SSP. As of 2013, only seven zoos in the US house bonobos and they care for about 80 individuals in total (The Bonobo & Congo Biodiversity Initiative). In European zoos, there are about 85 bonobos living in captivity. In contrast, there are over 2,000 chimpanzees living in captivity in the US alone which illuminates the rarity of bonobos in captivity and why they are understudied. Since the bonobo captive population is so restricted, the objective of the SSP is to ensure genetic diversity within this small gene pool and promote the health and well-being of captive bonobos. The Bonobo SSP also works in conjunction with the European Endangered Species Programme (EEP) to manage the captive bonobo population globally (The Bonobo & Congo Biodiversity Initiative). In addition to managing captive populations, the Bonobo SSP and the Bonobo & Congo Biodiversity Initiative (BCBI) aim to support and protect wild populations from the devastating effects of hunting and deforestation.

The management of bonobos under human care involves careful consideration of breeding genetically valuable individuals to ensure diversity. According to the Supervisor of Mammals at the Jacksonville Zoo & Gardens, a genetically valuable individual is a bonobo who does not have many relatives in captivity and whose genes are not heavily represented in the captive population. Again, these breeding decisions are outlined in a Species Survival Plan (SSP) for endangered animals like bonobos. Even though population numbers are so low, zoos cannot let bonobos breed freely in captivity. It is important that the institutions have enough resources, like funding, staff, and space in the exhibit, to care for a new infant before allowing a pair to breed. When a female bonobo is nursing her offspring, she is not sexually receptive and nursing acts like a natural contraceptive. If a female is not nursing her young and she should not be bred based on available resources and/or Bonobo SSP recommendations, she will be administered birth control to regulate her reproduction.

The organization in the US that outlines contraceptive methods for captive animals is the Association of Zoos and Aquariums (AZA). The rules and regulations established by the AZA are considered the national standard for animal welfare by the

United States Department of Agriculture (USDA) and the Occupational Safety and Health Administration (OSHA). They have rigorously tested and scientifically based standards that are verified by professionals from multiple disciplines. Zoos can be accredited by the AZA meaning they have been inspected by professionals in various fields to ensure they meet the requirements for vet care, conservation, education, guest services, physical facilities, safety, staffing, finance, and animal welfare outlined by the scientists behind AZA guidelines.

Due to their morphological similarities, bonobos and chimpanzees under human care receive similar methods of contraception. The Chimpanzee Care Manual (2010) created by the AZA details the various forms of contraception that are available for the species. The most preferred methods are ones that are short-term and reversible to ensure that normal behavior is maintained while using contraceptives and that the animal can still be bred (if recommended by the species' SSP) soon after contraception is stopped. In both chimpanzees and bonobos, the sexual swelling of the genitals has significant impacts on socio-sexual behavior. Therefore, it is important to achieve proper hormone dosage for the type of contraception being used. If the dosage is too high, it may prevent the female from reaching normal levels of sexual swelling. Conversely, if the dosage is too low then the contraceptive may be ineffective and the female could become pregnant unexpectedly. This is where an anthropological perspective becomes crucial. Treating bonobos with the same birth control as chimpanzees because they are somewhat similar is doing them a disservice. While they might appear biologically similar, I argue that distinct differences in socio-sexual behavior need to be taken into consideration when administering hormonal contraception. The nuanced physiology of bonobos that allows for longer periods of maximal sexual swelling significantly impacts behavior and bonobo society overall. Simply giving both species the same form of birth control overlooks these nuances in biology and obvious differences in behavior.

An anthropological perspective entails a holistic view of bonobos, taking both biology and behavior into consideration to ensure optimal management of captive bonobos.

There are several methods of contraception available, the main option being combination synthetic progestin and estrogen pills. These are exactly like the birth control pills that human females may take to prevent pregnancy. Pills are administered daily, preferably at the same time every day to effectively prevent pregnancy. Since chimpanzee and bonobo menstrual cycles are longer than human

females, higher doses may be used, but the typical dosage for humans has also worked for female chimpanzees. There are different types of pills that contain varying levels of progestin and estrogen, some of which are popular among humans because they eventually inhibit menstruation until the pill is no longer used. For chimpanzees, it is not recommended to use these pills that continually administer hormones throughout the menstrual cycle. Instead, birth control that has a pill-free or placebo week should be administered to ensure regulation of the sexual swelling cycle. In some female chimpanzees, contraceptive pills have had minimal to moderate effects on swelling which can greatly impact normal sexual behavior. Nonetheless, the pills impact the natural biological processes of sexual swelling for chimpanzees. There is not a Bonobo Care Manual available on the AZA website, but I presume that these same effects would be seen in bonobos. I hypothesize that sexual swelling will be impacted by birth control to a higher degree in bonobos because they tend to have a longer period of maximal swelling compared to chimpanzees. Prolonged maximal swelling might indicate a difference in the level of hormones that regulate sexual swelling, therefore the two species could be impacted differently by the same contraceptive pill.

At the JZG, birth control is administered daily in the form of a pill. The introduction of birth control to a female bonobo that has recently started exhibiting sexual swelling should be approached with caution. Starting birth control too soon can be potentially harmful according to the behavioral observation team at JZG. It is preferred to separate the maturing female from males in the group to avoid unplanned pregnancy since oral contraception is not considered a safe option.

Another method of contraception on the market is gonadotropin releasing hormone (GnRH) agonists, an experimental category of contraceptives that is available but not as widely used in populations of chimpanzees under human care. More research is required because the success rate and impact on socio-sexual behavior is unknown. Birth control pills, like many forms of contraceptives, target the female reproductive system, whereas GnRH agonists can be used in both males and females. This contraceptive works by first stimulating the reproductive system and subsequently suppressing the release of reproductive hormones. In males, testosterone and sperm production decreases and aggression is reduced. Females show a decrease in estrogen and progesterone and also experience ovulation suppression. If this is considered a reliable birth control option for male chimpanzees and bonobos,

it could reduce the need for female-centered contraceptives thereby eliminating the potentially negative impacts on sexual swelling cycles and socio-sexual behaviors.

Occasionally, sterilization is used to prevent pregnancy entirely. This involves a serious operation and should only be considered when the female would suffer severe health complications by becoming pregnant again or if they exhibit a reproductive pathology. For example, the oldest female bonobo at the JZG became pregnant unexpectedly and it was deemed very unsafe for her to give birth again after that pregnancy. She had the first case of a molar pregnancy seen in bonobos and it could have killed her. As a result, she underwent a hysterectomy procedure to sterilize her permanently. In the wild, reproduction is not regulated at all. Birth control and sterilization are significant ways that captivity differs from the wild and impacts a bonobo's natural biological functioning.

Research Methods

Originally, I planned to collaborate with JZG to compare their captive population of bonobos with results from existing research on wild populations. After discovering more about the group composition of their bonobos, I realized my original research questions could not be answered at this time with the data they had collected. Nonetheless, JZG provided insight to what a captive group of bonobos looks like which will serve as a basis for comparison to a wild setting. Additionally, I gained an understanding of how data collection works for primate behavioral observations.

The group of bonobos at the JZG is a multi-male and multi-female group that consists of six males and four females. The females are Lorel, Kuni, Jo-T, and Laney. The matriarch of the group is Lorel and she is the second oldest bonobo within the Bonobo Species Survival Plan (SSP) and the oldest at the JZG. She was among the first group of bonobos that were housed here in 1988. Lorel is 50 years old and has had eight offspring, one of which (Laney) resides with her. Birth control usage and breeding recommendations are outlined by the SSP to ensure the survival of the species. In the early 2000s, breeding was being encouraged to help increase population numbers. In more recent years, there has been a decline in breeding due to the lack of space and resources in the few zoos in the US that house bonobos (Personal conversation with Supervisor of Mammals at JZG). At JZG, there are currently no females that are on birth control because they are still nursing their young (Kuni and Jo-T), sexually immature (Laney), or are no longer fertile (Lorel).

Due to their reproductive states, they did not collect data on sexual swelling. This is interesting because researchers have found that wild female bonobos who are nursing still exhibit sexual swelling (Furuichi, 1987), but are just unable to conceive.

Initially, I intended to collect data myself on the socio-sexual behaviors of the JZG's bonobos. The timing of this coincided with renovations of their African Forest exhibit, which houses all the great apes, so I had to postpone my research. The updated enclosures provide more space and enrichment for the bonobos as well as the other great ape species housed at JZG. Previously, the exhibit consisted of only one enclosure where some of the bonobos would be out in the yard and visible to the zoo visitors while the rest of the group was kept separately inside their holding area. Now, the new exhibit consists of two yards, a north and south yard, plus access to an elevated walkway that leads to an artificial Kapok tree. Group members are rotated in and out of the areas based on fission-fusion to mimic the natural movement of bonobos in the wild. Keeping this fission-fusion system in mind, groups are sometimes given access to a combination of both yards, both yards and the holding area, one yard and the holding area, or one yard and the Kapok tree. Access to the holding area is always given when the temperature is below 55 degrees. Generally, the bonobos prefer warm weather and will stay in the holding area even if it is above that temperature, demonstrating that the bonobos are granted some autonomy in captivity to move between spaces at their choosing.

Behavioral observation data collection took place before and after the renovations. Observations are recorded on an iPad using a software called ZooMonitor. This allows the observer to systematically track behaviors using an interval and all-occurrence sampling method. For interval sampling, behaviors of each individual bonobo are recorded at an interval of five minutes for a total session duration of one hour long. At the beginning of the session, the observer will enter basic information about the context of the observation period such as which bonobos are out and being observed, what exhibit(s) they are in, the weather, time, enrichment available in the exhibit (burlap sacks, ball, etc.), and any special notes about other factors potentially impacting behavior for the session. Feeding time would be a good example of a special note that should be made before the session begins because feeding often elicits socio-sexual behaviors. Once the session has begun, a timer starts to prompt the observer with a buzzer sound every five minutes to enter the observations. At the buzzer, the observer scans the yard from left to right, takes a mental note of the

behaviors, then enters them into the iPad in order.

First, spatial or proximity data is recorded to identify whether individuals are touching, within arm's reach, or distant from each other. If two adult bonobos are touching, the observer would record the proximity information for each individual (i.e. one data point to represent Jo-T's contact with Lorel and another data point for Lorel's contact with Jo-T). Then, their behaviors are recorded based on an ethogram which lists classes of behaviors, their operational definitions, and a hierarchy that ranks the importance of recording one behavior over another if multiple behaviors are occurring at the same time. For example, if Jo-T is grooming Lorel, the observer would enter two data points: one for the initiator of the actions (i.e. Jo-T grooms Lorel) and one for the recipient (i.e. Lorel receives grooming from Jo-T). Infants are only included in behavioral observations as social modifiers. This means that their behavior and proximity is not recorded during the interval scans. They are not recorded as initiators of behavior. Instead, if an infant is nursing, the observer would record that the mother was receiving a prosocial behavior from the infant but they would not record that the infant initiated a prosocial behavior. This also applies to proximity; an adult would be recorded as being in contact with an infant, but the observer would not record the corresponding data for the infant. All-occurrence sampling is for behaviors that are salient or unusual and therefore are recorded each time they occur, even if it happens outside of the five-minute interval. The behavior labels in the ethogram created by the zoo include: aberrant, aggressive, submissive, reproductive, and display behaviors (See Appendix for operational definitions). Interestingly, JZG uses the term "reproductive behaviors" as opposed to "socio-sexual behaviors" which is the terminology commonly found in literature. Their word choice emphasizes the biological nature of copulation (for reproducing) as opposed to highlighting its social function in bonobos (for reducing group tension and strengthening social relationships). Again, this emphasizes the biological approach taken by zoos to manage bonobos.

During data collection, if there is anything important that occurred before or during the session that likely impacted the behaviors recorded that day, notes can be made by the observer so they can be referenced later while looking at the raw data. After completing and saving the session, it is uploaded into an Excel file. Data was collected prior to the renovation of the exhibit from March 2017 to July 2017. After the renovation was completed, observations resumed starting in September

2018 and continue to the present. To ensure inter-observer reliability, observers must reach a level of 85% agreement before collecting data. Training to officially collect data for the zoo involves practicing data collection with ZooMonitor. The novice observer will conduct observation sessions (without saving the data) until they are comfortable and ready to be tested by a trained observer. The observer in training must be in agreement with the trained observer for at least 85% of the observations to pass and reliably collect data for the zoo.

My intentions were to analyze their data to see if there were any correlates between female sexual swelling and the occurrence of socio-sexual behaviors and to compare the results to studies conducted in the wild. During the period of behavioral data collection, sexual swelling levels were not recorded for females due to their reproductive states. This research plan could be revisited and pursued in the future when the females are no longer nursing and the youngest reaches sexual maturity. Instead, I have analyzed and compared existing literature pertaining to the socio-sexual behaviors of wild and captive bonobo populations. My goals were to understand the differences exhibited by wild and captive bonobos and to find gaps where an anthropological perspective could benefit bonobo husbandry.

Literature Review on the Functions of Sexual Swelling

Sexual Swelling in the Wild

Ryu, Hill, and Furuichi (2015) proposed that female bonobo sexual swelling functions as a social cue to encourage interactions with other females to strengthen their relationships. They hypothesized that females with maximal swelling will engage in more GG-rubbing, have more females within close range to them, and spend more time grooming other females than those without maximal swelling. Data collection took place at the Wamba field site in the Democratic Republic of the Congo. The bonobos are wild and free-ranging, but they live in a reserve and are often the subject of wild studies. The first set of observations were collected from September 2011 until January 2012. Then data collection began again in June and concluded in September 2012. There were about 30 bonobos in the group across the two study sessions. Nine adult female bonobos were the focus of this study. Their sexual swelling was rated based on firmness since researchers noticed that size is not a reliable measurement due to individual variations in swelling (Ryu et al., 2015). The categories of swelling included non-swelling, intermediate swelling, and maximal

swelling. Researchers would follow the largest group during the day and one female in the group would be randomly selected for continuous focal sampling.

Copulations occurred more frequently for females exhibiting maximal sexual swelling. Additionally, young females copulated more often than old and middle-aged females and the old females only copulated during the maximal swelling period. GG-rubbing also occurred more often for females with maximal swelling. Of all the situations in which context could be determined, 89% of GG-rubbing occurred during times of feeding. For proximity, females exhibiting maximal swelling had more females within 1 meter of them. They also joined larger parties with more females than those without sexual swelling. Grooming interactions occurred more frequently for females with maximal swelling than those with intermediate or non-swelling status.

Since copulations occurred more often for females with maximal swelling, this supports the idea that swelling functions as a reproductive cue for males to increase breeding success. Researchers also found support for swelling as a social cue for female bonding. The swelling appears to make females more attractive to other females, facilitating GG-rubbing and grooming interactions. Additionally, the maximal swelling lasts for a prolonged period of time which would help to maintain high levels of female bonding. Since bonobos have a matriarchal society, it is suggested that sexual swelling increases the opportunities for female-female social bonding, thus supporting their high social status within the group. GG-rubbing occurred more often for females with maximal swelling and in feeding contexts than at any other time. Older females, typically with higher rank, often lead a group while they are foraging and get first access to the fruit tree. This also suggests that females with low rank would benefit from maintaining maximal swelling because they can engage in more GG-rubbing with higher ranked females to reduce tension, decrease distance between each other, and allow them greater access to food. In sum, sexual swelling functions as both a social and reproductive mechanism for female bonobos.

Furuichi (1987) also studied bonobos living in the wild at the Wamba site in the Democratic Republic of the Congo, formerly known as the Republic of Zaire at the time of his research. This group of bonobos contained 28 bonobos with 15 females and 13 males. Since juvenile and infant females are not sexually mature, the author focused on the sexual swelling and sexual behaviors of the ten adult females. The movements of the bonobos were followed through the forest in order

to collect observational data. Occasionally, sugar cane was given to the bonobos at their sleeping site to assess group membership and the level of sexual swelling. Also, there were two sites that were provisioned with sugar cane that the bonobos would visit when fruit was not readily available. About 12% of observations took place at these two sites. Sexual swelling was rated by firmness and size from a scale of 1 to 3: 1 being wrinkled and small (distance between the eyes and mouth of the focal female) and 3 being completely firm with no wrinkles and large (longer than the distance between the eyes and chin). Each female was observed for about 800 minutes each and copulations were recorded for the focal female and nearby females.

Similar to Ryu et al. (2015), periods of maximal swelling elicited the most copulations with 81.9% of copulations occurring during the highest swelling firmness rating of 3. Swelling size, compared to swelling firmness, was not predictive of copulation rates. This was likely because the younger females did not reach the same swelling sizes as the older females. Adult females with newborn infants rarely copulated but still exhibited regular sexual swelling cycles. Adult females with 3-year-olds copulated at the same rate as the other females who were not nursing or pregnant.

In this wild setting, Furuichi (1987) also observed that copulation frequency was related to the maximal swelling period. This could indicate that females are more attractive to males or are more sexually receptive at this time of her cycle. This study provides additional support for the biological function of swelling for reproduction. Interestingly, females with newborn infants who are not yet able to reproduce still showed regular swelling cycles, suggesting there is another reason to maintain swelling without sexual receptivity. For example, the prolonged period of non-receptive swelling could create the illusion that there are many estrous females in the group, thus reducing male mating competition. This would prevent males from fighting over females, as seen frequently in chimpanzees. Also, the non-receptive swelling may serve a social function for the females by encouraging GG-rubbing. This is only speculative as GG-rubbing data was not collected for this study.

Both studies were conducted at the Wamba field site, but at different points in time. For this population of bonobos, it appears that maximal sexual swelling elicits copulation more than other states of swelling. These studies support the primary biological function of sexual swelling in bonobos that is also observed in chimpanzees (Deschner, Heistermann, Hodges, & Boesch, 2004). While the species are similar regarding sexual swelling and reproduction, Ryu et al. (2015) clearly showed the

relationship between sexual swelling and GG-rubbing. Since GG-rubbing is a homosexual interaction and does not confer reproductive benefits, it is suggested that sexual swelling also promotes female-female bonding to ultimately reinforce the female dominated society in the wild.

Sexual Swelling in Captivity

Most captive studies of bonobos are carried out at one zoo or sanctuary location which makes it difficult to generalize the findings. Stevens, Vervaecke, and Van Elsacker (2008) conducted one of the first studies that considered the overall behavior of several captive groups of bonobos in one large study. Stevens observed four different captive groups: Wuppertal, Apenheul, Twycross, and Planckendael. Across the course of four years, Stevens focused on dominance relationships and socio-sexual behavior within these groups of bonobos. He observed bonobos continuously from morning to dusk using a combination of focal animal sampling, all occurrence sampling, and instantaneous scan sampling. All occurrence sampling included recording instances of aggression, grooming, and socio-sexual behaviors. He used instantaneous scan sampling to gather information about spatial proximity. During periods of frequent social interactions, video recordings were taken to be analyzed later.

Of all four groups, the Planckendael group of bonobos exhibited an unusually low rate of socio-sexual behavior at .13 interactions per hour. The socio-sexual behaviors included not only copulation, but GG-rubbing and genital manipulation as well. The rates of socio-sexual behavior for the other three groups was between .8 and .95 interactions per hour. For copulation alone, males across all four groups engaged in an average of .19 copulations per hour with a range from .01-.36. The researchers state that this number is close to the frequency of copulations reported for wild populations.

While most of the captive groups exhibited an average amount of socio-sexual behaviors overall, Planckendael was an outlier. The low frequency of socio-sexual behavior in the Planckendael group was explained in relation to group composition and age. In all four captive groups, a female bonobo's age was negatively correlated with the frequency of socio-sexual behaviors. In other words, as age increased, the rate of sexual behaviors decreased. Since there were several older females in this group, the researchers proposed that this relationship is why there was less socio-

sexual behavior in the group overall. This assumption is contrary to the results of Furuichi (1987) who found that there was not a statistically significant relationship between age and frequency of copulation in the wild. While the jury is out on the relationship between age and frequency of socio-sexual behaviors, I suggest that age played a role in the importance of the sexual swelling cycle, ultimately impacting sexual behavior.

While sexual swelling was not taken into consideration for this study, Stevens et al. (2008) mentioned that these older females at Planckendael were cycling regularly. Despite supposedly exhibiting regular sexual swelling, socio-sexual behavior was very infrequent since it occurred almost 6 times less than the other groups. If swelling was consistent, the results contrast with the findings of wild studies in which there is a marked increase in copulations and GG-rubbing in the maximum swelling stage (Ryu, Hill, & Furuichi, 2015). If there was this increase of socio-sexual behaviors during maximum sexual swelling, I think the frequency of socio-sexual behavior would be higher overall. I suggest that the rate of socio-sexual behavior was not impacted by sexual swelling because of the stability of the Planckendael group's composition. This was a well-established group at the time of Stevens' behavioral observations. According to Stevens et al. (2008), female-female bonds were stronger in this group 10 years prior. He suggests that this is because it was a new group with females who were unfamiliar with each other and required more frequent GG-rubbing to build their relationships. Prolonged maximal swelling was probably important to the newly formed group because it elicits more GG-rubbing. At the time of the study, the dominance hierarchies were solidified and the females were older. Their female-female bonds weakened over time and are unaffected by sexual swelling, resulting in an unusually low frequency of socio-sexual behaviors. I argue that maintaining the same group composition for 10 years in captivity dampened normal socio-sexual behavior.

Paoli, Palagi, Tacconi, and Borgognini Tarli (2006) investigated how the sexual swelling of female bonobos impacts the sexual behavior of both males and females in the group. Specifically, they examine how sexual swelling influences the rate of copulations between males and females and how the swelling affects the rate of genital-genital rubbing between females. Behavioral observation data was collected over four sessions for a total of 12 months between July 2000 and June 2003. Over the span of the observations, group composition changed with the

death of four bonobos and the birth of one. This group of bonobos is housed in the Apenheul Primate Park of The Netherlands. It is a unique colony because upon its establishment, six of the eight adults were born in the wild. Of these six, five of them came from their native environment in the Democratic Republic of the Congo (DRC). They were caught and kept at a rescue center in the DRC and transferred to the Apenheul Primate Park to establish the new colony and support the conservation of bonobos.

Behavioral data was recorded over the course of 6-hour sessions by using scan sampling at 5-minute intervals. In addition to recording all the bonobos' behaviors at every interval, focal animal sampling was used which entails following the behaviors and interactions of one animal for the entire observation period. Sexual behaviors, which include copulations and GG-rubbing, were recorded on an all-occurrence basis meaning at any time these behaviors occurred. Since the sexual behaviors are a key part of the hypothesis, it is advantageous to record them even when they occur outside of the scan sampling interval.

Copulation and GG-rubbing data was collected and analyzed for five females. Copulations occurred more frequently during periods of maximum sexual swelling for four out of the five females, but their analysis was not statistically significant when compared to periods of non-maximum swelling (paired t -test: $t=1.425$, $n=5$, NS). GG-rubbing occurred at higher rates during the maximal swelling phases compared to non-swelling and this result was statistically significant (paired t -test: $t=3.074$, $n=5$, $P<.05$). Copulatory rates were higher for female bonobos during periods of maximal sexual swelling. Despite not reaching statistical significance, this is an important finding considering there are other studies reporting similar results (Ryu, Hill, & Furuichi, 2015; Hohmann & Fruth, 2000). These other reports suggest that copulations are higher during maximal swelling for wild populations but not for captive populations. In captivity, rates of copulation remain stable throughout the swelling cycle (Blount, 1990). The reason for statistical non-significance could be that this group consisted of wild-born animals that were moved into a captive setting. Consequently, the typical male-female sexual relations may have been dampened by the restricted and artificial environment of the primate park.

Paoli et al. (2006) predicted that GG-rubbing would occur with the initiator having a different hierarchical ranking than the recipient which would suggest that it functions as an indicator of social status. GG-rubbing occurred more often during

periods of maximal sexual swelling and was not impacted by the social status of the initiator or recipient of the sexual contact. The idea of status indication through GG-rubbing was not supported. Since GG-rubbing occurred more often during maximal swelling, it was suggested that the swelling makes the females more attractive to other females to promote social integration through sexual behavior. In this setting, the functions of sexual swelling were to increase copulation for reproductive purposes and to increase GG-rubbing to strengthen social relations. While GG-rubbing occurred in a similar pattern to the wild study by Ryu et al. (2015), copulation differed in this captive setting.

Analytical Comparison Between Wild and Captive Studies

The sexual swelling of female bonobos has been studied extensively in the wild, naturalistic setting. In contrast, there are few captive studies whose primary focus is on the effects of captivity and sexual swelling on normal behaviors. While this subject warrants further research, a few conclusions can be drawn from the existing literature. First, socio-sexual behaviors are impacted by various factors including the level of sexual swelling, group composition, reproductive history of females, age, captive or wild setting, and place of birth (in captivity or in the wild). Additionally, maximal swelling influences socio-sexual behavior in both the captive and wild settings, but to a different extent. Lastly, despite my conversations with personnel at JZG suggesting that birth control is widely used in captive settings, there was no mention of it in the studies I encountered.

The groups of bonobos observed in each of the four studies were unique in their own way which makes it difficult to control for the impact of extraneous variables. For example, the two captive studies differed in terms of how well-established the bonobo groups were. The Apenheul Colony was established in 1998 and observations took place a few years later during the early 2000s. Based on anecdotal evidence from Stevens et al. (2008), a newly established colony often shows higher rates of socio-sexual behavior and female bonding than a well-established group. Not only was the Apenheul Colony a fairly new group, these bonobos were unrelated individuals transferred from a rescue center in the DRC and many of them were born in the wild. Animals born in the wild may exhibit a different range of normal behaviors than those born in captivity. As an illustration, male chimpanzees that are hand-reared by humans in captivity often don't engage in normal sexual behaviors. Instead,

they show more masturbation and less interest in copulation (Chimpanzee Care Manual, AZA). I propose that the results of the Apenheul Colony observations were more similar to the two wild studies because of the group's unfamiliarity with each other and retention of wild behaviors. If observed today, almost 20 years later, this colony might show low rates of socio-sexual behavior, similar to the Planckendael group from Stevens et al. (2008), because their social structure and dominance hierarchies would be well established.

In all of the studies, excluding Stevens et al., sexual swelling was positively correlated with socio-sexual behavior. The prolonged periods of maximal swelling may facilitate socio-sexual interactions to maintain low levels of stress in the group. In the wild, more stressors exist for bonobos such as the need to forage, the threat of hunters, the effects of deforestation on the abundance of fruit trees, and the potential to encounter neighboring bonobo groups and infringe on their territory. In Ryu, Hill, and Furuichi (2015), the wild group of bonobos showed more copulations, GG-rubbing, and grooming when females exhibited maximal swelling. In captivity, the only statistically significant result researchers found was that GG-rubbing occurred more frequently during the maximal swelling period, not copulation (Paoli et al., 2006). In a study about grooming preferences in captive bonobos, maximal swelling was not related to increases in grooming (Franz, 1999) like it was in the wild. As the amount of stress decreases for bonobos, the less influential the periods of maximal swelling are on behavior.

Although the rates of socio-sexual behavior in the captive studies were comparable to those found in the wild studies, there were slight differences. One of the four captive groups in the Stevens et al. (2008) study significantly differed from the rest in terms of the frequency of socio-sexual behavior. This could be due to how long the group was established as mentioned previously, but it could also be due to individual temperament. Studying non-human primates is so complex because every individual has their unique temperament and behavior. This is often overlooked in primate research because it is hard to quantify. In humans, we can administer personality tests to understand the impact of individual differences on behavior. The same thing cannot be done for bonobos, so we tend to lump them all together or attribute differences to sex, age, or social rank. For future research, it is important to understand the full scope of intra-group variation in temperament before making inter-group comparisons.

In addition to temperamental differences, I believe that the use of hormonal birth control could be why there are reports of different copulation patterns in captivity compared to the wild. Blount (1990) noted that copulation is consistent throughout the swelling cycle in captivity, suggesting that the sexual swelling cycle does not function in the same way as it does in the wild. I argue that the use of contraceptives is the culprit behind the differences in socio-sexual behavior. Bonobos and chimpanzees are commonly given the same types and dosages of birth control because zoological institutions view them as biologically similar species. Viewing them as equivalent undermines their unique differences in behavior and is potentially dampening the bonobo's normal range of socio-sexual behavior. An anthropological approach considers a wide range of perspectives and emphasizes the interconnectedness of various domains. This approach is critical for the management of bonobos because it encompasses the biological perspective predominantly used by zoos and how biology interacts with behavior to shape the unique society of this species.

Conclusions

While conducting my literature review, I found that there were far more studies conducted on wild bonobos and sexual swelling than in captive populations. This is surprising considering the potential dangers of studying bonobos in the war-torn DRC. Many of the authors for wild studies were recurring in my search, whereas this was not the case for captive studies. Sexual swelling may be difficult to study in captivity because pregnant, lactating, or juvenile females do not exhibit normal swelling with the associated socio-sexual behaviors. Additionally, the use of birth control was not mentioned in any of the captive studies I found. This may reflect a lack of birth control use in captive populations, or a lack of awareness of the use of birth control in the care of captive apes. The sample size of captive studies was small for this comparative research; therefore, it is difficult to generalize the results or make definitive conclusions. This further highlights the importance of collecting more data on captive populations.

Bonobos and chimpanzees are our closest living relatives. For many years, chimpanzees were chosen as the best evolutionary model for the last ancestor between our three species because they cooperated amongst each other, exhibited power hierarchies, and engaged in a similar form of warfare. When bonobos and chimpanzees diverged from each other, bonobos stayed south of the Congo river and

remained in the trees whereas the chimpanzees moved north of the river and adapted to a more open and dry environment. If bonobos stayed in the same habitat, they may be less specialized than chimpanzees (de Waal, 1995). As a result, this would make bonobos a better model for pre-humans because they have changed less over time. Bonobos are historically understudied because they were one of the last great apes to be discovered. It is important to continue researching their unique behavior and social structure because they may be the best representation of the last common ancestor between Pan and Homo.

There is more to be discovered about the full range of socio-sexual behaviors and their functions in bonobo society. More importantly, we need to understand how these behaviors differ while under human care in a captive setting. Since bonobos are endangered, it is crucial that they are well researched to ensure the best animal care and husbandry practices in zoos and sanctuaries that house bonobos. From my literature search and interviews with personnel at the Jacksonville Zoo and Gardens (JZG), birth control is administered to non-human primates in zoos if they are not recommended to breed. Interestingly, I did not find any research about how birth control affects bonobos specifically. This leads me to believe that chimpanzees may be relied on too heavily as a model for how birth control impacts a bonobo's normal behavior due to their biological similarity.

An anthropological perspective is unique from a solely biological viewpoint because it is holistic and captures multiple dimensions of a subject. In this case, an anthropological perspective in the care of captive bonobos would tremendously change how we manage the species. Since they were originally considered a pygmy chimpanzee, bonobos have often been directly compared to chimpanzees rather than seen as their own unique species. Though they look similar to each other, their unique behavior is what sets them apart, not their biology. At JZG, I witnessed the use of a primarily biological lens when looking at their ethogram which lists all the possible behaviors bonobos engage in and their operational definitions. Through my literature review, I found that the term "socio-sexual behavior" was preferred to encapsulate the social aspect of their sexual behavior. On the other hand, at JZG, they used the term "reproductive behavior" which only highlights one aspect of bonobo sexual behavior. Although this terminology is probably useful for answering the zoo's own research questions, it diminishes the importance of the social function of sexual behavior. Ultimately, I argue that a strictly biological viewpoint in the management of captive

bonobos relies too heavily on a physical comparison to chimpanzees and overlooks the unique quality of bonobos that is their socio-sexual behavior.

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Appendix

The Jacksonville Zoo and Gardens' Bonobo Behavior Ethogram

Table: Behavioral definitions of the condensed ethogram — modified from (Stoinski et al., 2004a).

Behavior	Social Modifier	Definition
<i>Affiliative</i>	Partner Initiator Receiver	or Subject engages in an interaction with another individual, (i.e. grooming, playing) or calmly seeks proximity to another individual. Never accompanied by piloerection. Divided into <u>prosocial interaction</u> or <u>approach</u> .
<i>Aggression</i>	Partner Initiator Receiver	or Subject directs to or is a recipient of agonistic social behaviors (i.e. charging, conspecific directed displays, chasing, slapping, kicking, biting). Usually accompanied by piloerection, tight-faced grimace, or loud vocalizations. Divided into <u>non-contact</u> and <u>contact</u> interactions.
<i>Submission</i>	Partner Initiator Receiver	or Subject exhibits or receives clear instances of avoidance or displacement in which an individual actively moves location based on the actions or proximity of another individual. Divided into <u>displace</u> or <u>displaced by</u> categories.
<i>Reproduction</i>	Partner Initiator Receiver	or Subject initiates or receives <u>copulation</u> or <u>genital manipulation</u> , or <u>genital investigation</u> (latter involving sight only)
<i>Aberrant</i>	None	Subject exhibits any species atypical behaviors. Behavioral modifiers include <u>self-injurious behaviors</u> (such as continual picking of scabs), <u>coprophagy</u> , <u>repetitive movement</u> (≥ 3 bouts), and <u>other</u> .

Behavior	Social Modifier	Definition
<i>Display</i>	None	Individual charges at <u>visitor</u> area, <u>holding</u> area or in an area with <u>no apparent recipient</u> . Can include chest beating, piloerection, vocalizations, or object throwing.
Locomotion	None	Subject is moving/changing location in a <u>horizontal</u> or <u>vertical</u> plane or <u>swinging</u> on ropes
Forage	None	Subject is searching for or ingesting food or liquid items. Divided <u>into eat or drink</u> .
Object	None	Subject actively manipulates a temporary or permanent (non-food) item within the enclosure. Divided into <u>enrichment</u> , <u>environment</u> , or <u>exhibit animal</u> .
Attention	Area	Subject directs attention to certain areas or individuals; face must be within 1 meter of separating glass or mesh. Behavioral modifiers are divided into <u>holding</u> areas or <u>second enclosure</u>
Self	None	Subject exhibits self-directed behaviors including auto-grooming, scratching, rubbing, etc.
Solitary Play	None	Individual engages in independent play using own body part or locomotive patterns
Inactive	None	Subject is not moving, eyes can be open or closed
Other	None	Subject exhibits any other behavior not included above

* Social behaviors (italicized) will be recorded as both scan behaviors and all-occurrence behaviors. All other behaviors will only be recorded as scan behaviors only.

** Underlined words indicate behavioral modifiers on ZooMonitor.