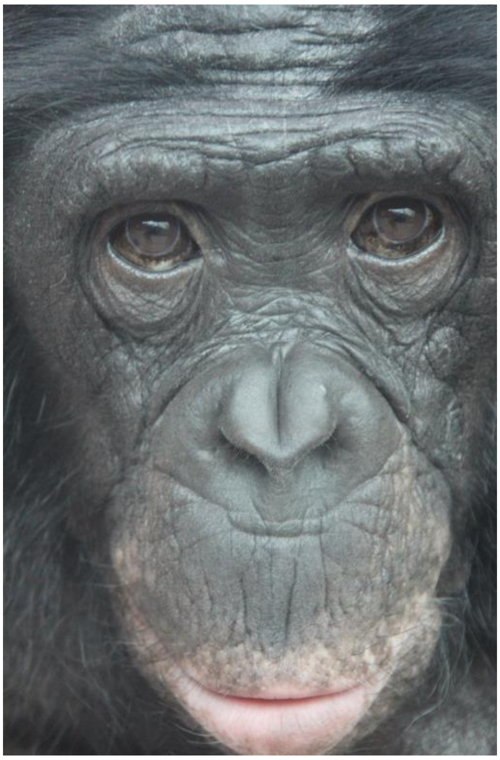
EAZA Best Practice Guidelines

Bonobo (*Pan paniscus*)



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EAZA Best Practice Guidelines disclaimer

EAZA Preamble

Right from the very beginning it has been the concern of EAZA and the EEPs to encourage and promote the highest possible standards for husbandry of zoo and aquarium animals. For this reason, quite early on, EAZA developed the “Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria”. These standards lay down general principles of animal keeping, to which the members of EAZA feel themselves committed. Above and beyond this, some countries have defined regulatory minimum standards for the keeping of individual species regarding the size and furnishings of enclosures etc., which, according to the opinion of authors, should definitely be fulfilled before allowing such animals to be kept within the area of the jurisdiction of those countries. These minimum standards are intended to determine the borderline of acceptable animal welfare. It is not permitted to fall short of these standards. How difficult it is to determine the standards, however, can be seen in the fact that minimum standards vary from country to country. Above and beyond this, specialists of the EEPs and TAGs have undertaken the considerable task of laying down guidelines for keeping individual animal species. Whilst some aspects of husbandry reported in the guidelines will define minimum standards, in general, these guidelines are not to be understood as minimum requirements; they represent best practice. As such the EAZA Best Practice Guidelines for keeping animals intend rather to describe the desirable design of enclosures and prerequisites for animal keeping that are, according to the present state of knowledge, considered as being optimal for each species. They intend above all to indicate how enclosures should be designed and what conditions should be fulfilled for the optimal care of individual species.

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Contents

Introduction

The bonobo (*Pan paniscus*) was the last of the African ape species to be “discovered” by Western scientists. Unfortunately, nowadays this species is endangered, and as in the other species of great apes, direct threats include commercial hunting for bushmeat, that is exacerbated by habitat fragmentation through slash and burn agriculture and timber harvest. Worldwide there are 225 bonobos in managed populations, including 136 individuals in 10 EAZA zoos (December 2019). The Bonobo Eaza Ex Situ Program (EEP) population is managed in a global breeding program together with the Species Survival Program (SSP) population, which houses 95 individuals in nine institutions (December 2019). The individuals housed in the sanctuary ‘Lola Ya Bonobo’; as well as a number of other individuals outside of the managed population are included in the International Studbook, but are not managed by EEP or SSP.

EAZA members have established Taxon Advisory Groups (TAGs) for different groups of animal species that are kept in zoos and aquariums. One of the main tasks of a TAG is to develop Regional Collection Plans that describe which species are recommended to be kept. The TAGs also identify which species need to be managed in a European breeding programme called EEP (EAZA, 2019).

The mission statement of the EAZA Great Ape TAG [2018] is:

“The mission of the Great Ape TAG is to maintain self-sustaining and healthy populations of all the taxa of great ape to sub specific level where possible, and to encourage and promote their conservation in the wild.The roles of zoo populations of great apes are primarily to be ambassadors for their wild counterparts for conservation-education, to support their global conservation and to be used for non-invasive research in line with the EAZA research standards. These zoo populations may also be necessary for future reinforcement of wild populations and should therefore be managed to preserve maximum genetic diversity and natural behaviour.”

In the regional collection plan of the EAZA Great Ape TAG [2011] the target population for bonobos, as defined by EAZA members needs/wishes (i.e. space allocated to the species) was set at approximately 200 individuals. This is more than the number that is strictly needed to maintain 90% of the current genetic diversity (which is approximately 111 individuals) for a minimum of a 100 years, but also takes into account the popularity of the species, as well as space needs for the other great ape species managed by the TAG.

In addition to the Mission Statement of the EAZA Great Ape TAG, the Bonobo EEP, together with the Bonobo SSP, formulated the following mission statement for the Global Breeding Program:

“*Recognizing the importance of preserving natural populations of species, the Bonobo SSP and EEP are designed to be an active component of a holistic approach to conservation of Pan paniscus, the bonobo or pygmy chimpanzee. Our mission is to manage the captive population of bonobos held in North American and European institutions, in a way which creates a self-sustaining captive population for many generations and which preserves the natural integrity of the species while in captivity to the fullest possible extent. In tandem with captive management, our mission is to support in situ conservation work that is vital to the preservation of wild bonobo populations. Because of the small* *size of both the SSP and EEP populations the SSP and EEP captive bonobo population will be managed as a world population.*

The SSP and EEP recognize the captive bonobo population as a valuable conservation resource and strive to optimize its utilization in the following ways:

1) *As an* ***educational resource*** *to increase public awareness of the natural heritage of the bonobo, which in turn can lead to:*
    a) *possible funding opportunities for in situ conservation of the bonobo and its habitat,*
    b) *increased public interest in the plight of the species and its natural environment, and*
2) *As an* ***ex situ source for non-invasive research*** *which contributes to species survival; increased scientific interest in the conservation biology of the bonobo;*
3) *as a species-specific* ***genetic and demographic model*** *for small population management and endangered species conservation;*
4) *As a resource for developing a repertoire of biological and management techniques and skills useful for in situ and ex situ conservation.*

The SSP and EEP seek to augment species conservation by meeting the following ***objectives****:*

1) *To manage the world captive population for long-term survival by:*
    a) *Preserving genetic diversity,*
    b) *Attaining and maintaining demographic stability,*
    c) *Encouraging species-specific behaviour to ensure survival of the bonobo's complex social and behavioural characteristics and to promote understanding of their intellectual attributes,*
    d) *Developing ways to improve the care and maintenance of the captive population, and*
    e) *Disseminating information pertinent to the above through open sharing of information and publication of appropriate materials (i.e. husbandry manual, action plan, Master Plan, etc.);*
2) *To encourage and support conservation initiatives in the Democratic Republic of Congo that benefit the bonobo and other wildlife, habitat and people by:*
    a) *Reviewing and reporting on the conservation status of the bonobo in DRC on a regular basis,*
    b) *Producing an action plan on a regular and timely basis,*
    c) *Encouraging SSP and EEP zoos to play an active role (direct or indirect) in addressing the priority recommendations of the action plan (e.g. financial and technical support),*
    d) *Developing the means to transfer technology, skills and other information between zoo personnel and other relevant people involved with field conservation and conservation education within DRC;*
3) *To develop the conservation potential of the captive bonobo population by:*
    a) *Promoting scientific research and development of husbandry techniques which enhance species conservation, propagation, improvement of captive management and animal welfare, and*
    b) *Encouraging educational activities that increase public awareness and appreciation of the bonobo's unique life history, behaviour, ecological significance, conservation status and natural environment;*
4) *To work in concert with the AZA and EAZA Ape Taxon Advisory Groups (TAG), conservation groups and scientific organizations in an effort to:*
    a) *Encourage development of complementary conservation goals,*

b) *Lend support to appropriate projects, and*
c) *Improve the opportunity for the captive population to be managed and utilized as part of the global bonobo population.*

These Best Practice Husbandry Guidelines follow the template suggested by EAZA for all their EEPs. The **first section** gives a detailed overview of our current knowledge on biology of the bonobo, based mainly on published research, to a lesser degree on information from PhD studies that were not always published or small articles from the “grey literature”, or even popularising books, and also to some degree on personal observations, or communications with various people. Although the EAZA template states this part should be based on data from the field, I have also included references to zoo-based research, where relevant, since so much of what we know about the bonobo’s biology has come through research in zoos. This part is written as an extensive scientific review and I have tried to include all relevant references. I realise this overview has become quite large and perhaps sometimes very detailed. This is partly because of my enthusiasm for bonobo science, but also because I wanted to give answers to questions that people have asked me over the years regarding bonobos. This section is also an up to date resource for education about the species.

The **second section** deals with bonobo management in zoos. This section is heavily based on the 1997 version of the Bonobo Husbandry Guidelines [Mills et al., 1997], which in turn was based on the 1992 SSP Husbandry Guidelines for chimpanzees [Fulk & Garland, 1992]. I have updated it with information collected and experiences gained by various zoos during the past 15 years. I also used the more recent SSP Care Guidelines for chimpanzees [Ross et al., 2009] and relevant chapters from the 2006 and 2017 editions of the Gorilla EEP Husbandry Guidelines [Abelló et al., 2017] and the Orangutan EEP Best Practice Guidelines [Bemment, 2018]. I am greatly indebted to all people who contributed to those volumes. I have included the references to contributions to these guidelines, when necessary. Since our ideas about bonobo management have changed considerably since 1997, and are always being readjusted, this section is also very much based on discussions and conversations I have had with various bonobo people throughout the years.

The chapters have been reviewed, and edited by:

Section 1: Matyas Liptovszky (Twycross Zoo); Zjef Pereboom (Antwerp Zoo); Sarah Lafaut (Antwerp Zoo);

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Section 2.7. Veterinary Care: Matyas Liptovszky (Twycross Zoo); Zjef Pereboom (Antwerp);

In **Section 3** a list of references is presented. These include the references that were used in writing section I and section II, and therefore include some references on chimpanzee and gorilla husbandry, too. In line with the tradition of the Royal Zoological Society of Antwerp EEPs, I constructed a broad scale bibliography, which also includes all other references to published work on bonobos (with exception of abstracts) that we have collected through the years, making it an extensive bibliography on bonobos, for those who are interested in aspects of bonobos (e.g. historical; cognitive; …) that were not specifically dealt with in section I and II of these guidelines.

A very special thank you goes to Dr Verena Behringer (Deutsches PrimatenZentrum) who went meticulously through this entire document, edited everything, up until the reference list, and gave me the courage to finish this document.

Enjoy!

Jeroen Stevens – 01 IX 2020

Section 1: Biology and Field data

Figure 1: Adolescent female bonobo (Zoo Planckendael – Jeroen Stevens)

1.1. Taxonomy

Order:	*Primates*
Suborder:	*Haplorrhini*
Infraorder:	*Simiiformes*
Superfamily:	*Hominoidea*
Family:	*Hominidae*
Genus:	*Pan*
Species:	*P. paniscus*

There are several early reports of “marungensis” apes living on the southern bank of the Congo river exist from 1880 on [Myers-Thompson, 2001a]. At the same time, several reports from captivity pointed out remarkable chimpanzees that later turned out to be bonobos [Portielje, 1916; Van Bree, 1963; Yerkes, 1925; Yerkes & Learned, 1925]. However, it wasn’t until 1929 that Ernst Schwartz officially described a new subspecies of chimpanzee, based on measurements of three adult skulls and one skin found in the Belgian museum of Tervuren, and named it “*Pan satyrus paniscus*” [Schwartz, 1929; Thijs-Van den Audenaerde, 1984 – see Figure 2]. In 1933, Hal Coolidge gave this taxon the full species status and named it “*Pan paniscus*”, based on investigations of a complete skeleton and skin of a female at the American Museum of Natural History [Coolidge, 1933, 1984]. It is ironic that this specimen is the smallest of all specimens collected [Doran, 1993; Jungers & Susman, 1984a], which led to the name of “pigmy chimpanzee”, by which the species was originally designated. An attempt in 1954 to place the species in a separate genus “*Bonobo paniscus*”, was not successful, but introduced “bonobo” as a vernacular name for the species [Heck, 1939; Pournelle 1960; Rempe, 1961; Tratz & Heck, 1954].

Figure 2: Type specimen for Pan paniscus (Tervuren Museum - Jeroen Stevens)

Nowadays, "*Pan paniscus*" is generally considered a **separate species** [e.g. Groves, 2018; McHenry, 1984; Kano, 1992; Shea & Coolidge, 1988; Stanyon et al., 1986], although this is sometimes disputed [e.g. Horn, 1979]. Based on genetic evidence, the divergence time between chimpanzees and bonobos is estimated to be around 0.86 – 2 million years before present [Bradley & Vigilant, 2002; Prüfer et al., 2012; Sarich, 1984; Stone et al., 2010; Won & Hey, 2005]. Genomic studies have found that gene flow occurred from bonobos into the ancestors of chimpanzees between 200.000 and 500.000 years ago [de Manuel et al., 2016]. Concurrent hybrids between a bonobo male and two chimpanzee females (*Pan troglodytes*) have occurred in a circus [Vervaecke & Van Elsacker, 1992; Vervaecke et al., 2004], but in the wild the two populations are allopatric and are separated by the Congo River [Vandebroeck, 1959]. The Congo River can reach a width of 20 km in the North and East, and is surrounded by inundated swamps in the East, so this massive river acts as a natural geographic barrier between the two species [Fruth et al., 1999]. Recent geological analyses have shown that the Congo River was formed around 34 million years ago, so long before ancestors of bonobos split off from ancestral chimpanzees; leading to an evolutionary scenario where in the Pleistocene, one or more founder populations of ancestral *Pan paniscus* crossed the Congo River to its left bank East of current Kisangani, during rare times when the Congo River discharge decreased, and colonised the area in the East of the current range, and spread out from there to the Western and Central area of the Congo Basin, through various migration routes [Takemoto et al., 2015, 2017a,b].

No official subspecies have been described for *Pan paniscus*. Kingdon [1997] mentions *Pan paniscus marungensis*, which lives in the southern area of the species' range, as a possible subspecies, but it is unclear whether the apes on the West side of lake Tanganyika, south of the Lukuga river in the Marungu mountains belongs to either *Pan paniscus* or *Pan troglodytes* [Butynski, 2001; Myers-Thompson, 1997]. Recent genetic analyses indicate that the Lomami river in the East may function as a weak genetic barrier, separating the Eastern bonobos from the other populations [Kawamoto et al., 2013], and some distinct dental and cranial characteristics have been noted [Pilbrow & Groves, 2013], but no subspecific status has been assigned to the bonobos living east of the Lomami river.

Originally the species was commonly referred to as "pygmy chimpanzee" [Susman, 1984a]; "dwarf chimpanzee" [e.g. Kirchshofer, 1963; Mortelmans, 1972; Moor-Jankowski et al., 1972] or "black-faced chimpanzee" [Schouteden, 1930], and terms were used interchangeably. Especially in the 1990s there was a vigorous debate about the use of the **vernacular name** "pigmy chimpanzee" versus "bonobo" [e.g. Kortlandt, 1992, 1997, 1998; Messinger 1993]. The latter has been more commonly used since then, although it is not an indigenous name [Kano, 1992]. The origin of the term "bonobo" is unclear, even to the people who introduced it [Heck, 1939], but is possibly derived from a misspelling on the crate in which the animals were shipped from the town of Bolobo [Susman, 1984a]. An alternative hypothesis links the origin of the word "bonobo" to the proto Bantou language for "riverine", "what is found on the other side of the river", indicating the animals would find themselves on the same side of the river as ancestors [André, 2006]. "Lesser chimpanzee" [Brehme, 1973] or "gracile chimpanzee" have also been proposed as alternative names [Butyinski, 2001; Kortlandt, 1997, 1998, 1999; White, 1996b], but this never received much support. The Lingala word used for both chimpanzees and bonobos is *mokomboso* [Kano, 1992] or *mokonbusu* [Kano & Nishida, 1999], but is often not recognized by local people in areas where bonobos occur [Kano, 1992]. Indigenous names are *edja* or *edja mbanda*, *engombe* (plural: *bingombe*), *elya* (plural: *bylia*), *elyamana*, or *elia* (plural: *bilia*); *ifuk* (plural: *tofuku*); *ebubu* [Callewaert, 1930; Kano, 1984a; 1992; Kano & Nishida, 1999; Lingomo & Kimura, 2009; Maniacky, 2006; Mubalamata, 1984; Narat et al., 2015b, Thompson 1999,2000]. '*Bilia'* has been proposed as a vernacular name for publications in English publications [Kano & Nishida, 1999; Maniacky, 2006], but this was not successful [e.g. Thompson 1999,2000], and the species is now usually referred to as "bonobo", in most languages.

1.2. Morphology

1.2.1. Body Size

The original description of *Pan paniscus* was based on one individual that was relatively small, which led to the conclusion that bonobos weighed 50% of chimpanzees [Coolidge, 1933]. Later research on larger samples indicate that bonobos are not a dwarf species [Gijzen 1974; Horn, 1979; Shea, 1984]. On average bonobos weigh 85% of common chimpanzees, with considerable overlap in body weight between bonobos and the Eastern subspecies of chimpanzees [Corrucini & McHenry, 1979; Horn 1979; Jungers & Susman, 1984; Zihlman & Cramer, 1978; Zihlman et al., 1978].

Bonobos are the least sexually dimorphic of all apes in their cranial and **postcranial skeleton dimensions** [Cramer & Zihlman, 1978] and canine morphology [Begun & Deane 2005]. The average crown to anus length is 776 mm as measured for four wild caught males (range: 730-828 mm) and 738 mm for four wild caught females (range: 700-760 mm) [Coolidge & Shea, 1982]. When standing upright, the height from top of head to heel is on average 1190 mm for the four males (range: 1123-1240 mm) and 1170 mm for the four females (range: 1010-1165 mm) [Coolidge & Shea, 1982].

Sexual dimorphism is somewhat more pronounced in body weights, but the difference between males and females is still smaller than in other apes. In wild individuals, the average body weight for adult males is 45.0 ± 8.4 kg (range 37-61 kg) and for females 33.2 ± 4.2 kg (range 27-38 kg) [Jungers & Susman, 1984]. Parish [1996] found similar body weights for zoo-housed bonobos: average weight for adult males = 43.4 ± 6.4 kg (range: 33 – 56.5 kg, N = 15), for adult females = 35.9 ± 5,9 kg (range: 27.5 – 48.6 kg, N = 19).

In zoos, new-born bonobos weigh on average between 1 and 2 kg [Neugebauer, 1980]. No data are available for body weights of new-born individuals in the wild.

1.2.2. General appearance

Bonobos resemble their sibling species chimpanzees a lot, but differences in **morphology** have been noted and are used to describe the species [Coolidge & Shea, 1982; Zihlman & Cramer, 1978]. The typical colour of skin and body hair is black [Coolidge, 1933; Miller, 1952], but occasionally individuals with dark brown hair [Kano, 1983, 1992] or reddish brown hair [Jahme, 2005; J. Thompson, pers. comm.] have been seen in the wild, as well in sanctuatries [J Stevens pers. Obs – see Figure 3a]. Many bonobos retain white tail tufts, or at least some white hairs in the anal region, even into adulthood [Miller, 1952]. The face is typically black with pink lips [Coolidge, 1933; Kano, 1992], but individuals can differ greatly in the shade andthe degree of the pink pigmentation around the mouth (Figure 3b,c). It is often stated that bonobo faces and hands are black at birth [Frechkop, 1935], but individuals with paler faces have also been born in zoos (e.g. Figure 3e). Bonobos have brown eyes, with brown iris, usuallysclera are lighter brown [Lacambra et al., 2005], but in some individuals sclera may be partly white [J. Stevens, pers. obs. – Figure 3d]. Like humans, bonobos' sclerae are lighter relative to the color of their irises; chimpanzee sclerae are darker than their irises [Perea-Garcia et al., 2019]. Eyelids can be of a lighter colour in some individuals [Kano, 1992; Urbain & Rode, 1940].

In general, the bonobo has a more gracile body build with slender linear chest, has smaller ears, a rounder head, with less pronounced eyebrows and less prognathism when compared to chimpanzees, and has relatively long hind limbs [Coolidge, 1933; Coolidge & Shea, 1982; Jungers & Susman, 1984a; Kano, 1992; McGrew, 1984; Shea, 1984]. However, these differences are not always very clear cut. A good way to tell the two species apart is by listening to their voice, which is much higher in bonobos, who make higher-pitched, almost bird-like or gibbon-like vocalisations [Coolidge, 1933; de Waal, 1988, 1989; Frechkop, 1935; Heck, 1939; Hohmann & Fruth, 1994; Hübsch, 1970; Kirchshofer, 1962; Mitani & Gros-Louis, 1995; Rempe, 1961; Rode, 1940; Tratz & Heck, 1954; Yerkes & Learned, 1925].

Syndactyly, the webbing of toes or fingers (see Figure 3f) is often mentioned in early descriptions of bonobos [Miller, 1952] and has been recorded in 46.4% of 183 wild individuals studied by Kano [1984b]; and in 52% of the 23 zoo-housed individuals described by Gijzen [1974]. Five of the individuals in the latter study were related however, and the traits seems strongly heritable. In the current zoo population, webbing of digits can be traced back to certain founders, while webbing of toes and fingers is not apparent in other founder lines. Third nipples, a small tail bud at the base of the spine or six toes have been noted in wild-caught individuals and may be evidence of physical isolation of small populations [Messinger, 2007]. Similarly, it has been suggested that hand deformities could be a result of inbreeding in bonobos [Zihlman, 1987].

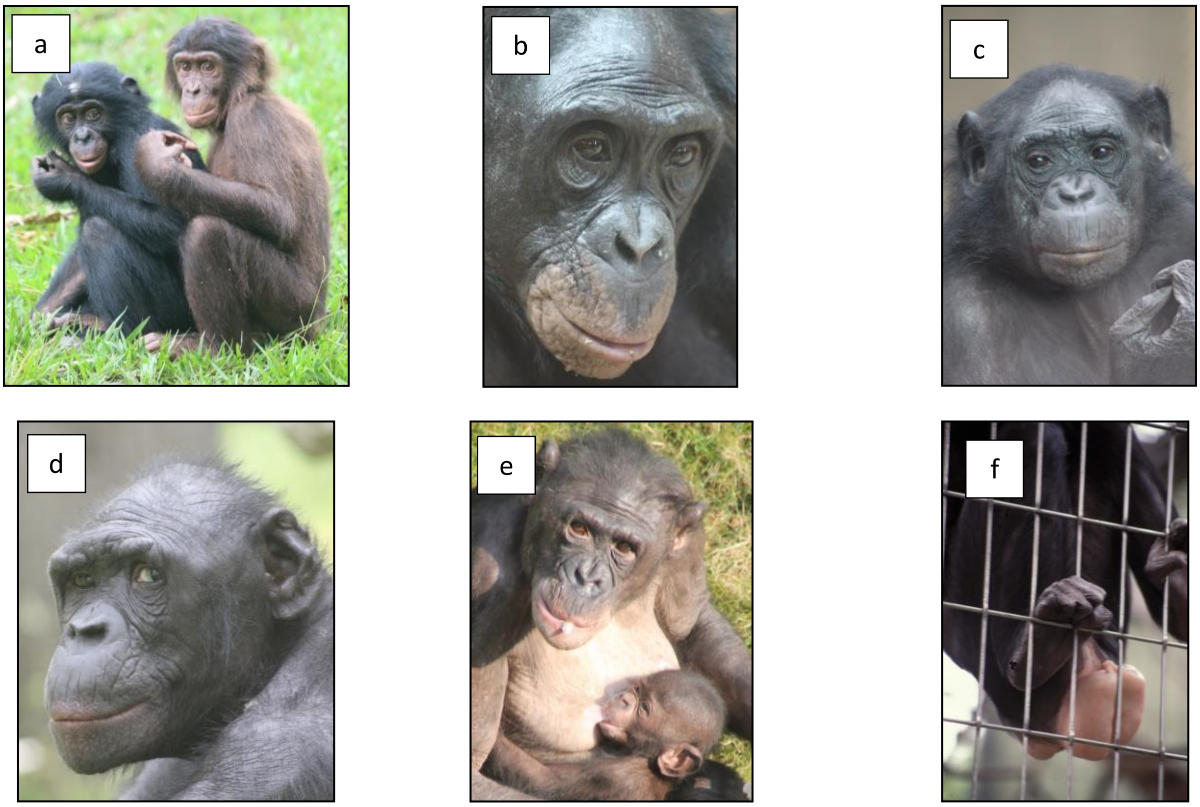

Figure 3: Variation in morphology in bonobos. A: some individuals have reddish brown hairs (Lola Ya Bonobo – Jeroen Stevens); b+c: Variation between individuals in the degree of pink pigmentation around the mouth (Twycross Zoo,Wilhelma Zoo Stuttgart – Jeroen Stevens); d: white patches on the sclera of an adult male (Frankfurt Zoo – Jeroen Stevens); e: very light pigmentation in very young bonobo male (Apenheul – Jeroen Stevens); f: webbed toes or syndactyly (Frankfurt Zoo – Jeroen Stevens).

The dental formula for deciduous teeth is di2/2, dc1/1, dm2/2, with no marked sexual dimorphism [Johanson, 1974; Kinzey, 1984]. It is suggested that dental eruption in zoo-housed bonobos is accelerated compared to wild ones [Bolter & Zihlman, 2011]. The **first deciduous teeth appear between four and six weeks and temporary dentition is complete at ten months** [Neugebauer, 1980]. Sequence of deciduous tooth eruption is [di1 di2] dm1[dm2 dc]/[di1 di2] dm1 [dm2 c] [Bolter & Zihlman, 2011]. Based on a small sample of five infant and juvenile bonobo females, Bolter & Zihlman [2011] conclude that **permanent tooth eruption occurs between 7 and 9 years of age**. For permanent teeth, the dental formula is: I2/2C 1/1, P2/2 M3/3, with only the canines showing sexual dimorphism: males have larger canines than females [Kinzey, 1984]. Sequence of permanent tooth eruption is [M1 I1 P4 M2] P3 I2 C M3/[M1 I1 P4 M2 I2] P3 C M3 [Bolter & Zihlman, 2011].

Several authors have called the bonobo a **paedomorphic species** [e.g. Behncke, 2015; Blount, 1990; Coolidge, 1933; Dahl, 1985; Doran, 1992, 1993; Kortlandt, 1999; Kuroda, 1979, 1989; Shea, 1983, 1984], retaining morphological and perhaps also behavioural characteristics of infancy into adulthood, such as the shape of the head, and in some individuals also the white tail tufts that in gorillas and chimpanzees only occur in infants [Coolidge, 1933]. Recently, it has been proposed that morphological paedomorphism in bonobos is a possible side effect of 'self-domestication' against aggression [Hare et al., 2012].

1.3. Physiology

There are no published records of bonobo heart rate, body temperature or respiration rates. Unpublished data from Antwerp Zoo/Planckendael suggest normal body temperature is around 37°C. Haemotological and biochemical values for blood are given in Appendix 1 [Loomis, 2003]. Bonobos show remarkably little polymorphism in blood groups, but show sharp serological differences from chimpanzees [Moor-Jankowski et al., 1972, 1975; Socha, 1984]. All bonobos tested have blood group A, and the antigens were indistinguishable from human A antigens [Gamble et al., 2011; Moor-Jankowski et al. 1972, 1975; Socha, 1984; Wiener & Socha, 1975]. In terms of the M-N blood system all tested bonobos had type M, but this agglutinogen differed from human and chimpanzee agglutinogens [Moor-Jankowski et al., 1972, 1975; Wiener & Socha, 1975]. Rh-Hr factors did not differ between chimpanzees and bonobos [Moor-Jankowski et al., 1972, 1975; Wiener & Socha, 1975]. In a large sample, 49 zoo housed bonobos were Rh-positive and two were negative, while in the bonobos of Lola Ya Bonobo orphanage nine tested positive and eleven tested negative [Gamble et al., 2011]. The tests for simian type blood factors showed differences between bonobos and chimpanzees. In the simian-type blood groups, all tested bonobos belonged to v.D and CEf types, while chimpanzees are also much more polymorphic for these factors [Moor-Jankowski et al., 1972, 1975; Wiener & Socha, 1975].

1.4. Longevity

Data for longevity in wild bonobos are scarce. The first field studies in Lomako and Wamba were only started in 1973, and had to be temporarily halted in the nineties because of political instability. In Wamba, some individuals could be re-identified after the war and data suggest a lifespan of about 45 years [Hashimoto et al., 2008; Kano, 1987a]. Ryu et al. [2016] mention three males and two females at Wamba older than 40 years. At Lomako, some females were also estimated to be older than 40 years; no old males in that age class were observed [Thompson-Handler, 1990]. Kano [1992] notes that for every possible illness, morbidity in wild bonobos is higher in males than females, suggesting that environmental pressure may be more severe on male than female bonobos. In zoos, the oldest living female, Margrit (Figure 4), is wild-born, so exact age is unknown, but she arrived in the zoo in 1957 at an estimated age of six, which makes her an estimated 68 years in 2019. In general, males seem to die at ayounger age, but the longevity record currently stands at 56 years, for Mato, Margrits son whowas born in Frankfurt zoo in 1963.

Figure 4: Margrit in 2019 at an estimated age of 68 (Frankfurt Zoo – Jeroen Stevens).

1.5. Zoogeography/Ecology/Conservation status

1.5.1. Zoogeography

The bonobo is endemic to the central Congo basin in the Democratic Republic of Congo (DRC). To the North and the West, the species range is bordered by the Congo River, which acts as a species barrier with *Pan troglodytes* and *Gorilla gorilla* [Kortlandt, 1995; Vandebroek, 1959]. Early reports of bonobos occurring North of the Congo river [e.g. Urbain & Rode, 1940] have been proven to be incorrect, and possibly these individuals were brought there by traders [Cousins, 1978; Kano, 1992]. The bonobos' geographical range is further bordered by the Lualaba river to the East and the Sankuru and Kasai rivers in the south [Butynski, 2001; Kano, 1992; Kortlandt, 1995; Vandebroek, 1959]. Recently, bonobos have been found to inhabit a forest block shouldering the right bank of the Lubefu River, an area south of the Kasai/Sankuru River system previously believed to be the southern limit of their distribution [Myers-Thompson, pers. com]. It has been speculated that until the 17th century the bonobo occurred much further south, up until Angola – but this evidence is mainly based on a painting by Tulp showing an ape "from Angola" which some believe to be a bonobo [Reynolds 1967; Thompson-Handler, 1990], but this is disputed [Gijzen, 1974; Thompson, 1997]. More surveys in the South are needed to determine the southern boundaries of the bonobo's range [Fruth et al., 2008]. The **historic range** is estimated to have been 565000 km², but is seriously fragmented and threatened by human activity [IUCN/ICCN, 2012; Hickey et al., 2013, see section 1.5.5.]. Only 28% (156,211 km²) of this range was predicted suitable habitat for bonobos [Hickey et al., 2013].

1.5.2. Ecology/habitat

Bonobos typically occur in **mature lowland tropical rainforest**, and until recently it was believed they were restricted to these forests, and were a relatively "stenoecious" species [Badrian et al., 1982; Boesch, 2002; Kano, 1984a, 1992]. However, in the southern Lukuru area some populations use hilly dry forest/savannah mosaic habitat as well [Myers-Thompson, 1997, 2002] and in the southern Lac Tumba area, in the Western range of the species, bonobo habitat consists of mostly terra firma island within swampy forest and savannah mosaic habitat [Inogwabini et al., 2007; Inogwabini & Matulinga, 2009; Pennec et al., 2016]. Bonobos use diverse habitats depending on their needs, and seem to prefer primary forest and aged secondary forest for feeding and sleeping; young secondary forest and swamp grassland are used for feeding, especially during periods when fruit is less abundant in primary forest; swamp forests can be used for sleeping, or foraging for local resources such as mushrooms [Fruth, 1995; Hashimoto et al., 1998; Inogwabini et al., 2012; Kano, 1983; Kano & Mulavwa, 1984; Mohnneke & Fruth, 2008; Mulavwa et al., 2010; Reinartz et al., 2008; Serckx et al., 2016; Terada et al., 2015; Trolliet et al., 2016]. Human presence has a negative impact on the occurrence of bonobos [Hickey et al., 2013; Reinartz et al., 2008], although in Wamba, where bonobos are not hunted, they have been seen to regularly use agricultural areas for foraging [Terada et al., 2015].

Altitudes in bonobo habitats vary between 300 – 600 m [Hohmann et al., 2010; Kano, 1984a, 1992; Kortlandt, 1995; Myers Thompson, 2002]. The average air **temperature** in this region ranges between 19,5° to 32,6° C [Bermejo et al., 1994; Fruth, 1995; Furuichi et al., 2008; Hohmann et al., 2010; Kano, 1992; Myers Thompson, 1997, 2002; Pennec et al., 2016]. The annual **rainfall** in areas where bonobos occur lies between 1500 and 2922 mm [Hohmann et al., 2010; Inogwabini et al., 2008; Kano 1992; Mulavwa et al., 2008; Myers Thompson, 1997, 2002; Pennec et al., 2016; Sabater-Pi & Veà, 1994]. Mean relative humidity rarely falls below 65% and can reach 87% - 90% [Horn, 1980; Inogwabini et al. 2008; Myers-Thompson, 1997].

Most of bonobo habitat shows only mild **seasonality** [Beaune et al., 2012; Kano, 1992; Kuroda, 1979; Malenky, 1990; Malenky & Wrangham, 1994; Mulavwa et al., 2008; White, 1998], and it has been proposed that this results in more constant availability of fruit, leading to reduced feeding competition in bonobos [Doran et al., 2002; Malenky, 1990; Wrangham, 1986]. In Lomako, fruit was found to be more scarce in the dry season, and bonobos were observed to consume more non-preferred food, but consumption of Terrestrial Herbaceous Vegetation (THV) (see section 1.6.1.) was constant [White, 1998]. In the Southern study site of Lukuru, seasonality is more pronounced and a rainy season from September through April followed by a dry season from May through August has been reported [Myers-Thompson, 2001]. Also,the Western sites have stronger seasonality with a long dry season from from May to August and a long rainy season in November and December, with annual variations [Pennec et al., 2016], and fruit availability follows a seasonal pattern [Serckx et al., 2014].

The following reports mention **other species** that live in bonobo habitat [Badrian & Badrian, 1977; Beaune et al., 2012; Dupain et al., 2000; Hart et al., 2009; Hohmann & Fruth, 2003c; Horn, 1980; Inogwabini et al., 2013; Kano, 1983, 1992; Malenky, 1990; Surbeck et al., 2017; Thompson-Handler, 1990; Trolliet et al., 2016; Uehara, 1988; Van Krunkelsven et al., 2000]. The species range overlaps with several smaller primates (*Allenopithecus nigroviridis*; *Cercopithecus wolfi*; *C. ascanius*; *C. neglectus*; *C. mona*; *C. dryas*; C. *lomamiensis*; *Lophocebus aterrimus*; C*olobus angolensis*; *Piliocolobus tholloni*; *Perodictius potto*; *Galago demidovi*), ungulates (*Cephalophus callipygus; C. dorsalis*; *C. monticola*; *C. nigrifrons*; *C. sylvicultor*;*Okapia johnstoni*; *Potamochoerus porcus*; *Hyemoschus aquaticus*; *Tragelaphus euryceros*; *T. spekei; Syncerus caffer nanus*), elephants (*Loxodonta cyclotis*), hippopotamus (*Hippopotamus amphibius*) and tree hyrax (*Dendrohyrax arboreus*); carnivores (*Panthera leo; P. pardus*; *Profelis aurata*; *Viverra civetta*; *Nandinia binotata*; *Genetta tigrina*); pangolins (*Manis gigantea*; *M. tricuspis*), bats (a.o. *Epomophorus grandis*; *Hypsignathus monstrosus*; *Lissonycteris angolensis*), aardvarks (*Orycteropus afer*) and rodents (a.o. *Funisciurus* and *Anomalurus* sp.; *Atherurus africanus*). Among the most notable birds that share the bonobo habitat are Congo peafowl (*Afropavo congensis*); Touracos (*Musophaga rossae*; *Tauraco persa*; *T. schuetti*; *Corythaeola cristata*); hornbills (*Ceratogymna atrata*; *Bycanistes albotibialis; B. fistulator; Tockus camurus*; *T. fasciatus*; *T. harlaubi*; *Tropicranus albocristatus)*; pigeons (a.o. *Treron australis*); and raptors (*Stephanoaetus coronatus*).

Bonobos play an important **role in the local ecosystem** as plant seed dispersers [Beaune et al., 2013a,b; Idani, 1986; Tsuji et al., 2010; Trolliet et al., 2016]. Bonobos also feature in the oral traditions of local people – many stories and legends tell of the close relationship between bonobos and humans, and in many tribes hunting or eating bonobos was considered taboo, although body parts of bonobos were used in traditional medicine [Callewaert, 1930; Inogwabini et al., 2013; Lingomo & Kamura, 2009; Myers Thompson et al., 2008; Narat et al., 2015b]. However, with people from other ethnic groups migrating in (including employees of logging companies, and armed soldiers during the 1990s war), the traditions have often been lost, especially among younger generations [Dupain & Van Elsacker, 2001; Dupain et al., 2000; Fruth et al., 2008; Idani et al., 2008; Kabongo, 1987; Lingomo & Kimura, 2009; Myers-Thompson, 2001b; Tashiro, 1995].

1.5.3. Field research

Bonobos have been studied at about a dozen field sites, which are indicated on Figure 5. The names with which these sites are referred to, sometimes vary. While research on other great ape species really took off in the 1960s, field research on bonobos only started in 1973, when two independent research camps were established at Wamba and Lomako, which are only 300 km apart, and are similar in habitat and climate [Kano, 1992; White, 1996]. In **Wamba Research station** (N0°11′, E22°37′), research was started by Takayoshi Kano, who was soon followed by multiple researchers [Kano, 1984a; 1992]. From 1991 on, research in Wamba was hindered by political unrest in DRC but researchers were able to come back regularly [Tashiro et al 2007]. In Lomako, three research projects have been conducted. After preliminary studies by Noel and Alison Badrian in 1973 [Badrian & Badrian, 1977, 1978, 1980], the "Lomako Forest Pygmy Chimpanzee Project" was initiated in 1980 by Randall Sussman, State University of New York at Stony Brook [Sussman et al., 1981], also referred to as the **Ndele** or Ndeli site (N 0.7994°, E21.143°) [Waller & White, 2016]; "Project Pan" was established in Isamondje (N0°51′, E21°5′) by Gottfried Hohmann and Barbara Fruth of Max Planck Institute Leipzig [Fruth, 1995; Hohmann & Fruth, 1993]. The "Bonobo in situ project" was initiated at Iyema by Jef Dupain and Ellen Van Krunkelsven of the Royal Zoological Society of Antwerp in 1995, at about 20 km from Isamondje [Dupain & Van Elsacker, 1999; 2001; Dupain et al., 1996, 2002; Van Krunkelsven et al., 1999]. For the first 25 years, most data on bonobo behaviour stemmed from these two locations. Smaller projects were also set up, at **Botuali** on the west side of Lac Tumba [Hansinger et al., 1974; Horn, 1980; Nishida, 1972], and at **Yalosidi** [Kano, 1983; Uehara, 1988], but these were less successful in habituating the bonobos. Between 1988 and 1990 bonobos were also studied in **Lilungu**, in the Ikela region by Jordi Sabater Pi and Joaquim Vea of the University of Barcelona, Spain [Bermejo et al., 1994; Sabater-Pi & Vea, 1990, 1994]. In 1992, a study at the **Lukuru** research site (S03°45′, E21°21′) was started by Jo Thompson, in the most southern limit of the species' geographic distribution [Myers-Thompson, 1997, 2001; Thompson & Tshina-tshina, 2003]. In 1997, the Milwaukee Zoological Society, working together with the Institut Congolais pour la Conservation de la Nature (ICCN) and the Royal

Zoological Society of Antwerp (RZSA), conducted a survey in the Northern sector of the Salonga National Park, and confirmed the occurrence of bonobos [Reinartz & Inogwabini, 2001; Van Krunkelsven et al., 2000; Van Krunkelsven, 2001].

During the Second Congo War (1998-2003), a main frontline cut through the bonobo range and researchers were forced to abandon the sites, and could only do short surveys [Draulans & Van Krunkelsven, 2002; Dupain & Van Elsacker, 2001; Furuichi, 2003; Waller & White, 2016]. After the civil war, researchers reopened the existing sites at Wamba, Lukuru, Lilungu and Lomako [Furuichi & Mwanza, 2003; Mulavwa & Balemba, 2008; Thompson & Tshina-tshina, 2003; Thompson et al., 2003a; White et al., 2008], and new sites were being opened. The existence of bonobos in Botuali forest on the West side of Lac Tumba was confirmed [Mwanza et al., 2003] and subsequent surveys showed more bonobo communities living in areas where bonobos were not known to occur, extending the known geographic range of the species [Inogwabini et al., 2007, 2008], which lead to the establishment of the WWF research site in **Malebo research station** (S2°33′, E16°29′)**,** where bonobos have been studied in Nkala Forest and Mpelu Forest [Serckx, 2014; Serckx et al., 2014a,b; Serckx et al., 2015]. Further research projects have been established in different forest patches, including **Manzano Forest** (Embirima, Bolobo district), 15 km away from Malebo [Beaune et al., 2017; Narat et al., 2015a, b,c]. In the Northern Part of the Salonga National park the **Etate research station** was founded by the Milwaukee Zoological Society [Reinartz, 2003]. In February 2002, the **LuiKotale research site** (S2°47′, E20°21′) was established at the fringe of the southern sector of the Salonga National Park [Hohmann and Fruth 2003c]. Around 2006, the **Nsondo research camp** (N0°12′, E22° 51′) was founded in the Kokolopori reserve, about 30 km away from Wamba [Georgiev et al., 2011]. A new permanent research camp in Kokolopori, named **Lonoa**, was set up in 2016 by Martin Surbeck of University of Harvard [Surbeck, 2018]. In 2010, the **Bembongo research site** was established near Iyondji and habituation of bonobos began, in preparation for potential tourism or scientific research [Sakamaki et al., 2012, 2016]. In addition to these research camps or sites, surveys of bonobo densities have been conducted at multiple locations [e.g. Grossman et al., 2008; Hart et al., 2008; Inogwabini & Ilambu, 2005; Mohnneke & Fruth, 2008].

The sites where bonobos are studied vary in time that they were used, in methods and scopes [Decoster & Gilleau, 1987; White, 1992c]. For example, in Wamba bonobos were provisioned with sugarcane and pineapple in the early years, which sped up the habituation process, and yielded vast amounts of social interaction data [Mori, 1984; Kano, 1982a, 1992]. In Lomako and the other sites no artificial provisioning was used, and there was a greater focus on ecological data before data on social interactions became available as habituation progressed [Fruth, 1995; Thompson-Handler, 1990; Van Krunkelsven et al., 1999; White 1992c, 1996a]. Habituated bonobo communities now exist at Wamba, LuiKotale, Kokolopori, Lomako and Malebo. As new data from different populations become available, bonobos seem to be more ecologically flexible than previously thought [Myers-Thompson, 1997; 2002; Serckx, 2014].

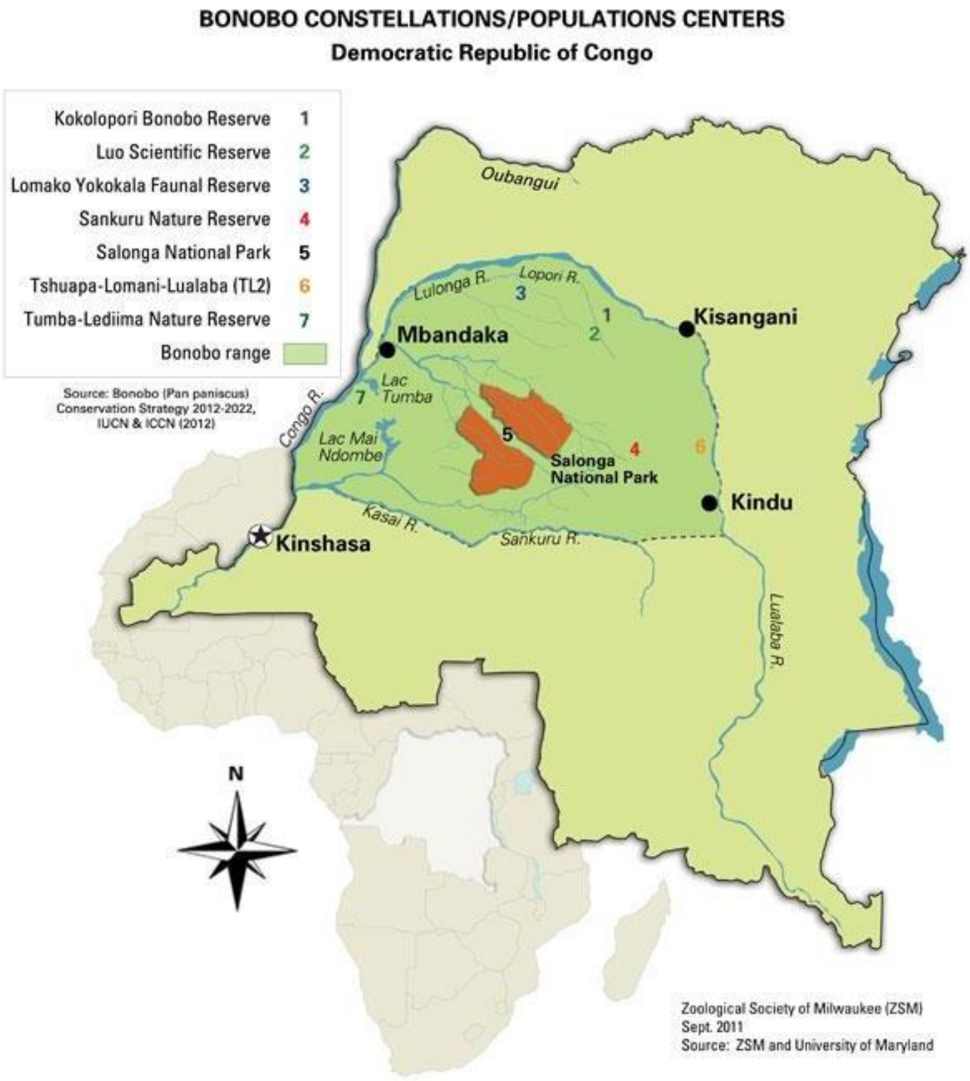

Figure 5: Distribution of map of bonobos within the Democratic Republic of Congo, showing the major Nature Reserves. (IUCN 2012).

1.5.4. Conservation status

Bonobos are listed as **Endangered** (EN A4cd) on the IUCN Red List of Threatened Species **since 1996** [Fruth et al., 2008; Stiles et al., 2012]. **The species is officially protected by** Congolese and international laws, and is listed in Appendix 1 of CITES since 1975 [CITES 2015] and on Class A of the African Convention on the Conservation of Nature and Natural Resources [African Union 1968]. Two domestic laws in DRC protect bonobos and other wildlife [André et al., 2008].

Before, and even after the first field studies on bonobos started, there was debate on **how rare bonobos actually were** [Kortlandt, 1977; MacKinnon, 1976; Reynolds, 1967]. But very soon reports started to appear, identifying hunting, habitat destruction and collecting, slash and burn agriculture, commercial logging, oil exploitation as threats to bonobo survival [Badrian & Badrian, 1977; Horn, 1980; Kabongo, 1984, 1987; Kano, 1984a; Malenky et al., 1989; Mubalamata, 1984; Susman et al., 1981]. Unfortunately, these threats still exist to this day.

The number of bonobos living in the wild is difficult to assess, because they live in remote areas, occur in naturally low population densities and are difficult to locate in their dense rainforest habitat of DRC [Hickey et al., 2012]. Within their total range bonobo occurrence seems patchy, and local population densities vary [Kano, 1984a, 1992; Kortlandt, 1995; Mohnneke & Fruth, 2008; Thompson-Handler et al., 1995]. Based on the estimates of the area in which bonobos potentially occur, and on local population estimates based on nest counts etc., a **minimum population size of 15.000 – 20.000 bonobos** is believed to exist [IUCN/ICCN, 2012]. There are many other population estimates [Coxe et al., 1999; Dupain & Van Elsacker, 2001; Kano, 1984a, 1992; Kortlandt, 1995; Myers-Thompson, 1997; Thompson-Handler et al., 1995], but these should be interpreted with extreme caution [Fruth et al., 2008], because of the wide confidence intervals – the estimate for Salonga alone was 7.100–20.400 [Grossmann et al. 2008].

1.5.5. Threats

Bonobos have disappeared in regions where they were known to have occurred previously [Thompson-Handler et al., 1995; Coxe et al., 1999]. The bonobo population is declining because of **three major direct threats**: poaching, habitat loss and disease transmission. The ranking exercise by IUCN/ICCN [2012] clearly shows that poaching is by far the most important direct threat to bonobos. Reducing bonobo mortality caused by poaching should therefore be the highest priority for this conservation strategy. Although there is agreement that habitat loss and disease are likely to become more important threats in the future, the ranking of the various threats was different in each stronghold, which means that the appropriate strategies will need to take into consideration the local context.

1. *Poaching, the most serious threat to bonobos across their range.*

Traditionally, bonobos have been hunted for **food and religious purpose**[1] in many areas [Kabongo, 1987; Kano, 1992; Nishida, 1972], although many tribes also have local taboos against hunting and/or eating bonobos [Callewaert, 1930; Inogwabini et al., 2013; Lingomo & Kamura, 2009; Myers Thompson, 2001; Myers Thompson et al., 2008; Narat et al 2015b]. Migration of Bantu farmers into the area 700 years ago, may have started hunting on bonobos [Kano, 1992]. With recent migrations, the increased availability of guns and facilitation of transport, the **commercial hunting** of bonobos increased substantially [e.g. Tashiro et al., 2007]. Also, bonobos can become victims of snares intended for other game, sustain serious and potentially lethal wounds [Kano, 1984b; Tokuyama et al., 2012; Tokuyama, 2019]. Hunting persists throughout much of the bonobo range, including in areas that are protected [Dupain & Van Elsacker, 2001; Hart et al., 2008; Inogwabini & Omari, 2005; Reinartz, 2003; Reinartz et al., 2008; Tashiro et al., 2007; Van Krunkelsven et al., 2000]. Hunting activity increases near openings and results in lower nest occurrence [Reinartz et al., 2008]. Although not a primary species for subsistence consumption, bonobos are eaten and can be sold for considerable profit in urban markets or as part of the pet trade [Dupain & Van Elsacker 2001; Dupain et al. 2000, 2001; Malenky et al., 1989; Mubalamata, 1984; Narat et al., 2015b, Reinartz & Inogwabini, 2001; Van Vliet et al., 2012]. A recent report pointed out the growing international illegal trade in apes, including bonobos; although bonobos have yet not been involved in large scale trafficking, they are almost certainly illegally trafficked [Stiles et al., 2013].

2. *Habitat loss, both in terms of habitat destruction and fragmentation*

Most of the forests that still have bonobo populations are subdivided into logging concessions [Dupain & Van Elsacker, 2001; Thompson et al., 2003b]. The rate of suitable habitat loss for bonobos is particularly high and estimated at 29% between the 1990's and 2000's [Junker et al. 2012]. **Habitat fragmentation** can be an important predictor of bonobo occurrence even while their habitat remains relatively intact [Hickey et al., 2013; Kano, 1984a;]. One of the consequences of the political turmoil in DRC at the end of the 1990s was that infrastructure such as transportation systems were destroyed, damaging local village economies, so that for example the villagers at Wamba increased slash and burn agricultural activity [Tashiro et al., 2007]. There is concern that the **palm oil industry** will lead to biodiversity losses in West and Central Africa, similar to those in Southeast Asia with 99.2% of current bonobo habitat is suitable oil palm area [Wich et al., 2014]. Apart from direct impact of logging, the **indirect consequences of logging** are considerable because it facilitates access into the forest and human and bushmeat transport [Amman, 1998; Dupain & Van Elsacker, 2001; IUCN/ICCN, 2012].

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[1] Known as 'gri-gri', local fetish beliefs suggest that superhuman powers can be derived from bonobo bones [Kabongo, 1987].

3. Disease transmission, a potential future concern

So far, the devastating effects of large-scale epidemics of Ebola, respiratory disease or poliomyelitis that have affected gorilla and chimpanzee populations have not been recorded in bonobo populations. A survey in Bolobo found no zoonotic transmission of gastro intestinal parasites between humans and bonobos [Narat et al., 2015a]. Given the bonobos' limited range, increasing encounters between apes and humans because of habitat fragmentation, and the fact that many diseases can be transmitted between apes and humans [Whittier et al., 2001] the potential risk of disease transmission is, however, great and small scale epidemics such as flu have been reported in bonobos, which could possibly have passed from humans to the bonobo population [Grützmacher et al., 2018; Sakamaki et al., 2009]. Yoshida et al. [2016] found that Lymphocryptovirus (LCV), one of the major gena in the herpesvirus family which usually exhibits latent infection, where stress and/or immune suppression can cause both viral expression and subsequent onset of a variety of diseases, was highly disseminated among wild bonobos while the prevalence is remarkably diverse in their population-dependent manner.

1.5.6. Conservation actions

In the IUCN/ICCN [2012] document the following vision and goal were formulated:

- Vision: By 2050, bonobo populations across their range are viable and increasing relative to 2008–2015 surveys, face minimal threats, and their long-term survival is ensured.
- Goal: By 2022, priority areas for bonobo conservation are effectively managed and protected, the current main threats are reduced, there is no further habitat loss, and known bonobo populations are stable relative to baseline surveys.

Five main intervention strategies have been suggested to reduce bonobo major threats, that should be applied in the next ten years:

1) **Strengthening institutional capacity**;

Objectives include creating new protected areas, eliminating poaching in protected areas, monitoring and controlling the bushmeat trade, eliminating the circulation of weapons and ammunition in protected areas, and working with logging companies to implement specific wildlife protection activities in their concessions.

2) Consultation and collaboration with local actors living close to the bonobos;

Objectives include integrating bonobo conservation issues into national development plans, developing land-use and macro-zoning plans, and implementing sustainable subsistence activities at key sites.

3) **Public awareness and lobbying to decrease ignorance and non-respect of the law**;

Objectives include developing a nationwide communications strategy, undertaking awareness-building activities at key sites, sensitising urban communities and private sector operators, and lobbying government administration at national and provincial levels.

4) **Research and conservation monitoring activities**;
The objective is to develop a clear monitoring framework. Implicit throughout this plan is that surveys and monitoring of both bonobos and the threats to bonobos (including disease/health monitoring) are necessary as a means to track changes in population size and distribution, to assess the level and location of threats, and ultimately to assess progress towards the Goal and Vision of the Strategy. There will also be a disease prevention plan, focussed on the prevention of human-bonobo disease spread, together with an early detection mechanism and an emergency intervention plan to address potentially catastrophic disease outbreaks.

5) **Sustainable funding such as payment for ecosystem services** (IUCN and ICCN 2012): The objective is to evaluate funding needs for bonobo conservation and create sustainable sources of funding.

Nature reserves, national parks and protected areas
In the context of the Congo Basin Forest Partnership (CBFP) 2005, an international project for the protection of forests, DRC possesses three landscapes important for bonobo conservation: 1) Lac Tele-Lac Tumba Landscape (Congo and DRC); 2) Maringa-Lopori-Wamba Landscape (DRC); and 3) Salonga-Lukenie-Sankuru Landscape (DRC) [Fruth et al., 2008]. In addition to those three areas, a fourth block between the Lomami, Lualaba and Tshuapa rivers (TL2) recently was found to harbour important populations of bonobos and other wildlife [Hart et al., 2009] and therefore is also included. These four areas are also known as the **four bonobo strongholds** [IUCN/ICCN, 2012].

Within these landscapes, the following protected areas have been set apart, or plans exist to protect them – these areas differ in degree of protection and many include involvement of several NGOs etc. [IUCN/ICCN, 2012].

The Northern block corresponds approximately to the Maringa-Lopori-Wamba landscape [Dupain et al., 2009; Hickey et al., 2012] and contains four areas offering various levels of protection. In 1988, the Research Center of Natural Science, or CRSN, and the local communities signed agreements that created a reserve named **the Reserve Scientifique de Luo**, which covers 481 km². The reserve was officially recognized by the Ministry of the Environment in March 1990 [Furuichi et al., 2012; Tashiro et al., 2007]. The park is divided by the Luo river in two parts: the Northern (147 km²) part encompasses Wamba forest and included the Wamba research station, and the southern sectors encompasses Ilongo Forest (334 km²) [Hashimoto & Furuichi, 2001; Idani et al., 2008]. In 2006 the **Lomako-Yokokala Faunal Reserve** was gazetted [Henson et al., 2009] and comprises 3,625 km² of continuous rain forest north of the Lomako River and south of the Yokokala river and is demarcated further by small tributaries to both the east and west of the forest block [Henson et al., 2009; Omasombo et al., 2005]. The 4.000 km² **Kokolopori Bonobo Reserve** is a community-based natural resource management (CBNRM) area [IUCN/ICCN, 2012]. The **Iyondji Community Bonobo Reserve** was established by the DRC Ministry of Environment in 2012 and encompasses approximately 1.100 km² of tropical moist forest. The reserve is adjacent to the southeast border of the Luo Scientific Reserve and to the Kokolopori Bonobo Reserve in the east [Sakamaki et al., 2012; Dupain et al., 2013].

In the Western Stronghold, which corresponds largely to the Lac Tele-Lac Tumba Landscape, the **Tumba-Lediima Natural Reserve** was created in 2006 with an area of 7.500 km² [Twagirashyaka & Inogwabini, 2008]. The Centre de Recherche en Ecologie et Foresterie manages the 2.6 km² **Mabali Scientific Reserve** [IUCN/ICCN, 2012]. At Manzano, a community protection program was initiated in 2001 [Narat et al., 2015].

In the Southern Stronghold/the Salonga-Lukenie-Sankuru landscape, the **Salonga National Park** (SNP) was created in 1970. It comprises 36.000 km² and is Africa's largest area of rain forest protection [Mohnneke & Fruth, 2008]. Since 1984, it has been on the list of world heritage sites representing the largest area for the protection of bonobos and other endemic species [Mohnneke & Fruth, 2008]. SNP is divided in a Northern and Southern part of about equal size, separated by an unprotected zone of about 45 km² [Myers-Thompson, 1997; Van Krunkelsven, 2001]. For a long time it was believed that no bonobos occurred in the Salonga [Badrian & Badrian, 1977; Kano, 1979], but in 1987 presence of bonobos in the Northern part was observed, and bonobos were not rare in the area [d'Huart, 1988; Meder et al., 1988]. Later surveys reconfirmed the presence of bonobo populations in both sectors of the Park [Grossmann et al., 2008; Inogwabini & Ilambu, 2005; Reinartz & Bila Isia, 2001; Reinartz et al., 2006, 2008; Van Krunkelsven 2001; Van Krunkelsven et al., 2000]. In 1997, the **Bososandja Faunal Refuge** (BFR) was established, and protected by local civil authority. In 2003, efforts in collaboration with ICCN began to elevate its status to a nationally recognized Community Forest protected area [Thompson & Tshina-tshina, 2003].

The significance of the Eastern block for biodiversity has only recently been realized, thanks to surveys in this area. Therefore, it was not included in the COMIFAC/CBFP landscapes [IUCN/ICCN, 2012]. In 2007, the bonobo conservation initiative announced the creation of a 23.161 km² **Sankuru Nature Reserve** [Hurley, 2007; Stokstad, 2007]. However, subsequent surveys covering just over half of the Sankuru Natural Reserve, west of the Tshuapa River, found that bonobos were present in just 17% of the reserve, and were absent in the south-central and southwest area and signs of intense hunting pressure were widespread [Hart et al. 2009; Liengola et al. 2009; IUCN/ICCN, 2012]. Over half of the reserve consists of secondary or degraded forests, fragmented by areas of human occupation. So, it was recommended that further funding should be targeted at areas with much greater bonobo conservation potential [Liengola et al., 2009]. In the **Tshuapa-Lomami-Lualaba** (TL2) region, bordering the Sankuru

Reserve where surveys have shown presence of bonobos [Hart et al., 2009; IUCN/ICCN, 2012]. A 9.000 km² National Park, surrounded by a buffer zone of approximately 16,380 km² with Wildlife Reserve status was created in 2016.

Hickey et al. [2013] estimated that the majority of Iyondji Community Bonobo Reserve, Lomako–Yokokala Faunal Reserve, SNP, and Kokolopori Bonobo Reserve were suitable bonobo habitat (87, 86, 82 and 64%, respectively) whereas less than 50% each of Luo Scientific Reserve, Sankuru Reserve, and Tumba–Lediima Reserve were predicted as suitable.

Sanctuary and reintroductions

From the beginnings of bonobo field research, researchers were confronted with orphaned infant bonobos [Badrian & Badrian, 1977, 1984]. These bonobos, as well as the occasional former pet bonobo were released into the forest, without much knowledge of what happened to them in the long term [Badrian & Badrian, 1984a; Ruwet, 1987]. Some early solutions were proposed to house the so-called "contraband bonobos" at Parc Président Mobutu at N'Sele, near Kinshasa [White & Susman, 1986; Reinartz, 1991] but these plans were never effectuated. Starting in 1987, several orphaned bonobos were cared for by Delfi Messinger at the Institut National de Recherche Bio-Médicale (INRB) in Kinshasa [Messinger, 2007; Messinger & Bi-Shamamba, 1997]. In 1997, the first birth of a bonobo in captivity in DRC was recorded at INRB. Eventually six of those bonobos were transferred from INRB to the EEP population in 1997 on breeding loan from DRC's Ministry of the Environment [Messinger, 2007; Messinger & Bi-Shamamba, 1997], and the remaining four bonobos were sent from INRB to Lola Ya Bonobo in 2004 (see below). In Congo-Brazzaville several infant bonobos also appeared on the market. Between 1989 and 2004, twenty orphaned bonobos were housed under the umbrella of Project Protection du Gorille, a gorilla orphanage in Brazzaville Zoo. During political unrest in Brazzaville these bonobos and gorillas were transferred to Tschimpounga, a reserve outside Pointe Noire, and later to Lesio-Louna Reserve, but in 2004 the eight surviving bonobos were also brought to Lola Ya Bonobo [King et al., 2005].

In 1993, a sanctuary for confiscated bonobos, named **Lola Ya Bonobo**, was founded by an NGO Amis des Bonobos du Congo (ABC), led by Claudine André who started caring for orphaned bonobos [André, 2006]. Starting in 1997, the first official confiscations were conducted by the Inspectors of the Ministry of Environment, working together with the Lola Ya Bonobo sanctuary. Currently the sanctuary exists near Kinshasa [André et al., 2008; Hirata & Tashiro, 2007], and has great value for conservation education [André et al., 2008]. The first birth here was recorded in 2005. On average five confiscated bonobos have arrived per year [Faust et al., 2017]. The population also grows through breeding, but contraception is also used [Faustet al., 2017]. A rehabilitation project named **Ekolo Ya Bonobo**, has been set up in a 20,000 hectare forest area near Basankusu, where since 2009 bonobos from the sanctuary have been released [Anonymous, 2009]. Six individuals were released in 2009, and seven in 2011 [Faust et al., 2017].

Zoo breeding programmes
An international bonobo studbook has been maintained at Antwerp Zoo since 1974 [Gijzen, 1974]. Because of the bonobo's endangered status and the existence of a well-documented breeding nucleus in zoos, the species was one of the first to receive an EEP status when the programmes were started in 1985 under the umbrella of EAZA. Antwerp Zoo has managed the coordination of the European breeding program since then. In 1988 the Wildlife Conservation and Management Committee of the American Zoo and Aquarium Association (AZA) approved the formation of a SSP for the species, managed by Milwaukee Zoo. Following a joint SSP/EEP meeting in Antwerp in 1989, it was decided to manage the zoo populations globally in order to maximize the genetic potential of the larger population. Intercontinental transfers have happened regularly (in 1991, 1993, 1999, 2001, 2012, 2018 – e.g. Ellis 2003), and regular SSP/EEP meetings have since been held in 1991 (San Diego – Barongi, 1991), 1998 (Columbus), 2007 (Chester), 2012 (San Diego), and 2018 (Karlsruhe). Several Master plans for the zoo populations have been edited on SSP, EEP and Global level [Reinartz, 1991; Reinartz et al., 2002]. The bonobos of Lola Ya Bonobo sanctuary (see above) are registered in the studbook, but they are not part of the managed population. After the arrival of six bonobos from the INRB to Apenheul in 1997, there have been no deliberate imports from DRC into the zoo populations. The current global zoo population descends from 36 founder animals, who based on genetic analyses are probably not closely related and originate from different areas within the bonobo natural range [Eriksson, 2004; Reinartz, 1997; Reinartz et al., 2000].

What Zoos can do
All EAZA zoos that maintain bonobos in their collections should ensure that they are priority species for conservation efforts, over and beyond holding and breeding them as part of the EEP. Zoos can assist field conservation efforts for bonobos in a number of ways, including:

- providing financial or logistic support to conservation in situ: A list of In situ conservation projects can be found under Appendix 2.

- Raising awareness of the plight of wild bonobos, including that bonobos are **endangered** and the reasons why.

- Describing what **bush meat** is and the scale of the problem that this presents for the long-term survival chances of wild bonobos.

- Describing what **palm oil** is and the scale of the problems that the use of non-sustainably produced palm oil is creating for wild bonobos. Zoos should explain to their visitors how they can contribute - which types of every day products contain palm oil, and how people can ensure that they only choose products that contain sustainably produced palm oil.

- Ensuring that zoos are '**practicing what they preach**' by ensuring where possible that products used by the zoo and products purchased for sale by the zoo, such as foods and confectionary sold in catering and retail outlets, only contain sustainably sourced palm oil. A full palm oil audit of products purchased by the zoo is recommended.

- **Raising awareness** and campaigning more widely for use of sustainably sourced palm oil, through local cafes, restaurants and businesses and schools.

- **Funding field conservation** efforts through the numerous NGO’s working in the field. A number of NGO’s working on bonobo field conservation can be found in “Appendix 2: Bonobo Conservation Organisations”.

1.6. Diet and feeding behaviour

1.6.1. Gastro-intestinal system

While no images of the bonobo gastrointestinal (GI) tract are available, it is said to closely resemble that of the chimpanzee (see Figure 6), which is also considered omnivorous with a diet high in plant material. The bonobo GI tract features a simple stomach, relatively short small intestine, and modified hindgut to process the less-digestible plant matter in their diet. This hindgut consists of a colon haustrated by three taeniae over its length, which continue along the cecum and end in a vermiform appendix (Primate NRC, 2003; Stevens and Hume, 1995).

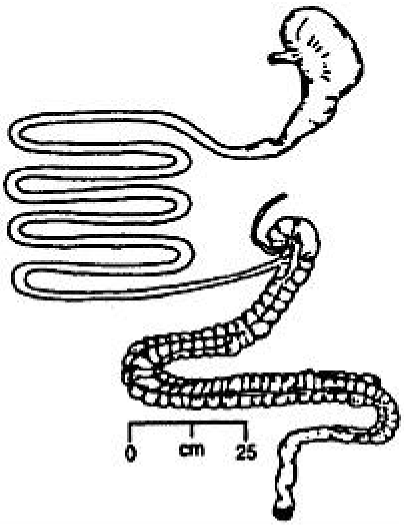

Figure 6: Gastrointestinal tract of the chimpanzee (Stevens & Hume, 1995)

1.6.2. Diet in the natural habitat

The diet of wild bonobos has been extrapolated from observations of feeding individuals, or from faecal analyses, [Idani et al., 1994; Kano, 1992; Sabater Pi & Veà, 1994; Serckx et al., 2015]. Including DNA analyses of faecal material [Hamad et al., 2014; Hofreiter et al., 2010], and more recently also from isotope analyses [Loudon et al., 2019; Oelze et al., 2011, 2016]. In general, wild bonobos have a **varied diet**, but are mainly frugivorous, with fruits being the most important food item in proportion of total diet and in frequency with which items are consumed, followed in importance by pith, leaves, leaf petioles, seeds, and flowers, and animal matter [Badrian & Malenky, 1984; Kano, 1992; Kano & Mulavwa, 1984; Sabater-Pi & Veà, 1994]. The total amount of food types recorded for free-ranging bonobos rises above 110 for the longest studied populations [Badrian & Malenky, 1984; Idani et al., 1994; Kano, 1992; Kano & Mulavwa, 1984]. Wild bonobos may eat up to ten different food types per day, and 40 different food types per month [Kano & Mulavwa, 1984].

Conklin Britain et al. (2001) summarized data from six studies at two field sites (Lomako and Wamba – see Table 1,) and reported that, compared to chimpanzees, bonobos show a **higher proportion of terrestrial herbaceous vegetation** (THV) in their diet, as had been suggested by

Malenky & Wrangham [1990] and Wrangham [1986]. Bonobos at Lomako consumed more THV than chimpanzees in Kibale, and THV is more abundant in bonobo habitat [Malenky & Wrangham, 1994]. However, when comparing data from Wamba and Lomako with multiple populations of chimpanzees, Doran et al. [2002] did not find that bonobos spend more time feeding on THV and leaves than chimpanzees, because chimpanzee populations in their study varied more in THV consumption than in the previous comparison. Harrison & Marshall [2011] also did not find that THV was more important as fallback food for bonobos compared to chimpanzees. More recent data from other bonobo sites also show great variability in the importance of THV for the bonobos' diet (see below). Thus, differences between sites have been reported in feeding patterns; in number of species eaten; and in food preferences. These can be partly explained by different sampling methods and efforts, and/or differences in availability and/or cultural differences between sites [Badrian & Malenky, 1984; Doran et al., 2002; Kano, 1992; Hohmann et al., 2010; Idani et al., 1994; Inogwabini & Matulinga, 2009; Malenky et al., 1994; Myers-Thompson, 2002].

Table 1: Proportion and range of food item in diet of wild bonobos [from Conklin-Britain et al., 2001]. THV =terrestrial herbaceous vegetation (which can also include small woody shrubs).

	Fruit	THV	Leaves	Flowers	Prey	Bark and miscellaneous
%	55	25	14	2	2	2
Range	0-100	0-100	0-28	0-7	0-3	0-11

In terms of **nutritional values**, not many data are available. Malenky & Wrangham [1994] report that in Lomako *Haumania liebrechtsiana* contained 30.6% protein, 1.7% water soluble carbohydrates (WSC) and 1.3% lipids, and that 19 fruit species averaged around 4.4% protein, 34.3% WSC; and 3.5% lipids. Hemicellulose and cellulose were not measured in this study. Hohmann et al. [2006, 2010] report the nutritional values of the bonobo diet at LuiKotale, and compare this with plants that were sampled at the same site, but that were not eaten by the bonobos (Table 2). Like chimpanzees, bonobos seem to select fruits that have higher levels of water, sugar, crude fat and lower levels of fibre components compared to non-food, which matches predictions of optimal diet theory [Sommer et al., 2011]. They avoid eating that contain high concentrations of alkaloids and cyanogenic glycosides [Bondjengo et al., 2017]. Bonobos do consume tannin rich fruit, suggesting that they are able to cope with the deleterious effects of dietary tannins [Beaune et al., 2017]. Some studies report that compared to chimpanzees, bonobos have higher intakes of protein and non-structural carbohydrates including starch [Hohmann et al., 2006; Serckx, 2014]. However, when information from more chimpanzee populations was included, this difference was not found [Hohmann et al., 2010]. A recent study found that bonobos in LuiKotale select aquatic plants who are very high in iodine [Hohmann et al., 2019a].

Table 2: Mean value and standard deviation of phytochemical components in plants collected in the habitats of bonobos, which belonged to the bonobos diet (left column), or that were not consumed (right column) [Hohmann et al., 2006].

	Food plants (N = 47 species)	Non-food plants (N = 39 species)
Energy	17.5 ± 2.5	18.1± 5.4
Dry mass	23.9 ± 12.8	25.9 ± 15.2
Crude Protein	8.3 ± 4.7	11.4 ± 4.7
Sugar	9.8 ± 6.9	7.0 ± 6.9
Starch	3.7 ±9.1	3.9 ± 9.0
Crude Fat	6.6 ± 8.9	3.3 ± 4.6
Neutral detergent fibre	26.8 ± 16.3	32.1 ± 15.3
Acid detergent fibre	16.6 ± 11.1	20.8 ±12.0
Acid detergent lignin	5.2 ± 5.1	6.9 ± 5.6
Cellulose	11.5 ± 7.2	13.9 ± 7.0
Hemicellulose	10.1 ± 8.1	11.3 ± 6.4
Total phenol	4.9 ± 5.1	4.7 ± 5.7
Total tannin	2.8 ± 3.0	3.0 ±4.0
Condensed tannin	4.7 ± 10.1	3.6 ± 5.4
Crude protein / acid detergent fibre	0.81 ± 0.7	0.87 ± 0.79

Bonobos have also been seen feeding on aquatic herbs [Badrian & Malenky, 1984; Bermejo et al., 1994; Hohmann et al., 2019a; Horn, 1980; Kano, 1983; Myers-Thompson, 2002; Uehara, 1988], algae [Myers-Thompson, 2002] and on the tissue of a subterranean parasitic plant (*Chlamydophytum aphyllum*: Georgiev et al., 2010]. Other items include honey, mushrooms, and roots [Bermejo et al., 1994; Georgiev et al., 2011; Kano, 1983, 1992; Kano & Mulavwa, 1984]. Preliminary data of the bonobos at Kokolopori suggest the bonobos there include large amounts of seeds in their diet in periods of fruit scarcity [Georviev et al., 2011]. Similar to what is observed in chimpanzees, bonobos in Lomako, Lilungu, Wamba and LuiKotale swallow the stems and leaves of *Manniophyton fulvum* during the rainy season, as a form of self-medication against parasite (*Oesophagostomum* sp.) infection [Dupain et al., 2002; Fruth et al., 2014; Sabater-Pi & Veà, 1994]. It is likely that bonobos use other forms of self medication [Ekutsu et al., 2016]. Bonobos have been reported to eat soil from termite nests [Kano, 1992; Kano & Mulavwa, 1984], but this has not been investigated further.

Fruit in bonobo diet
As mentioned above, fruits constitute a **major part of the diet of wild bonobos**, and most of the long-term field sites report around or above a 100 species of fruits eaten by bonobos [Beaune et al., 2013b; Badrian & Malenky, 1984; Kano, 1992; Kano & Mulavwa, 1984; Sabater-Pi & Veà, 1994]. Wild bonobos prefer fruit with lower proportions of fibre, and seem to maximise the input of macro-nutrients and minimise ingestion of non-digestible fibrous parts [Sommer et al., 2011]. Bonobos at LuiKotale avoid eating fruit species that contain high concentrations of alkaloids and cyanogenic glycosides [Bondjengo et al., 2017]. The fruit species consumed by bonobos differ between sites, but overlap. Sabater-Pi & Veà [1994] found between 20.6 and 33.3% overlap in number of species that were consumed by bonobos at Lilungu with reported studies from Lake Tumba, Yalosidi, Lomako and Wamba, but this comparison included some relatively short studies. Beaune et al. [2013] compiled a list of 133 plant species whose fruits were observed to be ingested by bonobos at LuiKotale, of which 91 were ingested including seeds. Their list overlapped at the generic level in 44.0% of the 113 species reported for Wamba by Kano & Mulavwa [1984] and 40.0% overlapped at the generic level with the 81 species reported by Badrian & Malenky [1984] for bonobos at Lomako. The fact that the overlap at the species level is small (8.0% and 9.0%, respectively) merits further investigation, and suggests a much higher diversity across the Congo Basin than usually anticipated [Beaune et al., 2013a]. Furthermore, bonobos living in forest/savannah mosaic habitats consume fruits of species only found at the savannah patches [Inogwabini & Matulinga, 2009; Myers-Thompson, 1997, 2001b, 2002]. Macronutrient analyses showed that these ripe grassland fruits had significantly higher level of proteins and tannins, and lower level of sugars compared to ripe forest fruits consumed at Wamba and Lomako, suggesting that these grassland fruits are not as attractive as forest fruits for primate feeders [Myers-Thompson 1997, 2003]. While Kano [1992] notes that bonobos in Wamba were conservative in exploiting new food resources and were not inclined to feed on cultivated fruit species, it has been reported that bonobos invade plantations and destroy crops. Bonobos at Lac Tumba sometimes eat cultivated fruits such as sugar cane (*Saccharum officinarum*), banana (*Musa paradisiaca*), maize (*Zea mays*), papaya (*Carica papaya*), pineapple (*Ananas sativus*), sweet potatoes (*Ipomea spp*) and cocoa (*Theobroma cacao*) [De Witte, 1931; Inogwabini & Matulinga, 2009; Kabongo, 1987; Nishida, 1972].

Despite the large variety of total fruit species eaten, at Lomako the ten most important species (three species of *Dialium; Uapaca guineensis*; two species of *Ficus; Antiaris toxicaria*, *Pancovia laurentii*, *Polyalthia suaveolens*, and *Anonidium mannii*) accounted for 70.0% of all fruit feeding episodes [Badrian & Malenky, 1984]. *Dialium sp.* are reported as a major fruit source in all bonobo sites [Kano, 1992], and contribute to the bonobos' dietary intake of sugar and protein [Beaune et al., 2013b].

Terrestrial Herbaceous Vegetation and leaves in bonobo diet

Bonobos at all sites regularly consume the **pith and new leaves** of a variety of herbaceous plant species [Badrian and Badrian, 1984; Badrian and Malenky 1984; Horn, 1980; Kano, 1979, 1983, 1992; Kano & Mulavwa 1984; Kuroda 1979; Malenky, 1990]. Badrian and Malenky [1984] report that, if judged by the frequency of consumption, THV is the second most important dietary component exploited in the Lomako Forest, after fruit pulp. At Yalosidi it was estimated that THV is equally important to bonobo diet as fruit [Kano, 1983]. At Lac Tumba, fruit represented around 42.0% of the fresh and recent food remains, while THV represented 48.0% (including young leaves and young shoots) and piths and flowers accounted for the remaining 10.0% (ca. 1.0% and ca. 9.0%, respectively) [Inogwabini & Matulinga, 2011]. Preliminary data from Kokolopori suggest bonobos there have very little THV (3.9-4.9% of average daily consumption) in their diet, but bonobos there consume large amounts of seeds in periods of fruit scarcity [Georgiev et al., 2011].

Bonobos are **selective** in which THV species and plant parts they pick. *Haumania liebrechtsiana* and *Sacrophrynium schweinfurthii* seem to be preferred species in Lomako [Badrian & Malenky, 1984]; *H. liebrechtsiana* and *Megaphrynium macrostachym* in Wamba [Kano, 1992]. Bonobos also show a preference for the immature leaves and/or the pithy ends of leaf petioles of these plants [Badrian & Malenky, 1984]. The plant parts chosen are high in proteins and relatively low in carbohydrates [Malenky & Stiles, 1991]. Bonobos will strip off harder outer husk and eat the tender inside [Kano, 1992]. The higher dental wear on incisors, has been related to eating the fibrous sheet of THV [Kinzey, 1984]. THV contains high amounts of plant protein and low concentrations of acid detergent fibre [Malenky & Stiles, 1991; Sommer et al., 2011]. However, between sites differences in protein/calorie values of THV have been noted [Malenky & Wrangham, 1994].

Several studies report that bonobos and chimpanzees differ substantially in their preferences and needs for THV, but the **importance of THV as a fall-back food for bonobos is still under debate** [Doran et al., 2002; Malenky & Wrangham, 1994; Wrangham, 1986; Yamakoshi, 2004]. Although it has been suggested that THV is used by bonobos as an alternative resource when fruit is in short supply [Badrian et al., 1981; Kano, 1983; Kuroda, 1979], White [1998] found no evidence that bonobos at Lomako consumed more THV when fruits were scarce in the dry season – so THV did not function as a fall-back food. It is generally assumed that THV is consistently available, but it may vary in quality between months, because the growth rate of the highly preferred large stems is related to the amount of recent rainfall [White, 1988].

Animal Prey in bonobo diet

Wild bonobos consume a wide **variety of invertebrates** such as crustaceans, molluscs, beetles, crickets, bees, snails, caterpillars, colonial spiders, giant millipedes, earthworms, larvae, termites and ants [Badrian & Badrian, 1977; Badrian et al., 1981; Badrian & Malenky, 1984; Bermejo et al., 1994; Georgiev et al., 2011; Hohmann & Fruth, 2003b; Horn, 1980; Inogwabini & Matsungila, 2009; Kano, 1979, 1992; Kano & Mulavwa, 1984; Oelze et al., 2011; Sabater-Pi & Veà, 1994], but have never been seen using tools to fish for termites or ants [Furuichi et al., 2015; Kano, 1992; Koops et al., 2015a,b; McGrew et al., 2007] even though in zoos they master fishing skills easily [Boose et al., 2013; Gruber et al., 2010; Jordan, 1977]. A recent study using molecular faecal analyses identified many insect families that are consumed by bonobos, including flies and moths (probably larvae/caterpillars) which were not known from behavioural observations or macroscopic faecal analyses, suggesting that secondary predation of invertebrate prey, while bonobos are eating plant parts may play a more important part than previously estimated [Hamad et al., 2014] .

Despite early knowledge of bonobos consuming invertebrates, until recently, they were considered very much as vegetarian apes that hardly consume **vertebrate prey**; however they do consume birds eggs [Kano, 1992], squirrels (*Anomalurus sp*: Bermejo et al., 1994; Hirata et al., 2010; Kano & Mulavwa, 1984; Sabater-Pi & Veà, 1994), flying squirrels (species unknown Ihobe, 1992b; Ingmanson & Ihobe, 1992), bats (*Eidolon sp.* : Bermejo et al., 1994; Sabater-Pi & Veà, 1994), shrews and small snakes [Badrian et al., 1981; Badrian & Malenky, 1984], juvenile and adult duiker (*Cephalophus dorsalis*, *C. nigrifrons*, *C. monticola, C. weynsi, C. callipygus*: Badrian & Badrian, 1984b; Badrian & Malenky, 1984; Fruth & Hohmann, 1993, 2008, 2018; White, 1992a; Sakamaki et al., 2016; Wakefield et al., 2019), and juvenile bush pigs (*Potamochoerus pictus*: A. Fowler, cited in Hofreiter et al., 2010]. More recently observations have been made of bonobos at LuiKotale and at Iyondji consuming the meat of other primate species (*Galago demidovii*: Hohmann & Fruth, 2008; *Cercopithecus ascanius*, *C. wolfi*: Surbeck & Hohmann, 2008; *Lophocebus aterrimus*: Surbeck et al., 2009; Sakamaki et al., 2016), and on at least three occasions even the meat of infant bonobos [Fowler & Hohmann, 2010; Tokuyama et al., 2017]. In LuiKotale it is estimated that bonobos hunt and/or ate meat on average twice per month [Fruth & Hohmann, 2018]. Differences in hunting behaviour across field sites may be due to “specialised prey images” [Ihobe, 1992b], but can also be explained by ecological differences between sites. For example, no red colobus monkeys occur in Lomako, which explains why bonobos there do not hunt them. Monkeys were more frequently encountered at Iyondji than at Wamba, which may partly explain why primate hunting occurs less frequently in the latter site [Sakamaki et al., 2016].

Although bonobos thus consume a variety of invertebrate and vertebrate prey, analyses of stable carbon and nitrogen isotopes in hair of wild bonobos at LuiKotale suggests that the **contribution of fauna to bonobo diet is marginal** and that plant food is the dietary protein source [Oelze et al., 2011].

1.6.3. Feeding behaviour

Wild bonobos show **two peaks in feeding behaviour**: one in the morning (between 06:00 and 09:00 hours) and the other at noon (between 15:00 and 17:00 hours) [Badrian et al., 1981]. In Wamba, bonobos feed on fruits in the morning and, starting from noon, feed on more fibrous foods such as THV or tree leaves are consumed later in the day [Kano, 1992]. Feeding is mostly done in trees, while sitting, or sometimes while hanging, standing bipedally or quadrupedally [Kano, 1983; Kano & Mulavwa, 1984; White, 1992a], but bonobos also forage on small foods while travelling [Badrian & Malenky, 1984], sometimes referred to as “feed as you go foraging” [Furuichi, 2009; Wrangham, 2000], when crossing grassland patches [Myers-Thompson, 2002] or when wading in ponds or streams [Hohmann & Fruth, 2003b; Myers-Thompson, 2002; Uehara, 1988]. Often bonobos will break off fruit bearing branches and take them to a more comfortable place [Kano, 1983]. Like chimpanzees, bonobos will sometimes make sponges from moss and soak up water from tree holes [Furuichi et al., 2015; Hohmann & Fruth, 2003b], or they will stuff food between their lower lip and teeth and suck on these “wadges” [Kano, 1983], a behaviour that is also common in zoo-housed bonobos. It is suggested in wild bonobos, this behaviour may be an adaptation to cope with high tannin levels in the mesocarp of some fruits [Beaune et al., 2017]. Bonobos have been observed to wash certain food items in pools of water [Bermejo et al., 1994]. Although hard shelled nuts are present, bonobos in Lomako have never been observed to use tools to crack open these nuts [Hohmann & Fruth, 2003b], but observations in sanctuaries have shown they are able to use this method [Neufuss et al., 2016]. Extractive foraging for insects or honey has also not been observed in wild bonobos [Furuichi et al., 2014; Koops et al., 2015a,b; McGrew et al., 2007], but digging holes (50 cm diameter, 30-40 cm deep) in the ground to look for mushrooms and/or earthworms has been reported [Bermejo et al., 1994; Kano, 1979, 1983, 1992].

According to some authors**, feeding competition** between bonobos is reduced, since bonobos feed more frequently in large trees than chimpanzees, and visit larger food patches [White, 1989a; White & Wrangham, 1988]. Bonobos in Lomako generally don’t sit closer than one meter (arm’s reach) in each other’s **proximity during feeding** [White & Lanjouw, 1992]. Among bonobo females in LuiKotale, food intake rate moderately increased while feeding effort decreased with female dominance rank, indicating that females engaged in competitive exclusion from high-quality food resources. However, these rank effects did not translate into variation in energy balance, as measured from urinary C-peptide levels [Nurmi et al., 2018]. Both in the wild and in zoos, penile erection and sexual behaviours increases around feeding time, especially when highly desirable or monopolisable food items are encountered [de Waal., 1987; Hare et al., 2007; Hohmann et al., 2009; Hübsch, 1970; Palagi et al., 2006; Parish, 1994; Savage-Rumbaugh & Wilkerson, 1978]. In groups without adult male-mother dyads, most females clearly have feeding priority over low ranking males without a mother in the group [Parish, 1994; J. Stevens pers. obs.]. However, when adult male-mother dyads are present, female feeding priority becomes more blurred [J. Stevens pers. obs.].

Food sharing is often observed and well documented for bonobos both in the wild and in zoos, although there is discussion to what degree this reflects tolerance around food [de Waal, 1992; Fruth & Hohmann, 2002; Goldstone et al., 2016; Hare & Kwetuenda, 2010; Hare et al., 2007; Hirata et al., 2010; Hohmann & Fruth, 1993, 1996; Jaeggi et al., 2010, 2012; Kano, 1980; Kuroda, 1980, 1984a; Parish, 1994; Tan & Hare, 2013; White, 1992b; Yamamoto, 2015]. Bonobos will share not only animal prey, but also plant material, including some very large fruits [Kano, 1980; Kuroda, 1980, 1984a; Fruth & Hohmann, 2002; Hirata et al., 2010; Hohmann & Fruth, 1996; White, 1992b], such as the seeds of *Treculia* fruits, which can weigh 5 to 10 kg per piece [Hohmann & Fruth, 1996; White, 1992b] the pericarp of *Annonidium manni*, which weigh 4 to 6 kg [Hirata et al., 2010; Yamamoto, 2015], or *Carpodinus gentilii*, which weighs only 0.9 kg [White, 1992b], and on occasion also faeces [Goldstone et al., 2016]. Typically, females are possessors of large monopolisable food, including meat, and share most frequently with their own infants, then with other females and least with adult males [Fruth & Hohmann, 2002; Hohmann & Fruth, 1996; White, 1992b; Yamamoto, 2015]. Meat from squirrels, birds, monkeys and duikers, as well as honey; is also shared between adults [Goldstone et al. 2016; Hohmann & Fruth, 1993; White, 1992b].

Coprophagy has been observed in wild bonobos [Beaune et al., 2017; Goldstone et al., 2016; Sakamaki, 2010], and is believed to be an adaptive behaviour in times of food scarcity, where bonobos re-ingest valuable food items such as hard seeds [Sakamaki, 2010]. It may also be a (cultural) behaviour in the bonobos of LuiKotale to cope with high tannin levels of *Canarium* fruits [Beaune et al., 2017].

1.7. Reproduction

Like chimpanzees, bonobos have a diploid **chromosome number** of 48 [Bogart & Benirschke, 1977, 1980; Dutrillaux et al., 1975; Khudr et al., 1973; Stanyon et al., 1986] and exhibit a number of derived karyological features making it the more chromosomally specialized than humans or chimpanzees [Stanyon et al., 1986].

Bonobos typically give birth to **singletons**, although so far twin births have been reported twice in the zoo breeding programme. There have been no reports yet of twin births in wild bonobos. The **interbirth interval** in the wild varies between sites and is 4.5-5 years in Wamba [Kano, 1992; Takahata et al., 1996], versus 9.0 years in Lomako [Fruth, in Knott 2001]. In zoo-housed bonobos, interbirth intervals are on average 4.9 ± 0.2 years (range: 1.9–7.6 years, N = 34), which does not differ significantly from the interbirth interval reported for wild bonobos in Wamba [de Lathouwers & Van Elsacker, 2005; Furuichi et al., 1998].

In Wamba, **a birth peak** seems to occur during the light rainy season from March to May, just after the season with the least rainfall [Furuichi et al., 1998]. There is no apparent seasonality in reproduction of bonobos in zoos [Thompson-Handler, 1990].

1.7.1. Female reproductive characteristics

Few data on **sexual maturity** exist for wild bonobos. In zoo-housed bonobos, urinary testosterone increases in females around the age of five, which suggest they experience earlier onset of sexual maturation compared to male bonobos, and compared to male and female chimpanzees [Behringer et al., 2014]. In the wild, the size of external bonobo female genitalia increases around 5-6 years and the genitals become heart-shaped but there is no swelling [Kano, 1992]. Oestrus starts at the age of eight or nine years and then they leave their natal group [Kuroda, 1989]. In zoo-housed bonobos, menarche occurs in females between the age of 6-11.3 years [Thompson-Handler, 1990; Vervaecke et al., 1999]. Adolescent sterility, between menarche and live birth, is on average 4.5 years for zoo-housed bonobos (range: 1.9 – 8.5 years, N = 5, Thompson-Handler, 1990]. In zoos, females give birth for the first time at 10.7 +/- 3.3 years (range: 8–15 years). This is significantly earlier compared to wild bonobos [de Lathouwers & Van Elsacker, 2006], who give first at an estimated age of 14.2 year [Kuroda, 1989].

As in chimpanzees, the sexual cycle of female bonobos includes **three closely synchronised processes**: the swelling cycle, the menstrual cycle and the ovulatory cycle. Each of those will be discussed below.

The swelling cycle is most conspicuous [Dahl, 1986a]. It is recommended that zoos keep track of females swelling phases using the swelling score sheets (see section 2.4.2., and Appendix 6). Here I describe the anatomy of the swelling and physiological processes underlying the cycles. In bonobos, the entire genital area is rotated anteriorally and the clitoris is fully external, well defined and end terminates in a distinct glans [Savage & Bakeman, 1978; Savage-Rumbaugh & Wilkerson, 1978], although this glans was not found by Dahl [1985]. The *Labia majora* are retained into adulthood in bonobos, whereas in chimpanzees they become diminished as females mature [Dahl, 1985]. At maximal swelling, the *frenulum* is located between the hind limbs, which allows pairs of females to stimulate each other's *frenulum* during ventro-ventral GG-rubbing, and may facilitate ventro-ventral copulations [Dahl, 1985; see section 1.8.5].

Swelling size can differ greatly between females, depending on age, parity and the phase of the swelling cycle [Douglas et al., 2016; Furuichi, 1987 – see Figure 7]. In infant and juvenile bonobos, the genitalia are a slightly distorted triangular shape and very small. When the female reaches five or six years old the size increases a little and the genitalia become a small heart shape but there is no swelling [Kano, 1992]. In young females, the difference in size of swellings between tumescent and maximal phase is small [Ryu et al., 2015]. The *perineum* of fully adult females is of medium size even during the non-swelling phase, and the *perineum* of young adult females is small, but visible, throughout the swelling cycle [Furuichi & Hashimoto, 2004]. Shape and size of swellings vary between individual females, and include oval, globular, long and narrow and nearly square swellings and some are "as large as extra-large bread rolls"

[Kano, 1992]. Therefore, **size of the swelling in itself is not a reliable indicator to monitor female swelling cycles**, but instead the degree of wrinkles and turgidity of the swelling and anus can be used to evaluate swelling cycles [Furuichi, 1987, 1992; Heistermann et al. 1996; Ryu et al., 2015; Vervaecke, 1999]. In a study of swelling cycles of four zoo-housed females, the shine and turgidity of the anus correlated with turgidity of the swelling, but the correlation was not perfect, while the presence of a faecal plug and the colour of the swelling were less reliable indicators [Vervaecke, 1999].

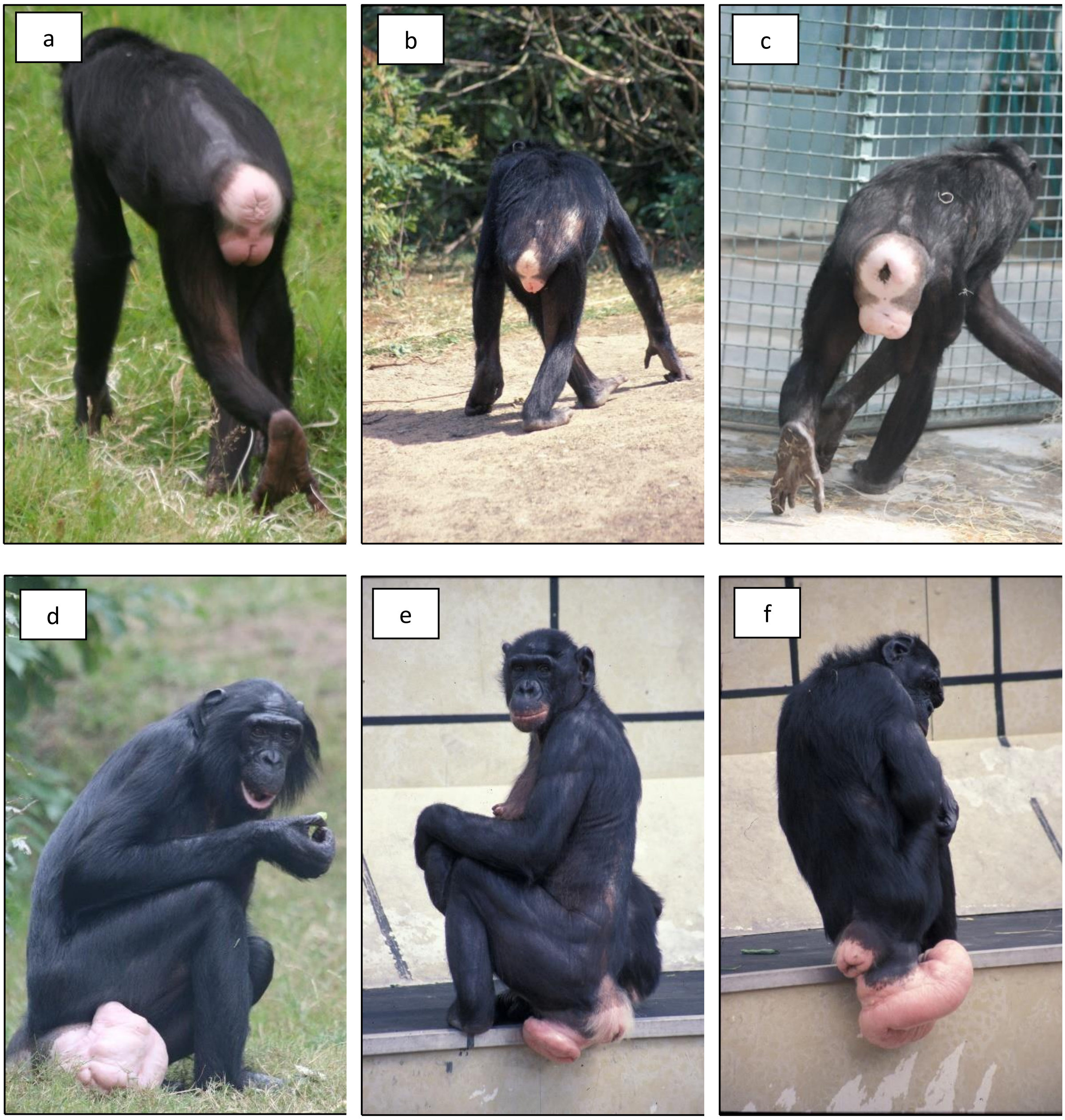

Figure 7: Swelling size in female bonobos of various ages. a: Lingoye in 2016 at age 8,5 yrs (Zoo Planckendael - J Stevens);b) Unga in 2001 at age 8.5 years (Zoo Planckendael - J Stevens); c) Unga in 2015 at age 22 yrs (Columbus Zoo - J Stevens); d: Chipita in 2019 at an estimated age of; e Hortense in 2001 at estimated age of 23 (Zoo Planckendael – J Stevens); f: Dzeeta in 2001 at estimated age of 30 (Zoo Planckendael – J Stevens).

The swelling cycle can be characterised by four different phases [Furuichi, 1987; Thompson-Handler 1990; Vervaecke 1999 – See Figure 8], that are caused by accumulation of interstitial fluid, although different scales have been used, using up to seven phases [Dahl, 1986a; White, 1992c]. Typically, around menses the swelling is minimal. Then there is a tumescent phase, followed by a maximal swelling phase, after which the swelling goes through a period of detumescence and returns to the minimal phase [Furuichi, 1992]. According to Dahl (1986a) the end of the perineal swelling period does not involve a single, abrupt detumescence; there is, instead, a gradual or "stepped" detumescence as evidenced by considerable swelling that continues for an average of 12 days after the first sign of detumescence. In a small study on three adult female bonobos, Vervaecke [1999] observed a super-maximal swelling phase, which lasted on average 6.8 days, range 3-10 days; N= six cycles) is marked by maximal shine on the swelling and the anus and coincided with ovulation, with higher attractiveness, more sexual inspections by the males and a trend for higher female proceptivity, but is not always clearly visible [Reichert et al., 2002]. Typically, the swelling cycle in young adolescent females can be quite irregular and they sometimes show long continuous swellings [Furuichi, 1992; Kano, 1992].

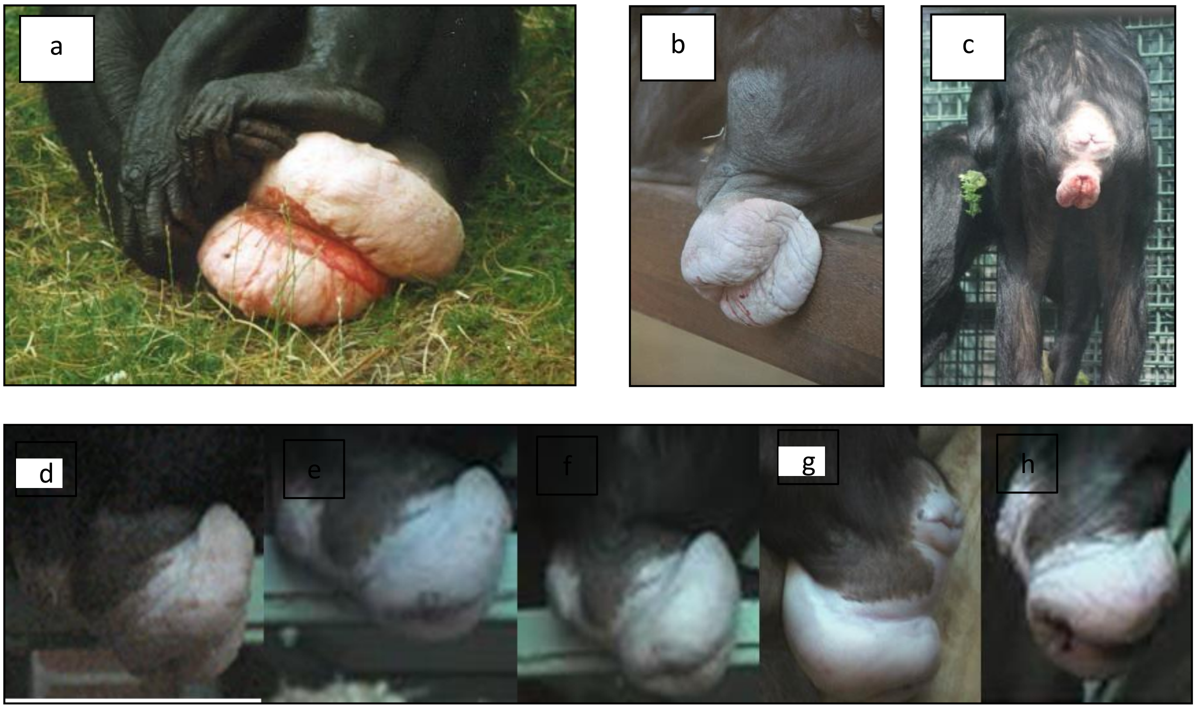

Figure 8: Swellling cycle in an adult bonobo female, including the major swelling phases; a-b-c: varying degrees of menstruation can be visible, these are examples of very visible menstruation; note the large absolute size of swellings during this non-fertile phase ; d--h: different swelling phases in the same female bonobo, Diatou at age 24 (Twycross Zoo - Jeroen Stevens). D: minimal swelling with menstruation ; e: increasing turgidity; f: maximum swelling size, no wrinkles; f: maximum swelling, no wrinkles and distinctive shine; g: decreasing swelling: wrinkles reappear

The length of the maximal swelling phase varies around 15 days [Douglas et al., 2016: average = 10.6, N = 70; range 1-31 days; Furuichi, 1987: average = 14.6 days; Paoli et al., 2006a: average = 13.47 days, N = 557, range = 2-24; Reichert et al., 2002: average = 16 days, range 3-30 days;

Savage-Rumbaugh & Wilkerson, 1978: average = 15.3 days; Vervaecke, 1999: average 12.4 days, N= 8 range 4-25 days], and can be highly variable both within and between females [Douglas et al., 2016]. Dahl [1986a] reports a swelling lasting 23.5 days, and if the days after first sign of detumescence are included, the swellings were reported to last 36 days. But these cycles seem to include some extremely long periods for swelling and may have overemphasized female oestrus period [Furuichi, 1992]. Because of the prolonged maximal swelling, and the fact that females still show swellings and are receptive during lactation and pregnancy, female bonobos spend a much greater proportion of their adulthood in oestrus than do female chimpanzees [Wrangham 1993; Furuichi & Hashimoto 2002], which may reduce competition between males and accordingly their harmful behaviours towards females or offspring (infanticide) or facilitate female choice of mates [Furuichi, 2012]. It has further been proposed that the prolonged sexual swellings of female bonobos also facilitate female-female interactions by making females with maximal swellings more attractive to other females [swelling for female attraction hypothesis: Ryu et al., 2015].

The menstrual cycle can be noted by menstruation. Menstruation, or menses, is sometimes visible when blood is apparent on the female genitalia or in the urine, but is not always very conspicuous, especially in the wild. Hematuria in urine can be measured using reagent strips. Vervaecke [1999] reports that menstrual bleeding usually coincided with the minimal swelling phase, but in one individual was also seen in the period of tumescence. Information on Inter Menstrual Intervals (IMI) is only available from zoo studies. Initially, some studies reported that IMI in bonobos were longer than those reported for chimpanzees [Dahl, 1986a: average IMI = 49 days; Neugebauer, 1980: average IMI = 44 days; Shimizu et al., 2003: average IMI = 47.7 days]. However, when larger sample sizes were taken into account, the duration of the IMI was reported to be more similar to that of chimpanzees [Bolser & Savage-Rumbaugh, 1989: average IMI = 35 days; Paoli et al., 2006a: average IMI = 35 days; Savage-Rumbaugh & Wilkerson, 1978: average IMI = 36 days; Thompson-Handler, 1990 average IMI = 35 days; Vervaecke et al., 1999 average IMI = 34 days]. There are however, as in humans, considerable intra- and interindividual differences in the length of these intervals [Vervaecke et al., 1999; Paoli et al., 2006a]. Possibly female dominance rank may influence length of the cycle, as Vervaecke et al. [1999] noted that the shortest cycles in their study belonged to the most dominant females. There is some indication that menstrual cycles are synchronised between female bonobos [Badrian & Badrian, 1984b; Thompson-Handler, 1990; Vervaecke et al., 1999], but sample sizes so far have been too small to confirm this statistically.

Ovulation is not visible externally. The ovulatory cycle can be determined by measuring the hormones oestrogens and progesterone in bonobo urine [Douglas et al., 2016; Heistermann et al., 1996; Jurke et al., 2000; 2001; Shimizu et al., 2003; Vervaecke, 1999 – see Figure 9]. In faeces, oestrogens cannot be detected reliably but progesterone and pregnanediol can [Heistermann et al. 1996; Jurke et al., 2000; Reichert et al., 2002]. The ovarian cycle is divided in a luteal phase (from menstruation until ovulation) and a follicular phase (from ovulation until the next menstruation). Endocrinologically, ovulation is marked by a preovulatory surge in urinary estrone conjugates (E1C), by a peak in follicle stimulating hormone (FSH) on the days around ovulation, and a postovulatory increase in urinary pregnanediol glucuronide (PdG) [Heistermann et al., 1996; Shimizu et al., 2003]. E1C shows a secondary peak during the luteal phase [Heistermann et al., 1996; Shimizu et al., 2003]. Shimizu et al. [2003] found that the patterns of urinary E1C and PdG were similar between bonobos and other ape species and humans, while patterns of urinary FSH differed in gorillas, but were similar in humans, chimpanzees, bonobos and orang-utans.

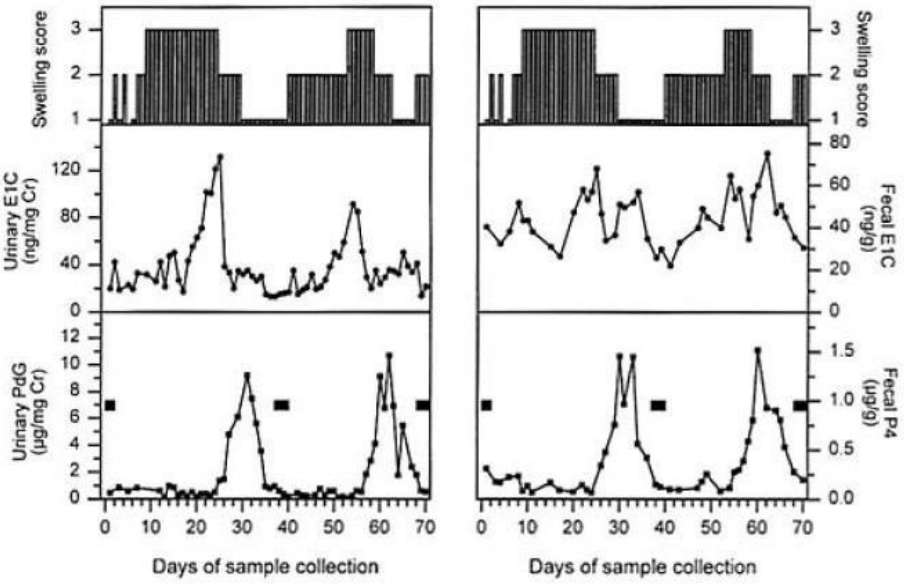

Figure 9: Hormonal profiles of 1) EC and PdG in urine (left) and 2) immunoreactive E1C and P, in feces (right) in relation to the stage of perineal swelling during two consecutive menstrual cycles in an individual female bonobo. Black bars indicate periods of menstruation. (Heistermann et al., 1996)

While in some primate species, the last day of tumescent swelling is an honest signal of ovulation and thus female fertility, and this has also been assumed to be the case for bonobos [Dahl, 1987]. However, endocrinological studies have shown that **swellings do not seem to be reliable indicators of fertility or ovulation in bonobos** [Douglas et al., 2016; Heistermann et al., 1996; Reichert et al., 2002]. First, bonobo females will continue to show a swelling during pregnancy when they are not fertile. The **postconception swellings** in bonobos continue longer than in chimpanzees, and have been reported in the first three months of pregnancy [Douglas et al., 2016;] until about one month before parturition [Furuichi, 1992; Furuichi & Hashimoto, 2002; Kano, 1992], although swelling cycles may become more irregular during pregnancy [Van Elsacker et al., 1997a], and females have been observed to copulate until 19 days before parturition [Kano, 1996]. Second, female bonobos often **resume sexual swelling within one year after parturition**, when they are still lactating [Dahl, 1986a; Dahl & Gould, 1997; Furuichi, 1987, 1989, 1992; Kano, 1987c; 1989, 1992, 1996], as early as three months post-partum [Douglas et al., 2016]. For zoo-housed bonobos, maximal turgidity of the swelling was observed on average from eleven months after birth [Van Elsacker et al., 1997a; range: 4-

17 months, N = 2 females, four cases], but first signs of swellings could occur as soon as one month after parturition, although patterns were erratic [Vervaecke, 1999]. Despite this short period of "postpartum amenorrhea" they do not conceive for another three years [Kano, 1992]. Finally, endocrinological research also suggests that in bonobos patterns of sexual swellings are not reliable indicators of ovulation, and the timing of ovulation can be highly variable [Douglas et al., 2016; Heistermann et al., 1996; Reichert et al., 2002]. It is common to find irregular swelling cycles in anovulatory cycles, and irregular cycles do not necessarily imply absence of ovulation [Douglas et al., 2016; Vervaecke, 1999]. Ovulation never took placein the first half of the maximum swelling period. In 70% of the 23 cases in captivity [Reichert et al., 2002] and in 69.2% of 18 cycles in wild bonobos [Douglas et al., 2012], ovulation occurred in the second half of the maximal swelling phase and in the remaining 30% of both populations, ovulations occurred after the onset of detumescence. A study of one female that showed a continuous swelling showed remarkably low oestrogen levels, but elevated levels ofluteinizing hormone [Lasley et al., 1977], further indicates that swellings in bonobos may not be fully linked to oestrogens.

It is suggested that a system of **concealed ovulation** in bonobos benefits the females in creating paternity confusion, reduces competition between males, and liberates females from sexual coercion [Douglas et al., 2016; Furuichi, 1992; Kano, 1992; Wrangham, 2002], possibly because the prolonged attractivity provides a source of leverage for females [Surbeck & Hohmann, 2013]. Both in zoos [Vervaecke, 1999] and in the wild [Surbeck & Hohmann, 2013] females with maximal swellings are more likely to win conflicts with males and are less likely to receive aggression from males. It has been suggested that competition between females may be partly responsible for variation in swelling length [Douglas et al., 2016; Vervaecke et al., 2003].

There is still debate about whether female bonobos experience **menopause**. Thompson-Handler [1990] observed old females in Lomako that showed no swelling cycle and no copulatory behaviour, leading her to believe that wild bonobos may reach menopause. On the other hand, a female at Wamba that was believed to be older than 40 years still had a one-year old infant and was still cycling [Furuichi, 1987]. A bonobo female that was estimated older than 40 years (Lokolema) ceased sexual cycling in the year before her death, and showed histological changes similar to those seen in postmenopausal women [Gould et al., 1981]. Jurke et al. [2000, 2001] indicated that hormonal data are needed to answer the question about menopause in bonobos, as they found that in zoos females older than 45 years can show regular cycling in their hormonal profile, even in the absence of a swelling cycle (Kitty), or they can show a regular swelling cycles including menses (Margrit), suggesting that there isno menopause in bonobos. However, Margrit stopped cycling in her fifties, and lived well beyond. The oldest female to have given birth so far in zoos is Natalie at age 44.

1.7.2. Male reproductive characteristics

The penis of bonobos has been described by Izor et al. [1981] and minor differences in morphology compared with the penis of chimpanzees were noted. The flaccid penis is carried within the preputial folds and is rarely visible, whereas the erect and free penis is conspicuous over its 13-16 cm length and pink coloration [Dahl & Gould, 1997 – See Figure 10]. The adult size of testicles varies between individuals, perhaps with body weight, and weight of testicles averages about 0.4% of adult body weight [Dahl & Gould, 1997]. There is very little published information available on characteristics of spermatozoa and of ejaculates in bonobos, but both seem to resemble those of chimpanzees [Seuanez, 1980].

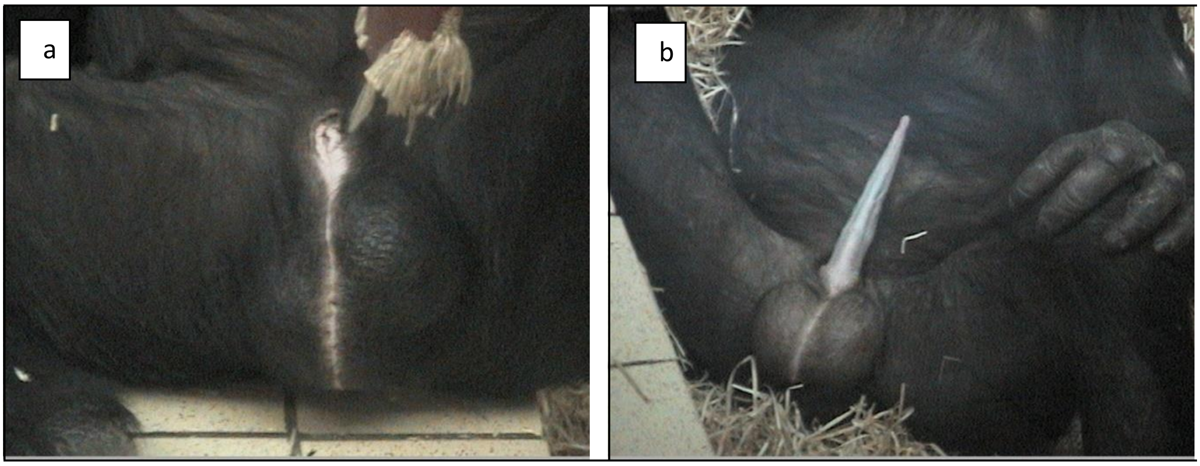

Figure 10; Testicles and penis of the same seven year old male.a: flaccid penis carried within the prputial folds ; b: erect penis (Twycross Zoo - J Stevens).

Urinary androgens increase in male bonobos around the age of eight years, suggesting that onset of sexual maturation starts around the same time as in chimpanzees [Behringer et al., 2014]. In wild bonobos, testicular descent occurs at nine years [Kuroda, 1989]. Dahl & Gould [1997] report that the testicles in six individuals are small during the first three years, increase in size during the fourth year, and show a huge increase in size between the sixth and tenth years. Not much is known about bonobo sperm quality or other indicators of male fertility in relation to their age. No data are available for age of first paternity in wild bonobos. Zoo born males (whose age is exactly known) are on average 12.3 years old at their first reproduction (range 7-17.2 years) [Reinartz et al., 2002]. These data should be interpreted with care as, management decisions can delay the age of first reproduction for younger, captive-born males [Reinartz et al., 2002]. In 2018, the oldest males who have become father, range around 45 years and 38 years for wild-born and zoo born males, respectively.

1.8. Behaviour

90 years after its scientific discovery, the bonobo is still referred to as the “unknown”, “last” or “forgotten” ape [de Waal & Lanting, 1997; Fruth et al., 1999; Kano, 1992]. In comparison with the vast literature on chimpanzees, there are relatively few publications on bonobos [Hare, 2009]. Although some early anecdotal reports about bonobo behaviour exist [Frechkop, 1935; Heck, 1939; Palmans, 1956; Rempe, 1961; Rode, 1941; Schouteden, 1928; 1930; Tratz & Heck, 1954; Yerkes & Learned, 1925], systematic studies on bonobo behaviour really only started in the 1970s, both in zoos [Gijzen, 1972; Hübsch, 1970; Jordan, 1977; Patterson, 1979] and in the field [Badrian & Badrian, 1977, 1978, 1980; Horn, 1980; Kano, 1979, 1980; Nishida, 1972; Susman et al., 1980]. Many of the early zoo studies were published in German and thus did not reach a broad scientific audience [de Waal, 2001]. Likewise, many early field study results from Wamba were published in Japanese, and translations in English only became available at the late 1970s. During the 1970s and 1980s, bonobo research focussed very much on behavioural differences between bonobos and their close relatives the chimpanzees [e.g. Blount, 1990a,b; Dahl, 1986b; de Waal, 1988, 1989a,b; Hübsch, 1970; Kano, 1987; Kitamura, 1983; Mori, 1983, 1984; Nishida & Hiraiwa-Hasegawa, 1987; Patterson, 1979; Savage-Rumbaugh & Wilkerson, 1978; Susman, 1987; Wrangham, 1986]. During the 1990s, some of these behavioural disparities between bonobos and chimpanzees have been challenged, and intraspecific variation in bonobos has become apparent [Boesch, 1996, 2002; Fruth, 1998; Fruth et al., 1999; Stanford, 1998; Stumpf, 2007; White, 1992, 1996a,b; Yamakoshi, 2004]. While clear interspecies differences still exist [e.g. Doran et al., 2002; Hare, 2009], there is also considerable overlap in behaviour and social orginastion. Chimpanzee studies across Africa reveal ever more diversity between populations, including cultural variation [Boesch, 2002]. For bonobos there is also some evidence for cultural differences in behaviour between the longest running field sites [Fruth et al., 2006; Hohmann & Fruth, 2003b; Stumpf, 2007; White 1996a], and between groups in zoos [Myers-Thompson, 1994]. As bonobos continue to be studied in different ecological conditions in the field [e.g. Myers-Thompson, 1997, 2002; Narat, 2015c; Serckx et al., 2014], and as zoo-housed groups become larger, more complex and are being managed more naturalistically, it can be expected that more flexibility in their behaviour will be revealed and more insights in the behavioural and ecological adaptations of bonobos will be discovered, but more research is needed to confirm this [Boesch, 2002; Fruth et al., 1999; Furuichi 2009; Stevens et al., 2008]. In the last decade, comparisons of physiology, neurobiology and genetics are providing major strides in understanding differences between bonobos and chimpanzees [e.g. Behringer et al., 2012a,b, 2014a, 2016a,2016b, 2018; Hopkins et al., 2009, 2017; Issa et al., 2019; Rilling et al., 2011; Staes et al., 2014; 2019; Stimpson et al., 2015].

1.8.1. Activity budgets

Bonobos are **diurnal**, and in the wild usually wake up 30 minutes after sunrise (between 5:20 and 6:20 am) and go to sleep about 40 minutes before sunset (between 4:45 and 5:45 pm) [Kano, 1992]. In Lomako, wild bonobos spend 40.4 % of their time feeding, 16.1 % travelling, 31.9% resting, and 6.3% in social interactions [White, 1992a]. In Wamba, Kano [1992] reports similar activity budgets with 43.0% resting, 20.0% foraging, 20.0% feeding in trees, 13.0% travel, 13.0% other (including social activities). Tsuji et al. [2010] found: 46.3 % feeding, 27.2% moving; 19.5% resting; 5.8% grooming; and other: 1.2%. At LuiKotale feeding made up 51.0% of daily activities [Beaune, 2012]. In zoo-housed bonobos, foraging time is typically lower, while social activities increase compared to data from the wild [Franz, 1998].

During the day, bonobos **travel** on average 1.8 - 3 km per day, at an average speed of 274 - 342 meter per hour, to meet their nutritional needs [Fruth, 1995; Fruth et al., 1999; Furuichi et al., 2008; Kano & Mulavwa, 1984; Tsuji et al., 2010; Waller, 2011].

Every evening, wild bonobos **build a new nest** every night from branches and foliage [Fruth, 1995; Horn, 1980; Kano, 1982, 1992]. Nests are usually made in nest groups, of on average nine nests [range: 1 – 24: Mulavwa et al., 2010] within a vicinity of 40 meters [Fruth, 1995; Fruth & Hohmann 1996; Maloueki., 2019; Mulavwa et al., 2010]. Typically, it takes 15-20 minutes for the bonobos to finish their nest [Kano, 1992]. Parties travelling separately but in the same vicinity start calling to one another with “sunset” calls [Kuroda, 1979; Furuichi, 2011]. Smaller parties will gather together at night and form sleeping clusters [Fruth & Hohmann, 1996] and will split up again in smaller parties the next morning [Mulavwa et al., 2010]. Nests are usually made up in the trees, between 2 and 50 metres above the ground, ata median height of 16 meters at Lomako, but this differs between field sites [Fruth & Hohmann, 1993, 1994; Kano, 1983]. Bonobos typically construct their nests near, but rarely infeeding trees [Fruth & Hohmann, 1996] and seldom re-use old nests [Fruth, 1995; Kano, 1983;1992; Sabater Pi & Vea, 1994;], except when trees are scarce [Fruth & Hohmann, 1996]. Bonobos often include several trees in the construction of one nest, which is rarely seen in chimpanzees [Fruth & Hohmann, 1993, 1994, 1996]. Ground nests are also constructed in some, but not all field sites, and are mainly used for daytime resting [Horn, 1980; Kano, 1979,1983, 1992; Inogwabini & Omari, 2005; Reinartz et al., 2006]. Sometimes bonobos cover themselves with leafy twigs when sleeping in nests, possibly to regulate temperature [Hohmann & Fruth, 2003b], or they put a leafy branch on their head when sitting in the rain, although this does not seem effective in keeping off the rain [Kano, 1982b]. Faeces are usuallydropped outside the nest [Fruth & Hohmann, 1996]. Females will build their nest at higher locations then males [Fruth & Hohmann, 1993]. Low-raking individuals nest on the periphery of nest groups [Fruth & Hohmann, 1996]. Day nests are used not only for resting, but also forfeeding, grooming, and play [Fruth & Hohmann, 1993, 1994]. It has been suggested that nestsmay indicate a “taboo zone” or indicate “personal space” [Fruth & Hohmann, 1993, 1996]. In zoos, female bonobos engage in nest building activities earlier than males; take more effort and time in constructing nest; and build nests on higher positions [Berle et al., 1995].

1.8.2. Locomotion

The bonobos' primary means of **travel** between feeding and resting sites is knuckle-walking quadrupedalism [Doran, 1993; Horn, 1980]. Arboreal travel is a significant component of bonobo overall travel [Doran, 1993; Doran & Hunt, 1994; Horn, 1980]. When travelling in trees, adult bonobos use five types of locomotion: palmigrade and knuckle-walking quadrupedalism; quadrumanous climbing and scrambling; bimanual suspension, including arm swinging and dropping; leaping and diving; bipedalism [Doran & Hunt, 1994; Susman et al., 1980; Susman, 1984]. Suspensory locomotion (hanging from branches or other surface) was more common in bonobos than chimpanzees [Doran & Hunt, 1994]. When jump height (defined as the vertical displacement of the body centre of mass during the airborne phase) was measured in zoos, it was found that bonobos reached jump heights above 0.7 m, which greatly exceeds typical human maximal performance (0.3–0.4 m) [Scholz et al., 2006].

It is often stated that bonobos have a greater predisposition to walk **bipedal**ly than chimpanzees [de Waal & Lanting, 1997; Kortlandt, 1999; Raeburn, 1983; Zihlman, 1996]. Wild bonobos will walk bipedally in the trees [Susman, 1984b], or on the ground when dragging branches in display [Susman, 1984b]; when wading in rivers or pools [Susman, 1984b; Myers-Thompson, 2002], or when crossing open short grass plains [Myers-Thompson, 2001b; 2002]. Comparative studies in zoos revealed that bonobos were not more often bipedal than chimpanzees, but the two species differed in function of bipedal locomotion, with bonobos showing more bipedality for carrying and vigilance, and chimpanzees showing more bipedality for display [Videan & McGrew, 2001; Smith & Delgado, 2015]. Aerts et al. [2000] and D'Août et al. [2002, 2004] compared several characteristics of bipedal versus quadrupedal locomotion in zoo-housed bonobos, and conclude that bipedal locomotion in bonobos is highly variable, and in many kinesiological characteristics significant differences from quadrupedal walking and from other locomotor modes are found, but suggest that the ability for terrestrial bipedalism may be a mere 'free bonus' locomotor mode and, in other words, unspecialized, bonobo- or ape-like terrestrial bipedalism may not be that difficult to accomplish.

1.8.3. Predation

Leopards (*Panthera pardus*) are confirmed predators of bonobos [d'Amour et al., 2005]. **Crowned hawk eagles** (*Stephanoaetus coronatus*) are known to prey on adult monkeys and may predate on infant bonobos, and bonobos have been seen to run for cover when a bird of prey flies over [Kano, 1983; Badrian & Malenky, 1984]. **Pythons** (*Python sebae*) are also considered as potential predators [Badrian & Malenky, 1984; Horn, 1980]. In the Northern part of Lac Tumba, **lions** (*Panthera leo*) occurred at least seasonally [Inogwabini & Matulinga, 2009] and could be potential predators, but seem to have disappeared since 2010 [Serckx, 2014].

Despite their reputation of being vegetarian, bonobos predate on a number of small mammals, including flying squirrels, duikers, galagos, guenons and black mangabey (see section 1.6).

1.8.4. Social behaviour

Social organisation

Bonobos live in **communities** (sometimes also called unit groups – see Van Elsacker et al. [1995] for a review of terminology) of about 10 to 63 individuals [Brand et al., 2016b; Bermejo & Omedes, 1998; Furuichi et al., 2008, 2012; Georgiev et al., 2011; Hashimoto et al., 1998; Hohmann et al., 2019b; Kano, 1982a, 1987a, 1992; Surbeck et al., 2011, 2017; Tokuyama et al., 2019; Waller, 2011] but groups as large as 100 individuals have been reported [Kano, 1982a, 1992; Kuroda, 1979; Uehara, 1988; Vandebroeck, 1959]. These communities occupy a territory of between 14 and 58 km² [Fruth, 1995; Hashimoto et al., 1998; Idani, 1990; Kano, 1982] that can overlap considerably with territories of neighbouring communities [Badrian & Badrian, 1984b; Fruth, 1995; Idani, 1990, 1991; Kano, 1982a, 1992; Kano & Mulavwa, 1984; Thompson-Handler, 1990; Waller, 2011]. Ranging areas are similar for males and females [White & Lanjouw, 1992]. Sex ratios in the community differ between locations. In Wamba and Lilungu, the number of males and females is about the same, resulting in Socionomic Sex Ratios[2] (SSR) around 0.5 [Furuichi, 2011; Kano, 1987a, 1992], but in Lomako and LuiKotale sex ratios tend to be female biased, and SSR values around 0.65, which is more comparable to those seen in chimpanzees [Fruth, 1995; Hohmann & Fruth, 1996; Hohmann et al., 1999; Surbeck et al., 2011; Waller, 2011].

Members of communities do not always travel together but, like chimpanzees, live in flexible **"fission fusion" societies** [Badrian & Badrian, 1984b; Kano, 1982a, 1987a, 1992; Kitamura, 1983; Uehara, 1988; White, 1988, 1989b, 1996a], where subgroups called "parties" form, of 2 to 50 individuals, that fluctuate in size and split up or regroup frequently in the course of one day [Kano, 1982a, 1992; for review see Van Elsacker et al., 1995]. Methods of estimating median party size differ between sites, and reported sizes vary in between four to six independent individuals at Lomako, and 4 to 14 adult individuals at LuiKotale, to 19 individuals at Wamba [Chapman et al., 1994; Hohmann & Fruth, 2002; Hohmann et al., 2019b; Kano, 1982a, Kano, 1992; Mulavwa et al., 2008; White, 1988; White & Lanjouw, 1992]. At Wamba all bonobos of the community travel together regularly [Kano, 1992], but at Lomako, all members of the community are rarely seen together and members of the same community can be separated by kilometres for days or weeks [White, 1992, 1996b] and changes in party composition occurred every 1 hour and 40 minutes [White, 1988]. Parties are larger in the morning, split up later and increase again in size towards the evening [Fruth, 1995]. Parties usually contain males and females; all male parties or lone females are rare, but lone males

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[2] Calculated as Number of Adult and Adolescent females / Total number of Adult and Adolescent individuals in the community (Fruth, 1995).

are sometimes observed [Badrian & Badrian, 1984b; Kano, 1982a, 1992; Kitamura, 1983; Kuroda, 1979; White, 1988]. Older females play an important role in deciding in which direction the party travels [Tokuyama & Furuichi, 1997]. This fission-fusion system is considered an adaptation for exploiting food patches that fluctuate in time and space [Hashimoto et al., 2004]. Occasionally bonobo communities have been observed to fission more permanently [Furuichi, 1987; Kano, 1987a, 1992]. Initially it was believed that party size in bonobos was larger than in chimpanzees [e.g. Kano, 1987c, 1992; Kitamura ,1983; Kuroda, 1979], but more recent analyses have shown that there is considerable within species variation, and bonobos fall in the range of chimpanzee party size [Chapman et al., 1994; Furuichi, 2009]. However, in bonobos, the relative party size (the average number of individuals in a party relative to the total number of individuals belonging to the group) is larger than in chimpanzee groups, suggesting that bonobos form more cohesive groups than chimpanzees [Furuichi, 2009, 2011].

Relationships between neighbouring bonobo groups seem more relaxed than in chimpanzees [Badrian & Badrian, 1984b; Furuichi, 2011; Furuichi & Ihobe, 1994; Idani, 1991a;Kano, 1982a, 1992; Myers-Thompson, 2002; Wrangham, 1999]. Bonobo groups encounter each other frequently and may range together for a few hours to a few days [Hohmann & Fruth, 2002; Idani, 1990; Kano, 1992; Sakamaki et al., 2018]. When bonobo groups meet, theyusually first exchange vocalisations, possibly to assess relative group strength. Males are usually very distant or show agonistic behaviours, but females and juveniles seem to freely interact with members of the other community, and show affiliative behaviour such as grooming, peering, sexual contacts and even play, sharing of food, and even forming coalitionswith females from other communities against a target male [Behncke, 2015; Fruth & Hohmann, 2018; Idani, 1990, 1991a; Tokuyama et al., 2019; White, 1996a], perhaps because they emigrated from the other group or recognise individuals that once belonged to their owngroup [Furuichi, 2011]. An anecdotal study at Wamba, however, suggests that ten months after emigration, a female bonobo did not afilliate with her mother and younger sibling in an intergroup encounter [Toda et al., 2015]. At Wamba, up to four different groups met simultaneously at one location [Sakamaki et al., 2018]. Despite the general peaceful nature [Kano, 1992; White, 1996], there is evidence for intergroup competition and aggression doesoccur. Smaller groups of bonobos seem to actively avoid larger groups. Small parties of females show signs of distress and tried to avoid contact with larger mixed sex parties from other communities by hiding and moving away, remaining silent and vigilant for the rest of the day [Hohmann & Fruth, 2002; Kano, 1982a]. It seems that larger parties bring benefits in intercommunity competition [Wrangham, 1986]. In Wamba, most intergroup encounters occur around the yearly peak in fruit abundance, suggesting that reduced food competition is linked to increased encounter frequency. During periods of relatively low fruit abundance, theprobability of an encounter was higher when a higher number of adult females with maximumsexual swellings were present, suggesting that the attractiveness of females with sexual swellings promoted group encounters during these periods [Sakamaki et al., 2018]. Intergroup encounters can sometimes be characterised by high levels of aggression, especially among males [Hohmann & Fruth, 2002; Kano & Mulavwa, 1984; Kano, 1992; Tokuyama et al., 2019] In Lomako, the number of males per party was larger the day after an intergroup encounter [Hohmann & Fruth, 2002]. However, lethal intergroup aggression, raiding or border patrolling has never been observed in bonobos [Hohmann & Fruth, 2002; Kano, 1987a; White, 1996b; Wilson et al., 2014].

Bonobos live in a habitual **male philopatric society**: males normally remain in their group of birth [Kano, 1987a, 1992], but on rare occasions have been seen to migrate into other communities [Hashimoto et al., 2008; Hohmann, 2001; Hohmann et al., 2019b; Sakamaki et al., 2015; Toda et al., 2018]. In some cases females have been observed to stay in their natal community after maturity [Moscovice et al., 2017], but females usually disappear out of their native group at age 6-10 and assumed to join other communities [Furuichi et al., 2012; Hashimoto et al., 2008; Kano, 1987a, 1992; Sakamaki et al., 2015; White, 1996a]. Typically, females visit several communities temporarily until they settle themselves permanently at the age of 11-13 years old, and then have their first offspring after which they normally remain in the community and become resident females themselves, and will be targeted by immigrating females as “specific senior females” [Furuichi, 1989, 2011; Furuichi et al., 2012; Kano, 1987a, 1992; Sakamaki et al., 2015], although some evidence exists of secondary dispersal of females with dependent offspring migrating into other groups [Hohmann, cited in Schubert et al., 2011]. Within the new community, newly arrived females first make contact with all females, but soon will seek affiliation with one resident female, referred to as “Specific Senior Female”, and groom and initiate sexual contacts with her often [Furuichi, 1989; Idani, 1991b; Pfalzer & Ehret, 1995]. Hostility towards these young immigrant females has been observed [Idani, 1991] but is generally reported as rare or absent [Gerloff et al., 1999].

The behavioural observations of male philopatry and female migration are supported by large scale **genetic studies** on mitochondrial DNA and Y nucleotides: relatedness between females is lower than between males in a community [Eriksson et al., 2004, 2006; Gerloff et al., 1999; Hashimoto et al., 1996; Hohmann et al., 1999; Ishizuma et al 2018; Moscovice et al., 2018], although a recent small scale investigation of genetic material in neighbouring bonobo communities, showed that some male-mediated gene flow exists in bonobos, possibly through a) male migration; b) secondary migration of females with male offspring and/or c) extra group copulations [Schubert et al., 2011]. All three mechanisms have anecdotally been described in bonobos [Gerloff et al., 1999; Hashimoto et al., 2008; Hohmann, 2001; Schubert et al., 2011; Toda et al., 2018], but the genetic evidence now suggests these may have greater consequences than previously believed [Schubert et al., 2011].

Affiliation and social bonding

Bonobos show a variety of affiliative behaviours, including grooming, play and sociosexual behaviours (see 1.8.5). Here I will describe briefly patterns of affiliation in different sex combinations.

Allogrooming is one of the most conspicuous measures of friendship in any primate. According to Patterson [1979] bonobos use their lips more during grooming than chimpanzees. Bonobos direct significantly most allogrooming to the face of conspecifics [Franz, 1999; Jordan, 1977; de Waal, 1988], and high- and low-ranking individuals, as well as males and females, differ significantly in their preferences for certain allogrooming sites. Subordinates and males tended to avoid facial grooming and preferred the back and ano-genital region, while high-ranking individuals and females directed most allogrooming to the face and head of grooming partners [Franz, 1999]. Compared to chimpanzees, polyadic grooming and mutual grooming is rare in bonobos; bonobos usually engage in grooming in a dyad, and when one individual is receiving grooming from another, it rarely grooms another individual [Sakamaki, 2013]. Grooming is possibly an exchange currency which can be exchanged for grooming or for support in conflicts [Stevens et al., 2005b; Surbeck & Hohmann, 2015; Vervaecke et al., 2000c] or food-sharing [Jaeggi et al., 2010, 2013], although the cognitive mechanisms behind such reciprocal exchange have been questioned. These correlations between grooming given and services received may be a by-product of a tendency to groom high ranking individuals [Stevens et al., 2005b; Vervaecke et al., 2000c], and it has been suggested that such reciprocal exchange may also be a by-product of overall and long-term friendships rather than of an actual mental book-keeping system [Jaeggi et al., 2013].

In wild bonobos, social **play** has been observed between newly immigrated adolescentfemales and resident adolescent males or immatures, and resident females played with theirinfants, but play between adults is rarely recorded; sometimes adult males and females engage in sexual play, but play does not occur between adult females [Enomoto, 1990; Idani,1991b, Kuroda, 1980; Sakamaki et al., 2015]. Various types of play have been described; typically play includes a huge amount of sexual behaviours [reviewed e.g. Palagi & Demuru, 2017]. In adult bonobos, play was absent in male-male dyads, but did not differ in proportionrough or calm play between male-female or female-female dyads, but females engaged moreoften in contact play [Palagi & Paoli, 2007]. Behncke [2015] reports that wild bonobos in Wamba have more diversity of partners in play than in sexual or grooming contacts and that play even extends between individuals from neighbouring communities in Wamba. In zoos, play was found to be more common among adult bonobos than among adult chimpanzees, adult bonobos also invited other adults more often to play, signalled play more clearly with aplay face, play was more of a rough nature compared to chimpanzees, and polyadic play is very common [Palagi, 2006, 2008; Palagi & Demuru, 2017]. Play was also found to increase inpre-feeding time, suggesting it may function as a tension-prevention mechanism [Palagi et al.,2006]. Tacconi & Palagi [2009] found no decrease in contact play (play fighting) when a group of bonobos was kept in a more restricted indoor enclosure, but found that play signals increased indoors, possibly to signal more clearly the benign intent of play. Compared to chimpanzees, social play sessions in juvenile bonobos escalated less frequently into overt aggression, lasted longer, and frequently involved more than two partners concurrently (polyadic play) [Palagi & Cordoni, 2012; Palagi & Demuru 2017]. It has been suggested that in bonobos, play can involve more risk-taking and trust, because of their more relaxed and tolerant relationships [Behncke, 2015], possibly also linked to their lower degree of social inhibitory control [Wobber et al., 2010; Palagi & Demuru, 2017].

Within the group, the strongest association and highest rates of affiliative behaviour are observed between **mothers and their sons** [Furuichi, 1989, 1997; Furuichi & Ihobe, 1994; Ihobe, 1991; Kano, 1982, 1987b, 1987c, 1992; Stevens et al., 2006, 2008; Surbeck et al., 2011; Surbeck et al., 2017b]. Variation in the strength of mother-son bonding has been reported [Ihobe, 1992a]. Even when they are mature, sons rely on their mothers, and their rank is often dependent of their mother's status, and mothers will actively support their sons [Furuichi, 1989, 1997; 2011; Furuichi & Ihobe, 1994; Ihobe, 1991; Kano, 1987a, 1992; Legrain et al., 2012; Surbeck et al., 2011]. When their mother died, or lost her dominance position to another female, some males lost their high status, while others could maintain their high rank [Furuichi, 1989; 1997; Furuichi & Ihobe, 1994; Kano, 1992]. Males with a mother are allowed to feed centrally with other females, while males without a mother are not [Furuichi, 1989]. Wild adult males resided twice as frequently with their mothers in bonobos than in chimpanzees, and immature bonobos were three times more likely to possess a living paternal grandmother than were immature chimpanzees [Schubert et al., 2013]. A mother may advantage her sons in two ways: a) in raising his dominance rank; b) in facilitating his access to mating partners [Furuichi, 1992; Kano, 1996; Surbeck et al., 2011]. Mothers support their sons in conflicts with other males by threatening or attacking opponents, including when these males are copulating or attempting to copulate but rarely receive support from their sons [Furuichi, 1989, 1997, 2011; Ihobe, 1992a; Surbeck et al., 2011]. Especially low and mid-ranking males gained substantially from the presence of, and possibly from interventions by, their mothers: the overall rate of mating with oestrous females increased when their mothers were present [Surbeck et al., 2011]. This may be a way for females to increase their chances on grandchildren [Furuichi, 2011]. This does not mean unconditional support, however and mothers will sometimes form coalition with their unrelated female friends against their own sons [Legrain et al., 2012].

Unrelated males and females may form long-term associations, including high rates of affiliative behaviour including grooming and food sharing, which are believed to result in higher mating success for males [Fruth et al., 1999; Hohmann & Fruth, 2003b; Surbeck et al., 2012b; White, 1992b]. In Lomako, the importance of male-female affiliation increases in larger party sizes [White, 1992c, 1996a,b; White & Burgman, 1990]. This may also explain differences between study sites in the relative importance of male-female bonding, as parties in Wamba are usually larger than those in Lomako [White, 1992c].

Female-female bonding has extensively been studied and debated in bonobos. Since females severe the social bond with their mother when they reach adolescence and migrate out of the community [Kano, 1987c], all or most females in a community are unrelated to each other [Hashimoto et al., 1998; Moscovice et al., 2017]. Socio-ecological theory predicts that they would not form social bonds if kinship is low, except when bonding is based on reciprocal altruism [Wrangham, 1979]. In the wild, non-related females will often form strong relationships based on association [Badrian & Badrian, 1984; Furuichi, 1989; Kano, 1992; Moscovice et al., 2017] but grooming is sometimes less frequent among females than among male-female dyads, especially when mother-son dyads are included [Furuichi, 1989; Kano, 1980; Kuroda, 1980]. When controlling for related dyads, grooming between females is not different from grooming between unrelated males and females [Hohmann et al., 1999; Stevens et al., 2006, 2008]. Food sharing is common between females [Fruth & Hohmann, 2002; Kano 1984; Kuroda, 1984; White, 1992b; 1996b]. Coalitions between females can be strong, especially in zoo-housed bonobos [Parish, 1994, 1996; Stevens et al., 2006; 2008; Vervaecke et al., 2000c], but also in the wild female-female coalitions occur more often than between males and females or among males and are often targeted against males, often when males charge at immatures [Nurmi et al., 2018; Surbeck & Hohmann, 2013; Tokuyama & Furuichi, 2016]. However, competition is also not absent among female bonobos: wild female bonobos engage in competitive exclusion from high-quality food resources, but these rank effects do not translate into variation in energy balance and it seems female bonobos trade off feeding opportunities for protection against male aggression [Nurmi et al., 2018].

Relationships between males are characteristically very weak at Lomako and LuiKotale, in that males rarely associate and rarely groom [Surbeck & Hohmann, 2015, 2017; Surbeck et al., 2017a,b; White, 1989a,b, 1992c, 1996a]. In at least one community in Wamba, spatial association and grooming between male bonobos appears to be no less intense than between male chimpanzees, whose groups are thought to be integrated primarily through male-bonding [Furuichi, 1989; Furuichi & Ihobe, 1994; Ihobe, 1991, 1992a; Muroyama & Sugiyama, 1994]. In LuiKotale, males maintained diversified relationships based on spatial association but not based on affiliative behaviours, and the strongest association occurred between maternal brothers [Surbeck & Hohmann, 2017]. Food-sharing between males is rare [Surbeck & Hohmann, 2017; White, 1992b, 1996b]. Coalitions between males are very rare, even between maternal brothers, who seem to be bound together only through their mother [Furuichi & Ihobe, 1994; Ihobe, 1992a; Kano, 1987a, 1987b; 1992; Surbeck & Hohmann, 2013, 2017; Surbeck et al., 2017a]. While male-male competition is sometimes believed to be weakor absent [Furuichi, 1989; Furuichi & Ihobe, 1994; Ihobe, 1992a; Kano, 1992], more recent evidence suggests that competition may be more intense as dominance predicts mating success [Kano, 1996] and to a certain degree also reproductive success [Gerloff et al., 1999;

Ishizuma et al., 2018; Surbeck et al., 2017c]. Aggression between males is lower in frequency and intensity in bonobos than in chimpanzees [Surbeck et al., 2017a], but nonetheless aggression between males also increases in the presence of oestrous females [Hohmann & Fruth, 2003a].

Males are very tolerant towards both related and unrelated infants and juveniles in the group, they will sometimes carry infants on their back or ventrum, and male-infant play is commonly observed [Enomoto, 1990; Hübsch, 1970; Ingmanson, 1992; Johnson, 1997; Kano, 1983, 1990, 1992, 1998; Patterson, 1979; Walker & Hare, 2017]. It has been suggested that males may maintain amicable relationships with infants and juveniles as a mating tactic to gain mating access to the offsprings' mother [Walker & Hare, 2017]. Male care of an orphaned bonobo has been reported in the wild [Hashimoto et al., 1996; Surbeck & Hohmann, 2017]. Male infanticide seems to be absent in bonobos [Fruth et al., 1999; Furuichi, 1989; Furuichi et al., 1998; Hohmann et al., 2019; Kano, 1987a; Wilson et al., 2014], although sometimes males may charge at juveniles, but not dependent infants, for no apparent reason, which provokes counter aggression by coalitions of resident females and males [Fruth & Hohmann, 2006; Hohmann & Fruth, 2002, 2003, 2011; Hohmann et al., 2019b; J. Stevens pers. obs.; Surbeck & Hohmann, 2013]. Long-term records from the field site of LuiKotale include several cases when infants either disappeared from their mothers or were found dead with the hints to infant mortality remaining ambiguous [Hohmann et al., 2019b].

When comparing data on social organisation between Lomako and Wamba, White [1992c, 1996a] found differences in the relative importance of **affiliation between males and females** compared with affiliation among females. In smaller parties female-female affiliation prevailed, while in larger parties male-female association and affiliation are more frequent [White, 1992c; White & Burgman, 1990]. As parties in Wamba are generally larger, this may explain inter-site differences [White, 1992c]. How bonobo communities from other locations (e.g., LuiKotale, Malebo, or Kokolopori) fit into this theory, still needs to be addressed.

Aggression and reconciliation

While it is true that aggressive interactions among bonobos are usually milder and lighter than those of chimpanzees [de Waal, 1992; Kuroda, 1980] and the peaceful nature of bonobos is often emphasized [Carmigini, 2000; Coxe, 2002; de Waal, 1995, 2001; Furuichi, 2011; Kano, 1990; Wrangham & Peterson, 1996] aggression is not absent in bonobos [de Waal, 1988], as is evident from the high frequency of injuries to toes, fingers and ears reported for wild bonobos in Wamba [Kano, 1984b]. Direct observations of serious aggression, especially of females against males, sometimes leading to serious wounds, have been recorded in the field as well as in zoos [Parish, 1996; Hohmann & Fruth, 2011; Sandin, 2005]. A study in zoos found that adolescent bonobos harass, or pester mainly lower ranking individuals, especially when these responded to harassment with agonistic responses – suggesting that this quasi aggression in juveniles but mainly in adolescents serves to learn about aggression and dominance behaviour and acquire information about novel, complex or unpredictable relationships as well as to acquire dominance and eventually outrank adults [Boose & White, 2017]. Several studies found that higher-ranking individuals direct aggression to others more [Hohmann et al., 2009; Surbeck et al., 2012a]. Typically, male bonobos show less aggression when compared to chimpanzees [Kuroda, 1980], but it is still the most common form of aggression observed in bonobos, followed by aggression from females to males, female aggression against females, and male to female aggression is least common [Hohmann & Fruth, 2003b; Idani, 1991b; Kano, 1980, 1987c; Kano & Mulavwa, 1984; White, 1989b, 1992c]. Male-male aggression over food is more common than competition over access to females [Kano, 1987a], although studies from Lomako and LuiKotale show that aggression between males increased at times of high mating activity [Hohmann & Fruth, 2003a; Surbeck et al., 2012a]. Typically, bonobo males aggress females far less frequently than the other way around [Clay & de Waal, 2013; Hohmann et al., 2009; Parish, 1994; 1996; Vervaecke et al., 2000a]. It has been proposed this allows females to dominate males [Parish, 1994], but the lack of male aggression towards females may also be adaptive for males, if female choice is based on affiliation. Indeed, sexual coercion is absent in bonobos [Fruth et al., 1999; Hohmann & Fruth, 2003b; Paoli, 2009; Paoli et al., 2009; Surbeck et al., 2011]. Adolescent male and female bonobos can show increased levels of displaying, “quasi aggressive” or “pestering” behaviour towards certain adult individuals [Kano, 1987c; Van Elsacker et al., 1994; J. Stevens, pers. obs.]; as in chimpanzees, this probably functions to test social boundaries, establish relationships in the hierarchy [Boose & White, 2017; Kano, 1987c].

Male infanticide is documented in many groups of chimpanzees and gorillas, but seems absent in bonobos [Fruth et al., 1999; Furuichi, 1989; Furuichi et al., 1998; Hohmann et al. 2019b; Kano, 1987a, 1998; Wilson et al., 2014]. The lack of evidence may be due to less observation time for bonobos, or to the less aggressive nature and more efficient female counterstrategies in bonobos [Stumpf, 2007]. In Lomako, resident males sometimes charged at females with small infants, which led to counterattacks from resident males and females [Hohmann & Fruth, 2002]. In one case the male disappeared after such an attack, and he was presumed to have fled from the community or he may have died [Fruth & Hohmann, 2006; Hohmann & Fruth, 2002, 2011]. Also at Lomako, one infant died after it was kidnapped by another female, opening the question about **female infanticide** [Fruth & Hohmann, 2006; Hohmann & Fruth, 2002; Vervaecke et al., 2003]. In three different groups (LuiKotale, Wamba and Kokolopori), female bonobos have been observed eating the meat of a dead infants, and sharing it with others, including the mother of the infant; the cause of death in these infants was not observed, but female infanticide cannot be ruled out in each of these cases [Fowler & Hohmann, 2010; Tokuyama et al., 2017].

In many primate species, former opponents will show affiliative behaviour after the conflict has ended, which has been labelled “**reconciliation**”. Initially de Waal [1987] reported a very high occurrence of reconciliation in bonobos in comparison to chimpanzees. Subsequent studies have found varying rates of reconciliation, that overlap with those reported for chimpanzees [Clay & de Waal, 2013a: CCT[3]= 22.3% +/- 23.6%; Palagi et al., 2004: 24.8% +/- 41.3%]. In bonobos, reconciliation is higher for female-female dyads than for male-female or male-male dyads [Palagi et al., 2004]. Male-male dyads in LuiKotale rarely reconciled [Surbeck et al., 2017c: CCT= 3%]. Typical for bonobos is that they will often use sexual behaviour to reconcile or console with group members [Clay & de Waal, 2014; de Waal, 1987, 1992; Furuichi & Ihobe, 1994], but one study suggests that affinitive behaviours such as grooming, touching and play may be equally important for reconciliation as sociosexual behaviours [Palagi et al., 2004]. Consolation, or third party post conflict affiliation, has also been observedin bonobos [Clay & de Waal, 2013; Palagi & Norscia, 2013; Palagi et al., 2004], whereby sociosexual behaviours were found to be more important in this context [Palagi et al., 2004].

Dominance relationships

Dominance relationships have been extensively studied, but results are still not conclusive. Unlike chimpanzees, bonobos do not seem to have ritualised communication to signal subordination [Furuichi, 1992; Furuichi & Ihobe, 1994; Kano, 1992; Stevens et al., 2005a], and dominance hierarchies can only be inferred from agonistic interactions, which can be rare, especially in the field [e.g. White & Wood, 2007]. Moreover, the absence or presence of group members that can act as potential coalition partners can influence the outcome of dominance encounters in bonobos [Vervaecke et al., 1999]. Some studies find evidence for egalitarian hierarchies where dominance is non-linear or hardly expressed [de Waal, 1995, 2001; Kano, 1987a, 1990; Palagi, 2006; Palagi & Paoli, 2007; Paoli et al., 2006b; White, 1996a; White & Wood, 2007], while others find strong, linear hierarchies in males [Furuichi, 1992, 1997; Furuichi & Ihobe, 1994; Hohmann & Fruth, 2003; Ihobe 1992; Ishizuka et al., 2018 Kano, 1992; Surbeck et al. 2011; White, 1996a] or in both sexes [Franz, 1999; Stevens et al., 2007; Surbeck & Hohmann, 2013; Vervaecke et al., 2000], but usually dominance relations are more expressed among males than among females [Kano, 1987c, 1992; Stevens et al., 2007; Vervaecke et al., 1999, 2000]. Often there is clear alpha male and female status, but dominance relationships between middle ranking individuals is less clear [Paoli et al., 2006], and dominance relationships between females may be more stratified [Moscovice et al., 2017]. Much of the variation in results can be explained by variation on which behavioural indicators for dominance have been used [Vervaecke et al., 2000a], and by different use and/or interpretation of terms such as “despotic” or “egalitarian” [Paoli et al., 2006b; Stevens et al., 2007]. Some studies only use the decided outcome of dyadic agonistic interactions [Hohmann & Fruth, 2003a; Jaeggi et al., 2010; Stevens et al., 2007, 2008; Vervaecke et al., 2000a] while other studies include agonistic outcomes but also include displacements [Franz, 1999; Furuichi, 1997; Paoli et al., 2006b; Surbeck & Hohmann, 2013]. Also it is likely that in

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[3] CCT stands for : Corrected Conciliatory Tendencies

small zoo groups, control of dominants is larger and dominance relationships can be more clearly expressed [Stevens et al., 2008].

Dominance rank is not consistently correlated with individual attributes such as age [Paoli et al., 2006b; Stevens et al., 2008] or body weight [Paoli et al., 2006b; Vervaecke et al., 2000] but predicts certain behaviours such as access to food [Vervaecke et al., 1999] or the amount of grooming received [Franz, 1998, 1999; Stevens et al., 2005b; Vervaecke et al., 1999, 2000b] and, in some studies, male mating success [Kano, 1996; Surbeck et al., 2011]; but the relationship between dominance and mating or reproductive success is not consistent, suggesting other factors such as female mate choice may also be at play [Furuichi & Hashimoto, 2004; Marvan et al., 2006; Stevens, 2005; Surbeck et al., 2017c; Takahata et al., 1996]. Although one preliminary study found a correlation between rank and testosterone in wild male bonobos [Marshall & Hohmann, 2005] other studies in zoos [Sannen et al., 2004a,b,c[4]] and in the wild [Surbeck et al., 2012b] suggest a more complex picture. Surbeck et al. [2012b] suggest that high-ranking bonobos males had lower testosterone levels and were less responsive in their testosterone increase, but were more often involved in friendly relationships with unrelated females.

Also, the **dominance position of females** is highly debated [Kano, 1987c; Parish & de Waal, 2000; Stanford, 1998; Surbeck & Hohmann, 2013; White & Wood, 2007]. Again, the discussion is obscured by many different terms and definitions that are being used to describe intersexual dominance relationships. Parish [1996] states that bonobo females are dominant over males. According to White & Wood [2007] at Lomako, bonobo males are dominant over females in dyadic encounters, but have feeding priority. The term "co-dominance" or "equal dominance" is often used in studies on wild bonobos [Fruth et al., 1999; Furuichi, 1989, 1997, 2009, 2011; Wrangham & Peterson, 1996], although definitions of "co-dominance" vary. Surbeck & Hohmann [2013] use the term "mixed-sex dominance", where "*adult females held the highest positions, adult males and some adult females held intermediate ranks, and sub-adult males as well as primiparous and nulliparous females held the lowest ranks*". This is in fact very similar to reports from zoos where, in all studies documented, the highest ranking position was taken by a female, usually the oldest female in the group, while the lowest ranking position is typically taken by males without a mother in the group [Franz, 1999; Paoli et al., 2006b; Parish, 1994; Stevens et al., 2007; Vervaecke et al., 1999a; 2000a] and the positions in between can vary, with some males succeeding in dominating some females, especially if these males have a mother in the group to support them in conflicts [Stevens et al., 2007, 2008]. This has been termed "non-exclusive female dominance" [Stevens et al., 2007, 2008; Vervaecke et al., 2000a], which seems to correspond with "mixed sex dominance"; but may in fact also be called "co-dominance", as has been done for wild bonobos. Because coalitions between females are commonly observed, and males are usually targets of these coalitions

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[4] Note that Hauser et al. [2008] found that the assay used in these papers was not appropriate

[Parish, 1996; Stevens et al., 2005b; Surbeck & Hohmann, 2013; Vervaecke et al., 2000b], it has been suggested that these coalitions enable the females to dominate males [Parish, 1994], but evidence for this hypothesis is mixed [Surbeck & Hohmann, 2013].

To conclude: social behaviour in bonobos seems a lot more flexible than previously believed, as evident from group differences reported in wild and zoo housed bonobos [Hohmann & Fruth, 2002; Stevens et al., 2008]. For zoo management this flexibility is important to keep in mind, when making decisions about group composition and stability.

1.8.5. Sexual behaviour

Bonobos are well known for their exuberant, frequent and variable sexual behaviour [e.g. de Waal, 1987, 1988, 1990, 2001; Kano, 1987a]. Initially observed in zoos [Hübsch, 1970; Jordan, 1977; Kirchshofer, 1962a; Patterson, 1979; Rempe, 1961; Savage & Bakeman, 1978; Tratz & Heck, 1954], subsequent studies in the wild soon confirmed that this sexual activity is not aberrant behaviour [Badrian & Badrian, 1984b; Enomoto, 1991; Kano, 1980, 1987a, 1987c, 1989, 1990; Kitamura, 1989; Thompson-Handler et al., 1984]. A study in orphanage raised bonobos suggests that juveniles do not need to learn sexual behaviour from adults [Woods & Hare, 2011]. In general, sexual behaviour can occur between any age-sex combination of individuals, including immature individuals [de Waal, 1990; Enomoto, 1990; Hashimoto & Furuichi, 1994; Kano, 1992; Kitamura, 1989] and besides heterosexual copulation, also different kinds of pseudo-copulatory behaviours have been described, such as non-copulatory mounting, genito-genital rubbing, rump-rump rubbing, and penis fencing [Hashimoto & Furuichi, 1994; Kano, 1989, 1992; Kitamura, 1989; Kuroda, 1980, Thompson-Handler et al., 1984]. The only combination that usually does not have sex, are mothers and their adult sons, although occasionally exceptions to this rule have been noted [Kano, 1987c, 1992] and have resulted in offspring in zoos [J. Stevens, pers. obs.]. Multi-individual sexual behaviour is not unusual, and up to five females rubbing their genitals on one another, have been recorded [Savage-Rumbaugh & Wilkerson, 1978]. Sexual activity typically increases when parties reunite, or when food is encountered [e.g. Clay & de Waal, 2014; Hare et al., 2007; Hohmann et al., 2009; Moscovice et al., 2015, 2019; Palagi et al., 2006; Parish, 1994; Roth, 1995; Thompson-Handler, 1990] and besides reproduction, sexual contacts can serve various social functions, such as play, tension regulation, social bonding, consolation and reconciliation after fights [Blount, 1990; Brown, 2005; Clay & de Waal, 2014; de Waal, 1987, 1990; Furuichi, 1989; Furuichi & Ihobe, 1995; Hashimoto & Furuichi, 1994; Hohmann & Fruth, 1996; Kano, 1992; Kuroda, 1980, 1984a; Parish, 1994; Thompson-Handler, 1990; Wrangham, 1993]. One study on zoo-housed bonobos did not find conclusive evidence for the tension reduction role of sexual behaviour, as targets of aggression did not have more sexual contact and did not solicit more sex with others, and salivary cortisol remained high in the alpha female, the male and immatures and decreased only in the four other adult females of the group [Hohmann et al., 2009]. Another study found that self-scratching, a behavioural indicator for stress, was reduced in victims of aggression after they had had sexual contact with group members [Clay & de Waal, 2014].

However, **sex in bonobo society is also often overrated** in public media, and especially older bonobos will not necessarily engage as much in sexual behaviour as youngsters do [Roth, 1995]. Thompson-Handler [1990] notes that copulations and GG-rubbing did not appear to be daily activities for the wild bonobos at Lomako. The copulation rates and promiscuity of bonobo males in Wamba was lower than that of adult chimpanzee males of Mahale and Gombe, and copulation rates of adolescent male bonobos were even lower [Takahata et al., 1996, 1999]. Also for bonobo females, the per-hour copulation rate is lower than for chimpanzee females [Hashimoto & Furuichi, 2006]. The copulation rate for adult female bonobos during the maximal swelling phase was lower (0.1 - 0.4 times per hour) than for chimpanzees (0.4 times per hour) [Furuichi & Hashimoto, 2002]. Of course, bonobos show a diversity of non-copulatory sexual behaviour as well. A study of 15 zoo-housed bonobos between 7 and 36 years old showed a negative correlation between age and sexual activity for male and female bonobos [Stevens et al., 2008].

One reason why sexual behaviour in bonobos has received so much attention is **the variation of the positions** in which bonobos have sex and more specifically the occurrence of ventro-ventral copulations, where bonobos look each other in the eye [de Waal, 1987, 1990; Jordan, 1977; Hübsch, 1970; Rempe, 1961; Savage & Bakeman, 1978; Thompson-Handler et al., 1984]. Based on the first few studies in zoos it was concluded that the majority of copulations occurs in this position [de Waal, 1987, 1990; Kirchshofer 1962a; Patterson, 1979; Rempe, 1961; Savage & Bakeman, 1978; Savage-Rumbaugh et al., 1977; Tratz & Heck, 1954]. However, subsequent studies from the wild and zoos have dispelled this, and 62 up to 90% of the observed copulations were in dorso-ventral position [Furuichi, 1987; Kano, 1992; Kano & Mulavwa, 1984; Kitamura, 1989; Thompson-Handler, 1990; Thompson-Handler et al., 1984]. Especially younger females will lift their abdomen off the ground during dorso-ventral copulations, because of the more ventral orientation of the vulva [de Waal, 1988]. Ventro-lateral posture, in which the body planes of the partners are 90° apart has been observed in the wild and zoos, but is relatively infrequent [Kitamura, 1989; Savage & Bakeman, 1978; J. Stevens, pers. obs.]. It seems that females and younger males prefer the ventro-ventral position, but as males mature they prefer the dorso-ventral position [Bourne, 1990; Furuichi, 1987; Hashimoto, 1997; Kano, 1992; Kitamura, 1989; Roth, 1995]. Genitogenital rubbing between females (see below) also typically occurs in ventro-ventral position. Apart from the typical dorso-ventral and ventro-ventral mounting, bonobos can have sexual contacts in a wide variety of positions, especially in immatures [de Waal, 1987; Hashimoto & Furuichi, 1994]. The dorso-dorsal position, sometimes also called “opposite position” [de Waal, 1987] is common in male-male contacts, where it has been labelled ‘rump-rump’ rubbing [Kano, 1989]; but this position is occasionally also observed in genital contacts between females [de Waal, 1987; J. Stevens pers. obs.]. It is not uncommon that copulating individuals change position during sexual contacts, and/or use their hands or feet to stimulate genitals of their copulation partners [Kitamura, 1989] or, more rarely, their own genitals [J. Stevens, pers. obs.].

Copulations are defined as sexual behaviour between mature males and females, including pelvic thrusting and intromission [Furuichi, 1992]. Ejaculation is usually difficult to observe and is often assumed to occur, especially in field studies [Kano, 1992]. According to Harvey [1997] ejaculation can be inferred if one or more of the following are observed: 1) ejaculatorypause: during ejaculation thrusting ceases and there is a pause which lasts for several seconds in which the male's body is momentarily rigid. Slight quivering of the male's flanks during ejaculatory pause may be visible; 2) ejaculate seen on tip of penis; 3) female seen cleaning ejaculate from perineum; 4) female perineum is wet (glistens). Occasionally an ejaculation plug can be observed in the swelling of the female after a copulation [Kano, 1992; Reichert etal., 2002; J. Stevens, pers. obs.]. Mean duration of copulations varies around 13-15 seconds [de Waal, 1987; Kano, 1989; Thompson-Handler, 1990; Thompson-Handler et al., 1984], witha mean number of 2.3-2.7 thrusts/second [de Waal, 1987; Kano, 1989].

Initially it was stated that bonobos **copulate throughout the swelling cycle** [e.g. Savage-Rumbaugh & Wilkerson, 1978; Thompson-Handler et al., 1984]. Subsequent research, using degree of wrinkles and firmness, instead of size as a criterion for scoring swellings (see paragraph 2.4.2.) found that the majority of copulations occur during the maximal swelling phase [Dahl, 1986a; Furuichi, 1987, 1992; Furuichi & Hashimoto, 2004; Kano, 1989; 1992; Paoli et al., 2006a; Reichert et al., 2002; Ryu et al., 2015; Surbeck et al., 2011; Takahata et al., 1996; White 1992c], although female bonobos are attractive and receptive, to some extent, during the non-swelling phase [Dahl, 1987; Furuichi & Hashimoto, 2004]. Lower-ranking or younger females may be more continuously receptive to male initiated copulations than high ranking or older females [Dahl, 1987,;Dahl & Nadler, 1989; Ryu et al., 2015]. Low-ranked female bonobos interacted with all females, sexual interactions between high-ranked females were rare [Clay & Zuberbühler, 2012]. Newly immigrated adolescent female bonobos copulated more than adult female bonobos do [Idani, 1991b; Thompson-Handler, 1990; Takahata et al., 1996, 1999], and also showed much higher levels of GG rubbing [see below; Idani, 1991b] and this is believed to be related to a means of gaining acceptance in their new group without incurring serious hostility [Kano, 1992]. Although they can remain sexually active during pregnancy and lactation [Kano, 1992, 1996], Furuichi [1987] noted that pregnant females and females with one year old infants showed very low frequencies of copulation. Several studies report that most copulations are initiated by males [Dahl, 1987; Furuichi, 1992; Furuichi & Hashimoto, 2004, 2006; Kano, 1989, 1992; Reichert et al., 2002; Takahata et al., 1999] and males will initiate more copulations during the maximal swelling phase of the female [Furuichi, 1992; Furuichi & Hashimoto, 2004].

In chimpanzees, three **mating patterns** are described: promiscuous mating, consortships, and possessive behaviour. In bonobos most mating is opportunistic or promiscuous [Kano, 1989, 1996; Takahata et al., 1999]. Sexual coercion or forced copulations have not been observed in bonobos [Fruth et al., 1999; Kano, 1989; Paoli, 2009]. However, **consortships** have been reported for Lomako, albeit rarely [Gerloff et al., 1999; White, 1996b], and possessive behaviour under the form of mating harassment, is observed in the wild as well as in zoos, but male harassment is relatively rare, consists usually of mild aggression and typically it is dominant males that harass or interrupt copulations of lower ranking males [de Waal, 1990; Furuichi, 1992, 1997; Furuichi & Ihobe, 1994; Kano, 1989, 1992; Hohmann & Fruth, 2003b; Stevens, 2005; Vervaecke & Van Elsacker, 2000]. Female mating harassment has also been recorded for zoo-housed bonobos and may indicate female competition [Vervaecke & Van Elsacker, 2000; Vervaecke et al., 2003]. As a further indication of male possessive behaviour, some studies found that male dominance rank predicts mating success [Furuichi, 1992; Kano, 1996; Paoli et al., 2006b; Surbeck et al., 2011; but see Furuichi & Hashimoto, 2004; Marvan et al., 2006; Takahata et al., 1996] and also reproductive success, with as many as 62% of the offspring sired by a single dominant male in Lui Kotale [Gerloff et al., 1999; Ishizuka et al., 2018; Surbeck et al., 2017c]. This suggests competition among male bonobos may be more intense than previously believed [Furuichi, 1992; Kano, 1992]. A genetic study in wild bonobo groups also showed that males have higher paternity success when their mother is living in the group at the time of the offspring’s conception in bonobos but not in chimpanzees [Surbeck et al., 2019]. As counter tactics, lower ranking males may use subtle ways to lure females away, such as leaf clipping displays [Kano, 1997], and sneaky copulations have been observed [Vervaecke & Van Elsacker, 2000; Stevens, 2005]. Lower ranking males also sire offspring in zoos [Marvan et al., 2006]. In wild bonobos extra-group copulations are common and may result in extra-group paternity [Gerloff et al., 1999]. Data from Lomako suggest that males may invest in long-term relationships with particular females, that exceeds the period of maximal tumescent swellings [Fruth et al., 1999; Hohmann et al., 1999; Hohmann & Fruth, 2002; Surbeck et al., 2012b]. The effects of female mate choice is presumed to be very high in bonobos, but has not been extensively studied [Furuichi, 1992, 2011; Kano, 1996; Gerloff et al., 1999; Stevens, 2005]. There is also potential of cryptic female choice, where females selectively eject sperm of non-preferred partners [Gerloff et al., 1999].

Male-female sexual interactions are often considered as **non-copulatory mounts** (or non-sexual mounts, or pseudo-copulations), when there is no normal solicitation process, or no erection, intromission and/or pelvic thrusts are observed, and mainly occur in tense situations, such as discovery of food [Furuichi, 1987, 1992; Kano, 1989, 1992]. Typically, non-copulatory mounts occur irrespectively of the female swelling cycle [Furuichi, 1992].

Female-female sexual contact usually consists of ventral mounting between females where participants embrace each other ventro-ventrally and rub their genital swellings laterally against each other, so that often the tips of the genitals (*frenulum clitoris*) rub against each other [Kano, 1989]. This behaviour has been labelled genito-genital rubbing, or GG-rubbing for short (Kano, 1980; Kuroda, 1980) and is common in both wild and zoo-housed bonobo groups [de Waal, 1987, 2001; Fruth & Hohmann, 2006; Furuichi, 1989; Hohmann & Fruth, 2000; Idani, 1991b; Jordan, 1977; Kano, 1980; Kirchshofer 1962a; Kitamura, 1989; Kuroda, 1980; Moscovice et al., 2015, 2019; Paoli et al., 2006a; Rempe, 1961; Savage & Bakeman, 1978; Savage-Rumbaugh & Wilkerson, 1978; Thompson-Handler, 1990; Thompson-Handler etal., 1984]. Other positions, including facing in opposite directions, or hanging from branches have also been observed [de Waal, 1990; Fruth & Hohmann, 2006]. Duration of GG-rubbing varies between 8-15 seconds [de Waal, 1987; Thompson-Handler, 1990]. Infant bonobos havealso been observed to participate often in GG-rubbing, and this behaviour has been seen between mothers and daughters [Thompson-Handler, 1984; Paoli et al., 2006a]. Several authors report that GG-rubbing occurs more when females are in the maximal swelling phase[Hohmann & Fruth, 2000; Kano, 1987c; Paoli et al., 2006a; Ryu et al., 2015]. A study on wild bonobos at LuiKotale found that following GG-rubbing, but not following male-female copulations, urinary oxytocin increased, suggesting a strong proximate bonding mechanism infemale bonobos [Moscovice et al., 2019]. While GG-rubbing is mostly associated with tensionreduction, often around feeding context [de Waal, 1987; Kano, 1980, 1987a; Kuroda, 1984a; Mori, 1984; Ryu et al., 2015], Hohmann & Fruth [2000] concluded that GG-rubbing is a multifunctional behaviour that can be used to reduce tension or to reconcile, but alsodemonstrates status, as typically lower ranking females will solicit the behaviour, and the higher ranking individual will usually assume the top position. Idani [1991b] reports that newlyimmigrated females showed much higher rates of GG rubbing than resident females. Paoli etal. [2006] found no relationship between dominance and the position in GG-rubbing for a zoo-housed group, and suggested that the behaviour functions as a tool for social assessment between females. GG-rubbing females can remain silent, but sometimes one or both participants emit vocal sounds acoustically identical to copulatory screams [Clay & Zuberbühler, 2011b; Fruth & Hohmann, 2006; Kano, 1989].

Male-male sexual contacts are less frequent than male-female or female-female contacts [Fruth & Hohmann, 2006; Hashimoto & Furuichi, 1994; Kitamura, 1989] and may include ventro-ventral mounting dorso-ventral mounting, dorso-dorsal mounting (called "rump-rump-rubbing) and penis fencing [de Waal, 1990; Kano, 1989; Kitamura, 1989]. Penis-fencing, where two males hang face to face from a branch while rubbing their erect penises together, has been recorded rarely, and only in Wamba but not in Lomako or in zoos [de Waal, 2001; Kuroda, 1989]. Intromission occurs very rarely in male-male sexual contacts [Fruth & Hohmann, 2006]. While de Waal [1990] noted that male-male contact does not include ejaculation in his study at San Diego Zoo, later observations in several zoos showed that males do ejaculate in non-copulatory mounts [J. Stevens, pers. obs.]. Sexual contact between males occurs mostly following display behaviour or aggressive interaction and thus seem to function mainly for tension reduction [Hashimoto & Furuichi, 1994].

Besides the different forms of mounting described above, bonobos can show a variety of **other sexual behaviours** including oral contacts such as mouth-to-mouth kissing, fellatio and manual massage of another individuals' genitals [de Waal, 1987, 1990].

As mentioned before, sexual behaviour in bonobos can also **include immatures** [de Waal, 1990; Hashimoto, 1997; Kano, 1992; Wood & Hare, 2011]. In general, male infants are sexually more precocious than females [Fruth & Hohmann, 2006; Hashimoto, 1997; Hashimoto & Furuichi, 1994; Kano, 1992; White, 1992a], but in zoos also female infants have been observed to initiate sexual contact with adults and adolescents [de Waal, 1990]. Infant bonobos as young as 3-4 months have been observed to engage in sexual interactions [Hashimoto, 1997; Hashimoto & Furuichi, 1994; Johnson, 1997; Jordan, 1977; Van Elsacker et al., 1997]. Usually these interactions involve the infants' kin or their own mother, who may rub her genitals against the genitals of the infant, possibly to reduce their own emotional arousal [Hashimoto & Furuichi, 1994; Johnson, 1997]. In zoos, sexual contacts between mothers and their sons generally cease after the age of two or three [Johnson, 1997; Van Elsacker et al., 1997a]. Most adult males do not mate with their own mother, but some exceptions have been noted [Kano, 1987a, 1992]. Also in some rare cases in zoos, mothers have been observed to allow their sons to copulate with them even when they are adult, even when they were mother-reared [J. Stevens, pers. obs.]. This may have been due to the lack of other sexually attractive partners, or to personality and/or maternal styles. While this seems to be the exception rather than the rule, this mother-son mating has resulted in surviving offspring on a number of occasions [Pereboom et al., 2011]. Sexual contacts between young infants and adult males can occur in a play like context, but as infants grow older may also involve conflict resolution when the infants are being attacked or threatened by adults [Hashimoto, 1997; Hashimoto & Furuichi, 1994]. Juveniles will also engage in sexual contacts with individuals other than their mother and join adult or adolescent individuals by mounting on the back or clinging to the chest of one of the adults, but will rarely attempt to disrupt sexual behaviour of adults [Hashimoto & Furuichi, 1994; Johnson, 1997], although in one case in a zoo a 4-year old female responded negatively to all three males that attempted to mate with her mother [J. Stevens, pers. obs.]. In wild bonobos, genital contacts between immature females and mature females were rarely observed [Hashimoto, 1997].

For male bonobos in the wild, the frequency of sexual activity drops after the age of six years and remains relatively low during adolescence, after which it goes up again in adulthood, as copulation rates but also sexual contacts with other males increase, but it does not reach the high peak of early childhood again [Hashimoto, 1997]. For female bonobos there is a peak in late juveniles and probably adolescents, as GG-rubbing increases [Hashimoto, 1997; Kano, 1987c]. In zoo-housed individuals, Roth [1995] found highest rates of sexual activity in adolescent bonobos, followed by juveniles and then adults. Stevens et al. [2008] found a negative correlation between age and sociosexual activity in both male and female zoo-housed bonobos between 7 and 38 years of age.

1.8.6. Communication

In this section, I will review how bonobos communicate with each other. For information about the language studies involving bonobos using computer symbols, I refer to a good review by Tomasello [2017] and the relevant literature in the Bibliography [e.g. Hopkins & Savage-Rumbaugh, 1991; Savage-Rumbaugh et al., 1996; Taglialatela et al., 2003].

Bonobos combine postural, facial, vocal and gestural signals to communicate with conspecifics [Bermejo & Omedes, 1998; de Waal, 1988; Graham et al., 2016; Pollick & de Waal, 2007; Smith & Delgado, 2015]. It has been suggested that in the wild, male bonobos use branches as communication tools to indicate travel direction or distance [Schamberg et al., 2017]. In general, bonobos seem to be using multimodal communication (for example combine gestures with vocalisations or facial expressions) more than chimpanzees [Bermejo & Omedes, 1998; Genty et al., 2014; Pollick & de Waal, 2007], resulting in a complex, but very flexible mode of communication. Within a combination, the facial or vocal signal tends to occur first, just before the gesture [Pollick et al., 2008]. When bonobos combine gestures with facial/vocal signals, they are more effective at eliciting a response than when they use gestures alone [Pollick & de Waal, 2007]. Combinations may indicate a different intention or context – e.g. 'contest hooting' can be used in agonistic or in playful contexts, but this is signalled by combining the vocalisation with appropriate gestures [Genty et al., 2014]. Duringcontact play and play fighting, bonobos increase the combined use of playful facial expressionsand gestures, possibly to signal no harmful intent, especially in contexts with multiple players[Demuru et al., 2015].

Facial expressions have been studied less than other forms of communication, perhaps because they require close up monitoring [Pollick et al., 2008]. Also facial behaviour varies inter-individually within the same context, be it an experimental condition or a natural situation in a consistent (intra-individual) manner [Gaspar, 2006]. The number of facial expressions describes varies from 5 to 46, depending on which criteria are used [Bard et al., 2011; de Waal, 1988; Gaspar 2001]. In general the facial expression described for bonobos appear similar to those of chimpanzees [Bard et al., 2011; de Waal, 1988; Gaspar 2001], but bonobos sometimes invent "funny faces" [de Waal, 1988; Gaspar, 2001], which has been suggested to indicate a degree of voluntary control over their facial musculature [Pollick & de Waal, 2007]. The communicative function of facial expressions remains understudied, but one study demonstrated contagious yawning in bonobos [Demuru & Palagi, 2012]. Like chimpanzees, bonobos two variations (play face and full play face), but adults bonobos use the second type more compared to chimps [Palagi, 2006]. Play faces are more common 1) during rough play in bonobos than chimpanzees [Palagi 2006], 2) during social play than in solitary play [Palagi, 2008] and 3) occur more during contact social play than locomotor social play [Palagi & Paoli, 2007]; 4) when bonobos are in a confined space [Tacconi & Palagi, 2009]. Bonobos may deliberately alter their facial expressions, such as play faces to manipulate and manage play sessions as they progress [Demuru et al., 2015; Palagi & Demuru, 2017].

Vocal communication has been studied by several authors, including sonographic analyses – resulting in different classification systems of sounds, or vocal ethograms, which will not be further discussed here [Bermejo & Omedes, 1988; de Waal, 1988; Genty et al., 2014; Hohmann & Fruth, 1994; Hopkins & Savage-Rumbaugh, 1991; Jordan, 1977; Mori, 1983; Okayasu, 1991; Patterson, 1979; Pollick & de Waal, 2007; Van Krunkelsven, 1993; Van Krunkelsven et al., 1996]. Bonobos produce higher pitched calls than chimpanzees, linked to differences in laryngeal and vocal tract production mechanisms [Demolin & Delvaux, 2006; Grawunder et al., 2018, 2019; Mitani, 1996; Mitani & Gros-Luis, 1995]. Although the types of vocalisations are similar for bonobos, chimpanzees and gorillas, the three species also differ in acoustic structure of calls, rate of call production and vocal usage [Mitani, 1996]. Members of bonobo subgroups are continually communicating with one another through vocalisations: during relaxed interactions, while there is some excitement or when there is a conflict [Bermejo & Omedes, 1998]. Wild bonobos use call combinations, call exchanges and call subtypes to coordinate their movement between parties [Schamberg et al., 2016, 2017a,b]. Vocal communication appears more dialogue-like in bonobos, and includes soft peeps to draw attention to and ‘‘comment’’ on novel items or environmental events [de Waal, 1988; Pollick & de Waal, 2007]. Dyadic vocal interactions are characterized by call overlap avoidance and short inter-call intervals [Levrero et al., 2019]. It has been suggested that some vocalisations are not context specific, and can be used flexibly by bonobos across different contexts [Clay et al., 2015b]. Several studies indicate that the sequence of vocalisations conveys meaningful information to group members [Bermejo & Omedes, 1998; Clay & Zuberbühler, 2009, 2011a]. “Food peeps” seem unique to bonobos [Mitani, 1996]. Clay & Zuberbühler [2009] could acoustically distinguish five food-related vocalisations in zoo-housed bonobos (“barks”, “peeps”, “peep-yelps”, “yelps” and “grunts”), which were usually uttered in sequences and the composition of these sequences, rather than the individual call types, varies in accordance with food preference. Although these sequences do not meet the formal criteria of functional reference or the properties of human syntax [Clay, 2011], subsequent play back experiments have indicated that bonobos could extract information from the sequences [Clay & Zuberbühler, 2011a]. Female “copulation calls” or “copulation screams” have received considerable interest and seem to serve as broader social signals in flexible and potentially strategic ways [Clay et al., 2011; Clay & Zuberbühler, 2011b, 2012]. Females are more likely to call in sexual contacts with males than with other females, they are more likely to call when having sex with a high-raking partner, and as swelling size increases, copulation calls increase during sexual contacts with male, but not female partners [Clay et al., 2011b]. Acoustic analyses of the calls showed that copulation calls convey information about caller identity, but not about swelling size, or rank of mating partner [Clay & Zuberbühler, 2011b, 2012]. Apart from these close range vocalisations, bonobos use vocalisations for communication over large distances such as “low hoots” and “high hoots”, to communicate between different parties [de Waal, 1988; Mori, 1983; Hohmann & Fruth, 1995; White et al., 2014], for example about the availability of food [White & Lanjouw, 1992], or to gather in the evening at nests sites

[Hohmann & Fruth, 1994]. Like other apes, bonobos have large internal air sacs [Rietschel & Kleeschulte, 1989], which probably are used for amplification of vocalizations. In zoos, low hoots are heard in response to environmental changes and disturbances [de Waal, 1988] and high hoots increased when feeding time was expected, but the quantity of food did not influence the number of high hoots [Van Krunkelsven, 1993]. In Lomako, low hoots were directed at human observers, or elicited by vocalisations of distant community members [Hohmann & Fruth, 1996]. “High hoots” are heard throughout the day, but most often in the morning and in late afternoon [Hohmann & Fruth, 1994], and coincide mostly with corresponding calls of conspecifics, calls of black mangabeys or other loud noises; high rates of hooting marked capture of prey, the beginning of food sharing episodes, or the invasion of feeding trees [Hohmann & Fruth, 1995]. Although there is considerable overlap, sexual differences are found with females producing lower frequency calls than males [Hohmann & Fruth, 1994]. Long distance vocalisations are often combined with drumming with hands and feet on buttress roots of large trees [Hohmann & Fruth, 2003b]. In zoos, it has been shown that bonobos respond to vocal calls of social partners even if they have been separated for five years [Keenan et al., 2016].

Gestural communication has also been studied extensively in bonobos [Demuru et al., 2014; Fröhlich et al., 2016; Genty & Zuberbühler, 2014; Graham et al., 2016, 2018; Kuroda, 1984b; Pika et al., 2005; Pollick & de Waal, 2007; Schneider et al., 2010, 2012; Smith & Delgado, 2015; Veà & Sabater-Pi, 1998; Zimmerman et al., 2009]. Bonobo gestures are very similar in repertoire and meaning to those used by chimpanzees [Graham et al., 2016, 2018]. The gestural repertoires of bonobos are characterized by a high degree of variability within and between groups, and compared to chimpanzees, bonobos seem to use gestures more flexibly [Pika et al., 2005; Pollick & de Waal, 2007], and use more gestures that involve touching [Pollick et al., 2008]. Many idiosynchronous gestures have been described that are only expressed by one or few individuals [de Waal, 1988; Douglas & Moscovice, 2015; Ingmanson 1987; Myers-Thompson, 1994; Pika et al., 2005; Pollick & de Waal, 2007]. Gestural communication is mostly done with the arms and hands, but foot gestures do occur [de Waal, 1988]. Bonobos use head gestures more frequently than chimpanzees, and in a greater variety of contexts, which suggests that bonobos are more sophisticated in their use of the head as a signal medium when compared with the other ape species [Dielentheis & Niemitz, 1991; Schneider et al., 2010]. Bonobos use manual and bodily gestures significantly more when recipients are attentive to them, suggesting these movements are intentionally communicative [Demuru et al., 2014; Smith & Delgado, 2015], and they seem to anticipate and respond to signals before they have been fully articulated [Fröhlich et al., 2016], with a timing between the initiation of an action and its response is similar to what has been documented in adult human interaction [Rossano, 2013]. It is believed that bonobos learn social gestural communication primarily through ontogenetic ritualization, and there is little evidence for social learning through for example imitation of the mother [Halina et al., 2014;

Myers-Thompson, 1994; Pika et al., 2005; Schneider et al., 2012]. The majority of gestures in bonobos are **imperative,** which means that they are used to get another individual to help in attaining a goal [Pika et al., 2005], but **referential gestures**, such as pointing or beckoning have been reported [Douglas & Moscovice, 2015; Genty & Zuberbühler, 2014; Veà & Sabater-Pi, 1998; Zimmerman et al., 2009]. **Iconic** hand signals, to signal information regarding the position to be assumed during copulation, have been reported for one male bonobo [Savage & Bakeman, 1978; Savage-Rumbaugh et al., 1977], but a follow up study on 20 bonobos from three zoo-housed groups found no evidence for either iconic use of gestures or gestures that were correlated with positioning or that were utilised to negotiate a copulatory position [Roth, 1995]. A study in LuiKotale suggested bonobo females may use iconice gestures when initiating sexual behaviour [Douglas & Moscovice, 2015], and bonobos in Lola Ya Bonobo use beckoning as an iconic gesture [Clay & Genty, 2017; Genty & Zuberbühler, 2014].

Section 2: Management in zoos

2.0. Welfare of bonobos in zoos

The practical considerations for keeping bonobos in zoos described below have been written with the intent to provide the best welfare to zoo housed bonobos. For this, it is important to give a brief understanding of what we mean by welfare. We refer to the WAZA Welfare Strategy [Mellor et al., 2015], for a more detailed perspective on welfare of zoo animals. Throughout the Bonobo EEP Best Practice Guidelines we follow the vision in this Welfare Strategy that bonobo holders should direct bonobo welfare attention towards the highest categories of Maslow's pyramid of wellness and well-being (Figure 11). This means that, besides the basic physiological needs, veterinary care and safety needs of animals, zoos should also provide the bonobos with optimal welfare, including social needs, mental stimulation and a maximum amount of choice.

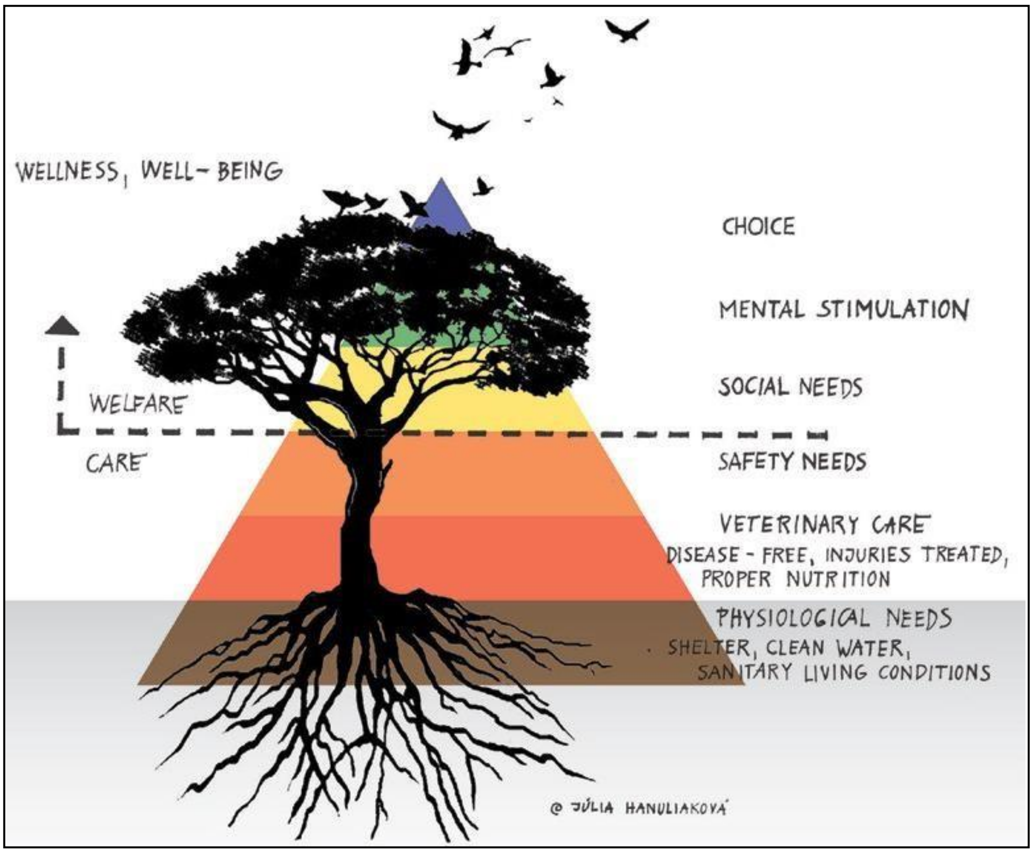


Figure 11: The aspiration of the World Zoo and Aquarium Animal Welfare Strategy; that is, to direct animal welfare attention towards the highest categories of Maslow's pyramid of wellness and well-being. The tree's roots represent the critical foundational requirements for survival, including nutrition systems, understood through experience and science. In the trunk, health care meets the animals' physical and safety needs. The crown is the site of the most varied and complex welfare-related activities that the best zoo and aquarium design and management would make available to the animals. The birds taking flight from the tree represent perhaps an ideal of zoos and aquariums—retaining and encouraging natural abilities. As a tree provides a complex habitat for other species, a zoo or aquarium can foster the welfare of animals beyond its own confines [Mellor et al., 2015].

While there are many welfare definitions around, as in the WAZA Welfare Strategy, we follow the following **description of animal welfare** (World Organisation for Animal Health – OIE):

"Animal welfare means how an animal is coping with the conditions in which it lives. An animal is in a good state of welfare if (as indicated by scientific evidence) it is healthy, comfortable, well nourished, safe, able to express innate behaviour, and if it is not suffering from unpleasant states such as pain, fear and distress. Good animal welfare requires disease prevention and veterinary treatment, appropriate shelter, management, nutrition, humane handling and humane slaughter/killing. Animal welfare refers to the state of the animal; the treatment that an animal receives is covered by other terms such as animal care, animal husbandry and humane treatment."

It is important to realise that animal welfare refers to the **overall state of an individual**. It is seen as the **balance** between positive and negative interactions. Overall, this balance should be positive. Therefore, it is equally important to realise that the above statement refers to an overall state and does not mean that all states of discomfort should always be eliminated for all individuals – for example during introductions, or rank reversals. Low ranking individual bonobos are sometimes the victim of coalitionary attacks. The balance to what degree this level of aggression is acceptable, needs to be closely monitored in open discussion with the EEP coordinator, other EEP species committee members and the TAG chair.

Equally important to bonobo welfare is the **concept of five domains animal welfare** [Mellor & Beausoleil, 2015; Mellor et al., 2015 – see Figure 12] :

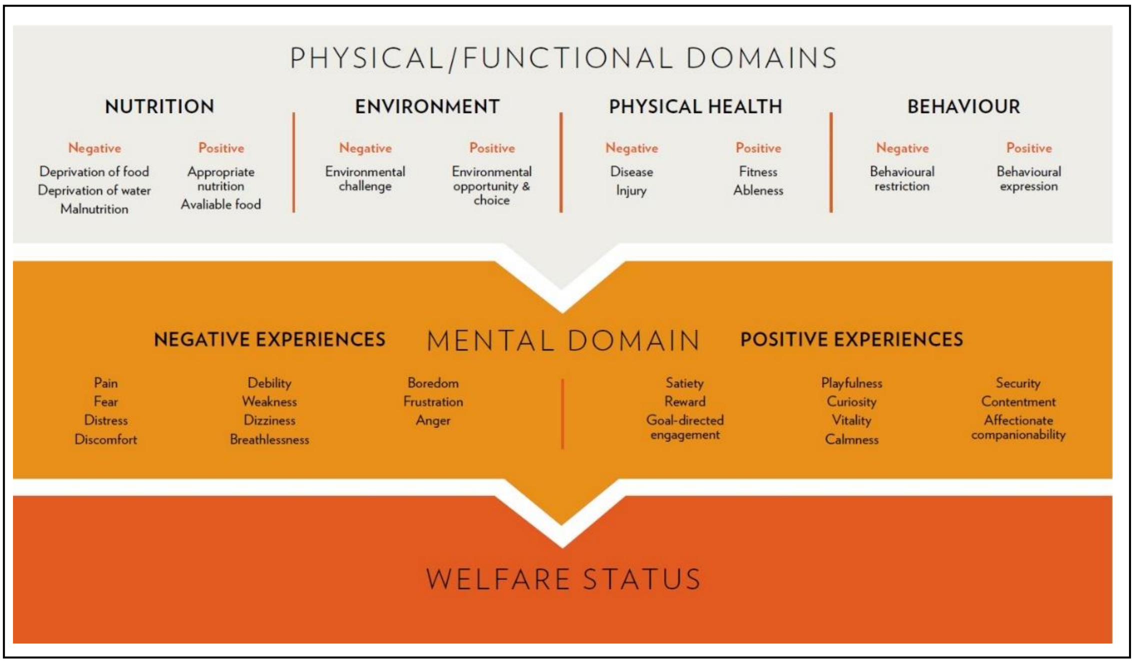


Figure 12: The five Domains model for understanding animal welfare, divided into physical/functional and mental components, provides examples of how internal and external conditions give rise to negative (aversive) and positive (pleasant) subjective experiences, the integrated effects of which give rise to an animal's welfare status [Mellor et al., 2015].

A third major concept that is crucial in maintaining good welfare in zoo animals, that also applies to bonobos, is the **24/7 across lifespan** (Figure 13) animal welfare concept developed by Brando & Buchanan Smith [2017]. Institutions holding bonobos are encouraged to think about how to improve bonobo welfare 24/7. To quote the authors: "*Care staff spends a limited number of hours at a zoo, wildlife centre, or sanctuary. The animals however, are there 24/7, year round for life unless they are part of a reintroduction program (or escape!). Indeed, the human working day dictates the care provided to captive animals. Husbandry activities typically occur during 6–8 daylight hours, which are not necessarily biologically relevant times for the animals. Care staff are not normally present to observe and provide for the needs and preferences of captive animals most of the time (i.e. 16–18 h/day). Given that animal care personnel are fundamental to promoting good welfare, we propose a tool for care staff to determine how well they are providing habitats that meet animals' needs*"

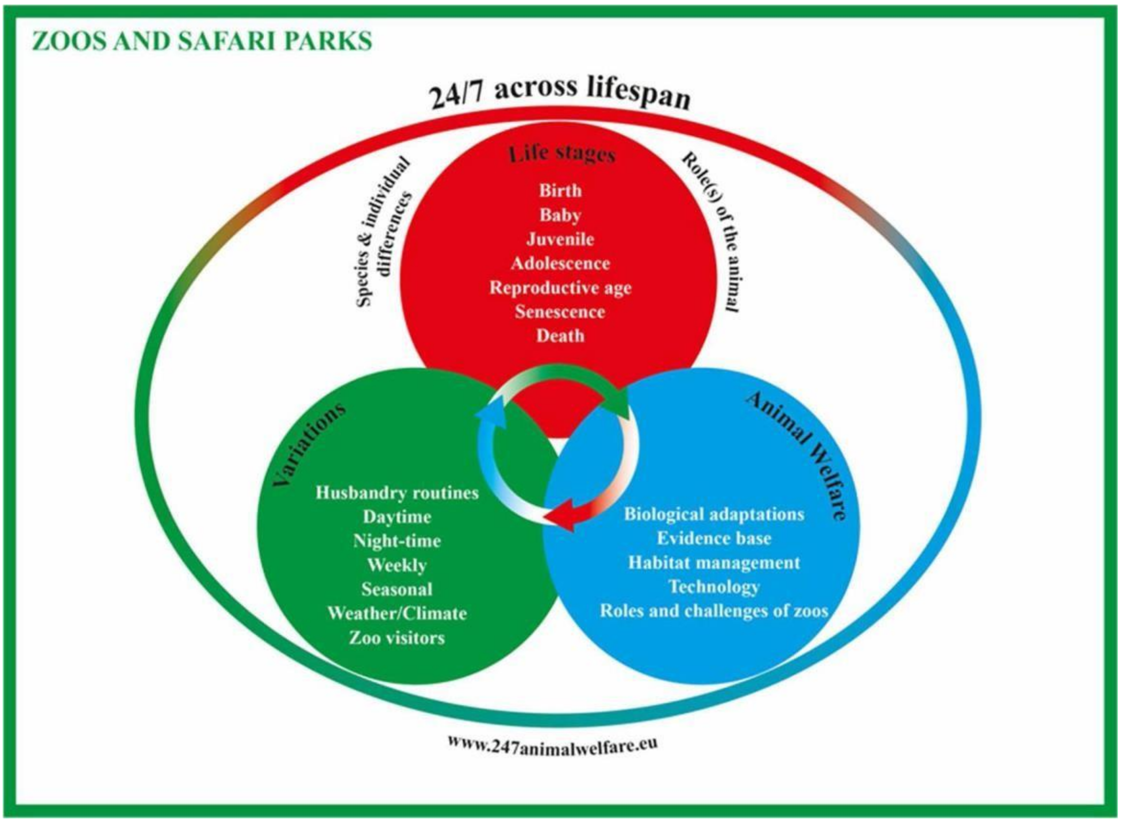


Figure 13: Schematic overview of 24/7 across lifetime welfare in zoo animals [Brando & Buchanan-Smith, 2017].

2.1. Enclosure

Figure 14: Well planted, netted outside enclosure [Cologne Zoo – Jeroen Stevens].

Important general remark: Zoos planning to reconstruct their bonobo enclosures or build new enclosures for bonobos are expected to contact the species coordinator for approval as early as possible. Not complying with this will affect transfer recommendations.

It is recommended that new holders should build for a minimum of ten adult bonobos.

Sufficient space and environmental complexity should be provided to:

- **House a multi-male, multi-female breeding group. Male offspring will likely be kept with their mothers on a long-term basis, creating the need for growing space.**
- **Promote the expression of species-appropriate locomotor, social, foraging, play, mating, parenting, exploratory, and display behaviours.**
- **Allow individuals to retreat from other bonobos and visitors.**
- **Allow and actively support the spontaneous formation of subgroups (fission-fusion behaviour) and when necessary allow for temporary formation and separation of subgroups for management reasons, such as medical, social or reproductive reasons ("managed fission fusion").**

For all enclosures, the **three most important dimensions** to promote both physiological and psychological well-being are: 1) environmental complexity; 2) environmental control; 3) enclosure size. **Environmental complexity** refers to the overall variation and changeability in the environment [Coe et al., 2001; Fulk & Garland, 1992]. Designing features that mimic the complexity and variety of experiences that wild apes have will greatly aid the promotion of species-appropriate behaviors and development [Fulk and Garland 1992]. **Control over the environment**, i.e. having the opportunity to make choices has been shown to greatly enhance psychological well-being in zoo-housed primates [e.g. Kurtyczs et al., 2014; Videan et al., 2005]. In practice, it may be difficult to give zoo housed apes much control, as they live very much in a human controlled environment. Therefore, we should strive to allow them maximum choice within the boundaries set by the zoo environment, for example by giving them the choice between in- and outside enclosures (but see restrictions below); the choice whom to interact with and whom to avoid (including conspecifics, keepers and zoo visitors); the choice to occupy or use resources within the enclosure etc.

As with other apes, the strength, intelligence, behaviour and social complexity of bonobos present unique requirements for designing enclosures that promote high quality care and high quality of life [Coe et al., 2001]. Bonobos may utilize new facilities in unexpected ways and substantial modifications may be required after opening. Experience shows that **unpredicted outcomes** are in fact to be expected.

In the temperate European climate, both an indoor and an outdoor enclosure should be provided. In warmer areas a sufficient indoor area is needed, to provide shelter and shade and to allow splitting and regrouping of animals when necessary. Besides staff facilities such as food preparation areas, storage for cleaning material, storage for enrichment etc., bonobo holding facilities should include: 1) at least one indoor enclosure, visible to the public (sometimes referred to as “habitat” or “on exhibit enclosure”); 2) several indoor holding enclosures (sometimes referred to as “off-exhibit enclosures”); 3) at least one outdoor enclosure. I describe each of these facilities below.

2.1.1. Indoor enclosures

The indoor enclosure(s) **function(s)** to keep and display the group of bonobos during the day (especially when weather conditions, or health issues don’t allow the bonobos access to the outdoor enclosure), but also to keep them during the night. Separate sleeping dens are not required for every individual. Occasionally some individuals may prefer to sleep on their own or only with certain conspecifics, but in general the group can sleep together. The indoor enclosure on its own, without the outdoor enclosure(s) should provide sufficient space and environmental complexity to keep a social group of bonobos healthy and happy.

Given the species’ arboreal lifestyle in the wild, and their capacity to jump high and far, so-called **‘open top’ indoor enclosures are not recommended**, because enclosures that are covered by a roof or a net provide much more possibilities to create an effective three-dimensional environment for the bonobos (Figure 14). In case sufficient space is present to allow for an ‘open top’ indoor enclosure and still allow bonobos a three-dimensional environment, wet or dry moats can be used (see section 2.1.4).

An **indoor enclosure consisting of several rooms** is preferred above one single larger volume, and it is recommended to build several indoor rooms that are interconnected in such a way that one or more circuits are created (see below and Figure 15). (Off-exhibit) Holding areas can also be made accessible to bonobos during the day. Ideally, at least one off-exhibit room should be available to the bonobos at all times, so that bonobos can retreat from visitors, especially if there is evidence that animals are disturbed by the public [Van Puijenbroeck & De Bois, 1997]. Rooms can be connected through doors, hallways or chutes/tunnels (see below). This design prevents individuals that may be attacked from being trapped in dead-ends. It also gives the individual bonobos a high degree of control over their level of contact with other group members, which reduces social stress and stimulates the species natural fission-fusion dynamics, as well as optimises welfare (see section 2.0). This will also create flexibility to combine rooms to create large areas, or to split them up to allow formation of temporary subgroups when required for the purpose of breeding or social management (see section 2.3.1. Managed fission-fusion). Each of the rooms should have adequate height, light, temperature and humidity conditions (see 2.1.7. Environment), and care should be taken to maintain these parameters also when the doors are closed to divide the enclosure to manage subgroups. To increase animal welfare and provide more choice to the animals, rooms can vary in some parameters, within the required boundaries, but it should be avoided that “best spots” are monopolised by dominant individuals.

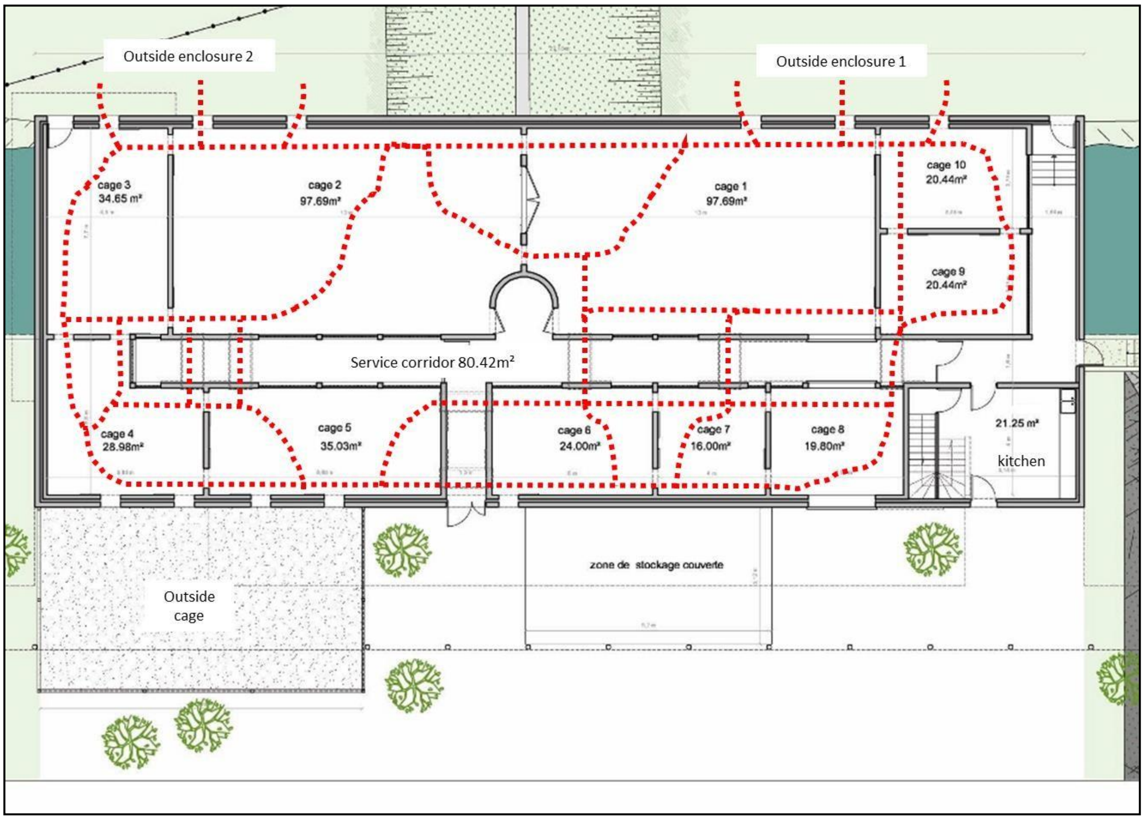


Figure 15: Ground plan of the inside enclosures at La Vallée des Singes, Romagne. Two large rooms (cage 1 and cage 2) are visible to the public from the first floor; the other eight smaller rooms are holding enclosures and are not visible to the public. Five overhead tunnels connect cage 1 and cage 2 with cages 4-8. The red lines indicate potential routes for the bonobos in the enclosure.

A **minimum height** of 3.5 metres is recommended for all indoor enclosures (except for some holding/quarantine enclosures for sedation, recovery, or treatment of sick animals, see below). This distance allows a climbing bonobo to stay out of reach of adversaries on ground level, e.g. in case of conflict. Because of the bonobos' arboreal nature, it is recommended to have in each indoor enclosure at least one room of five to ten metres high, where climbing structures and ropes allow the bonobos a high degree of arboreal locomotion. In all rooms, every effort should be made to stimulate the bonobos to use all three dimensions of their enclosure, by adding climbing structures, resting platforms, etc.. This also implies that keepers should have safe access to all three dimensions too, to allow hygienic cleaning of areas that the bonobos use, and to be able to change enrichment devices, fixing ropes etc..

To avoid animals being trapped or cornered, each room that the animals have permanent access to, should have **more than one entrance/exit**. Adjacent rooms that are permanently used should be connected by two sliding doors that are two or three metres apart, to allow lower-ranking individuals to enter or exit an enclosure if one door is being occupied by a more dominant individual. It is recommended to avoid narrow corners of less than 90°, as this can lead to problems when an animal gets trapped when it is chased by group members during conflicts.

Each enclosure (ideally each room) should **be easily accessible to keepers from keeper's areas**. Access doors should be wide enough to allow for comfortable passage with a wheelbarrow and high enough for any person to pass upright. In practice 1.20 metres wide and 2.20 metres high will be more than sufficient. In order to replace biofloor soil, exhibit furniture or technical service equipment, additional service doors should have larger dimensions with a recommended width of at least three meters. Doors should be locked in at least two, preferably three different heights; ideally doors should open into the enclosure and be self-locking (slam lock). It is recommended that keepers have good visibility on each of the rooms, and can directly access bonobos in each room when necessary. Preferably it should be possible to at least see, but also reach (e.g. with blowpipe) all corners of the inside enclosure from the keepers' area, for example if animals have to be sedated in case of an emergency. This is often difficult, as enclosures should also be complex, but can be achieved by having multiple access points to each room. Mesh is recommended to separate keepers from bonobos (see section 2.1.4. Enclosure boundaries), because it allows for good visual access. At the same time, it is recommended to include solid barriers between keepers and bonobos, to reduce noise levels. This can be achieved by creating double doors, where a solid door can be closed when access is not needed, and a mesh door that is locked as long as the bonobos are inside. When keepers need access to the bonobos, the solid door can be opened, but it can remain closed when no contact is needed. This also prevents bonobos of becoming "obsessed" with what is happening in the keepers' area. Examples of alternatives with partitioned doors can be found in the Figure 16 a-c.

Figure 16: Examples of "double doors" where visibility is guaranteed, but noise levels can be reduced (a: Leipzig Zoo – Jeroen Stevens; b: Frankfurt Zoo – Jeroen Stevens, c: La Vallée des Singes – Jeroen Stevens).

Because all three dimensions should be available to the bonobos, keepers should also be able to reach the higher parts of the enclosure and even ceilings should be easy to clean. A wire mesh ceiling is considered practical, as it offers many opportunities for attaching ropes, hammocks, nets, and for distributing food; it can also keep technical installations out of reach of the bonobos (remember that they can use sticks to reach or poke).

Depending on the circumstances and background of the individuals, **visual access to other bonobos** can be perceived as enriching or stressful, as useful or as undesirable. It is recommended to use solid walls in between most of the rooms that house bonobos, as bonobos may stir each other up, display continuously towards each other etcetera when they are in adjacent enclosures separated by glass or mesh wire. This is known as the "neighbour effect" in chimpanzees, and although there is no empirical evidence available, anecdotal evidence does suggest in some situations this effect also affects bonobos. In some areas, visual access through mesh partition walls or doors can be useful, for example to introduce new animals to each other, or to provide separated individuals with some visual contact with the group. When mesh wire is used between adjacent rooms, this should be double layered, to prevent for example copulations through the mesh in case the group has to be separated for breeding management. The recommended distance between two layers of mesh to prevent mating through the mesh is then minimum 14 centimetres (see Figure 17: Double mesh separating adjacent bonobo enclosures to prevent through the wire copulations [Frankfurt Zoo – Jeroen Stevens].).

Figure 17: Double mesh separating adjacent bonobo enclosures to prevent through the wire copulations [Frankfurt Zoo – Jeroen Stevens].

Glass barriers are recommended to **separate public from apes** in indoor enclosures, as they allow optimal vision, but avoid direct contacts and the risks of public feeding, disease transmission, etc. (see section 2.1.4.). When wire mesh is used to separate the bonobos from the public, the distance between apes and public should be so large enough to prevent direct contact (at least five metres if no other barriers are provided; 1.5 metres if additional barriers such as plants prevent the public to approach closer or touch the apes). Also, it should be taken into account that bonobos have been known to spit, throw faeces or even urinate on public through mesh fences. The noise produced by public on busy days can also cause excitement in the bonobos. Vice versa, the noise of bonobos screaming inside buildings can also be quite disturbing for visitors. On the other hand, mesh barriers allow the public to experience (smell, hear, etc) bonobos in a different way.

2.1.2. Holding enclosures / quarantine enclosures

Holding enclosures function to keep the bonobos while the main enclosure is being cleaned, or when bonobos need temporary separation, or for training sessions, veterinary treatment etc.. Bonobos should not be kept permanently in holding enclosures. Rather, movement through all rooms available provides an enriching experience for all individuals. In theory, holding enclosures do not have to be off-exhibit, if animals can be shifted between larger indoor enclosures. However, most institutions prefer to have at least some “off-exhibit” holding enclosures available, which are not visible to the public. The number of holding enclosures can vary depending on the total intended group size of the building. As mentioned before, ideally there should always be at least one room available, to allow the bonobos to retreat from visitors, especially if there is evidence that the presence of visitors has a negative influence on the behaviour of the individuals. While the dimensions of holding areas are usually smaller than those of exhibit rooms, they should have the same minimum height (3.5 metres), light, temperature and humidity conditions, and care should be undertaken to maintain these parameters, also when the doors are closed to divide the enclosure to manage subgroups differently. Each holding room should also have a source of clean water for drinking, accessible to the bonobos at all times.

Quarantine enclosures function to separate individuals from the group when they are seriously ill, or when new individuals arrive. Bonobo exhibit facilities should be complex/flexible enough, so that isolation of members of an existing group can easily be done within the exhibit facility and adjacent to the rest of the bonobo group. It is recommended that no bonobo should be individually housed for any longer period, even in case of illness or injury. Under most circumstances, it is recommended that one or more familiar companion animals would be housed with the individual that is being treated for minor medical issues. Ideally, at least two connected off-exhibit rooms that can be used for isolation/quarantine should be present in the same building as the indoor enclosure, so that ill individuals can be separated but still have at least auditory or visual (through windows!) contact with group members, in case they have to be separated. Alternatively, two individuals can be quarantined together.

A **quarantine enclosure** should ideally be composed of at least two rooms of each minimum 25 cubic metres, totalling for 50m^3 if the two units are combined, which should be sufficient in case animals have to be isolated for more than a few weeks. A set-up with two rooms allows bonobos in quarantine to be shifted in one of these two, while the other is being cleaned. In quarantine enclosures, the substrate, furniture and all walls should be of a hard, non-porous and easy to clean surface. At least one elevated resting platform per individual should be present, nesting material should be provided at all times, and a permanent source of drinking water should be always available in each room. It should be possible to turn off the water from outside the enclosure, in case water access has to be restricted for medical reasons.

It should be possible to raise the **temperature** in the quarantine area to 24° C or more. The quarantine area should have an entrance that enables to safely release a bonobo from a transport crate directly into the quarantine enclosure, without tranquilisation. This will also enable crate training, thereby providing some opportunity that the move down to the exhibit facility after the quarantine is finished will not require an additional immobilization. Monitoring and treatment/ immobilization of the isolated animal should be possible at all times. A camera system to record behaviour in the quarantine enclosures is useful. Dead corners and blind spots should be avoided, so that animals can reliably be darted when needed. The height of quarantine enclosures should ideally be no more than two metres, to prevent the bonobo from falling too deep when darted, or when recovering from anaesthesia. Ideally, the unit should be interconnected with the indoor enclosure or holding enclosures, so that the animal(s) can be shifted without sedation. Care should be undertaken to prevent direct contact with the group through slides, or to prevent contamination through urine etc. Drainage and ventilation systems for the quarantine enclosures should be designed in such a way that contamination of other indoor areas is prevented. Ideally a separate air circulation system should be provided.

2.1.3. Outdoor enclosures

Outdoor enclosures are open to ambient weather conditions and are often the primary daytime residence of bonobos. They give bonobos a wider range of environmental stimuli, direct access to sunlight, wind, interact with native wildlife, etc. Each new bonobo facility should contain at least one outdoor enclosure. Ideally, two outdoor enclosures are available, so that when subgroups have to be formed for management reasons, each group can have access to an outdoor enclosure. If this is not possible, alternative solutions can include a) rotation of subgroups on the same outdoor enclosure, by providing access to the outdoor enclosure via several routes; b) providing an indoor enclosure where the roof can be opened to give at least access to direct sunlight, and bonobos are prevented to escape by adding a mesh wire. An outdoor enclosure should be designed to maximize the time the bonobos can spend outside. For outside enclosures, zoos have used traditional cages, more modern wire mesh/netted cages, islands with dry moats or islands with wet moats (Figure 18).

Figure 18: Examples of different designs of outside enclosures for bonobo (a: dry moated enclosure (San Diego Safari – Jeroen Stevens); b) water moated enclosure (Apenheul – Jeroen Stevens); c) netted enclosure (Cologne Zoo – Jeroen Stevens).

Similar to guidelines for the indoor enclosures, **space and complexity** are the major dimensions for outdoor enclosures. Complexity can be provided by offering variation in the environment (topography, trees, shade, sunny areas, climbing structures, termite mounds, tall grass, bare areas, swampy areas, streams, pools, large rocks, smooth areas, rough areas, and various sights and sounds – see also Section 2.1.6. Furnishing and Maintenance). Topography of outdoor enclosures should be irregular to provide variability as well as hiding places. Small hillocks, with or without rock outcroppings, can provide bonobos with places to observe other bonobos or visitors, but can also serve as visual cover. Differing elevations is important, but it is not good to have an entire enclosure on a slope, because bonobos prefer to sit or to sleep on a flat area and will not like an enclosed space that is too steeply sloped. Sufficient shelter from wind, sun or rain should be provided. Especially in colder temperate regions, outdoor enclosures should have a southern orientation to maximise available sunlight. Bonobos prefer warm, shady areas with no wind, but in summer avoid sitting in direct sunlight. Microclimates can be created by providing trees, shrubs, shelters, pools or rivers etc. Further complexity can be added by appropriate furnishing (see section 2.1.6). It is necessary to provide ample climbing opportunities for bonobos to allow for arboreal locomotion.

Direct and easy access to the outdoor from within the inside enclosure is recommended for the bonobos. More than one entrance should connect indoor and outdoor enclosures, so that dominant individuals cannot block the way for lower ranking group members. If multiple inside enclosures are provided (as is recommended), it is a good idea to have several of them connect to the outdoor enclosure(s), which facilitates access to the outdoor enclosure when subgroups have to be managed.

As with indoor enclosures, it is recommended to provide convenient, safe **access to the outside enclosure for keepers**, designed to allow free movement of the equipment needed in daily care, and a wide service gate that accommodates construction equipment, or the possibility to build temporary bridges that cross water moats. Some institutions have used a double door (mesh door in combination with solid door) that gives direct access to the island from within the keeper area, so that keepers can get close contact to bonobos on the island, if necessary.

Outdoor exhibits should restrict **public viewing** to one side of the enclosure or at distinct, discrete sites, rather than along the entire perimeter. Preferably, the public should be at grade with the bonobos, and should not look down on them, and the bonobos should have access to climbing opportunities that will place them well above head level of the public viewing the exhibit. With appropriately furnished exhibits, bonobos seem to accept the activities, sounds and smells of public in zoos, and even may prefer to be near public viewing areas, so long as they have sufficient control to remove themselves from these areas as well.

2.1.4. Enclosure boundaries

Several types of enclosure boundaries can be used, each with certain characteristics, advantages and disadvantages – but these can also differ, depending on physical parameters of each institution (e.g. space, outside climate, budget, etc.).

Walls

a **s** have the advantage that they take up little horizontal space and can be less costly than glass walls or moats. They can be made out of a variety or combination of materials such as concrete, metal or glass (see below and Figure 19). The disadvantage is that they can be visually disturbing in naturalistic surroundings, which is usually disguised with geologic textures (rockwork), painting techniques, or protected planting, thereby increasing their cost. The distance from climbing structures to the walls should be at least four metres, to prevent leaping out, which can seriously reduce the vertical climbing space available for the animals. Vertical climbing space is important for bonobos, and for smaller walled enclosures, it is therefore better to make a wire-mesh roof, which increases access to vertical space without the danger of escape. When no roof is provided, the minimum height of walls should be five metres. The goal, obviously, is to create non-climbable walls. The texture must be relatively smooth to prevent foot or finger holds. Doors with their hinges, or nuts and bolts, which are used for attaching constructive elements to the walls, may be critical points. Overhangs may have to be added to prevent scaling. The layout of the walls should avoid perpendicular or acute angles to adjoining walls to prevent "chimneying" out, or they should be capped at these dangerous intersections. Overhangs may be provided to prevent climbing (Figure 19b). A completely enclosed walled space can be very stressful for great apes, as they can often hear noises from behind the walls but cannot see anything that is happening. In such enclosures, each wall should have several windows. An additional disadvantage of the completely enclosed wall is that wind cannot cool the enclosure when temperatures are very high [Becker et al., 2017].

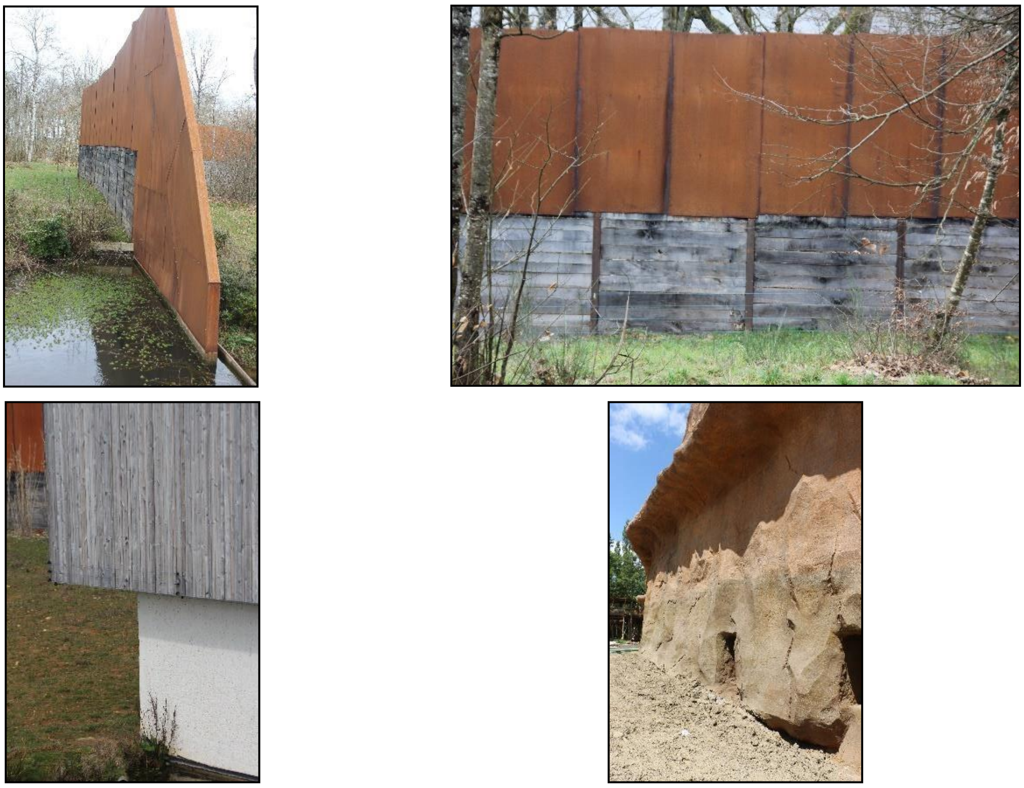


Figure 19; Examples of designs for enclosure walls that have proven to be effective a-b: Wall covered with metal sheet, note that in front of the base of the wall electric fences and planting have been used (La Vallée des Singes - Jeroen Stevens); c: overhang, with additional electric fence as secondary barrier (La Vallée des Singes – Jeroen Stevens); d: rockwork wall with overhang (Zoo Planckendael – Jeroen Stevens).

Dry moats

Dry moats exclude the risk of drowning, and still can give visitors an unobstructed view on the bonobo exhibit, but at the moment they are not used by any facility in the EEP. “U-shaped” dry moats should not be used for apes (Figure 20), as they risk falling in the moat [Becker et al., 2017; de Jongh et al., 2017]. Rather, dry moats should be V-shaped (Figure 20), with a gentle slope descending from the apes’ side and a vertical wall on the side of the visitors meeting the same criteria (distance from climbing structures, minimum height) as in the cases of the other walls (see paragraph above). The disadvantage of these V shaped dry moats can be that bonobos are invisible to the public when they sit close to the wall (e.g. to look up shade). It is estimated that chimpanzees can jump six meters wide but can increase this distance by adding a running distance [Coe et al., 2001]. Comparable data for bonobos are not available, but it is recommended to keep a seven metre horizontal distance. Bonobos can also jump high, and can use sticks to increase their reach. The minimum height for barriers should be five metres. This is assuming that the vertical barrier is smooth and without vegetation, and that no tools or moveable objects are available to the bonobos that might be used to decrease the effective height of a vertical barrier. Any plant material that grows over the exhibit barrier can reduce the distance and, therefore, should be pruned right away. The specific measurements necessary for adequate containment may vary from institution to institution [Van Puijenbroeck & De Bois, 1997].

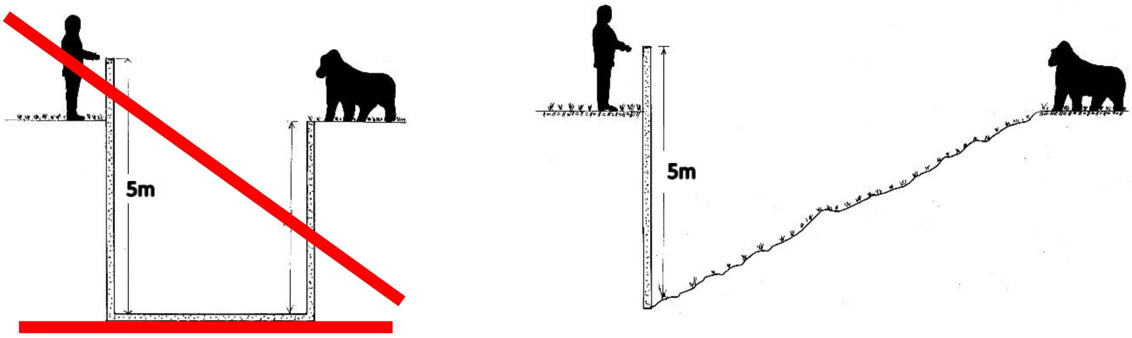


Figure 20: Schematic view of "U-shaped" moats which are NOT recommended, vs. "V-shaped" dry moats [de Jongh et al., 2006].

Wet moats

Wet moats are aesthetically pleasing and can look natural, but they put a large distance between public and bonobos (Figure 21). Because they may take up space that would otherwise be available for the bonobos, wet moats should only be considered when adequate space is available. Given the estimated horizontal jumping distance [based on chimpanzee records: Coe et al., 2001] the moats are recommended to be seven metres wide. A minimum depth of 150 cm is recommended. When designing water moats, care should be taken to avoid the risks of drowning. Although bonobos seem less afraid of water than chimpanzees, and have been kept on islands in EAZA facilities for over two decades, some incidences of drowning have occurred (although much more rarely than in other ape species). A wet moat should contain a shallow "swamp" part on the side of the bonobos, a gentle slope towards the deeper end at the side of the visitors, and opportunities for the bonobos to exit the moat must be provided (Figure 21). A slope of maximum 25 cm per meter has been recommended for other apes, and works for bonobos. The swamp area forces the bonobos to slow down so that they cannot run into the moat at full speed. Some zoos have used chain link nets or ropes on the slope and/or the water edge, which allows bonobos to clamber out of the water if they slip and fall in the water. Electric wire as a secondary barrier has been used in all EAZA institutes that keep bonobos on islands, and this is recommended. See notes below on the appropriate use of electric fences. The place of the electric wire varies and can be on the side of the bonobos on the island, in the middle of the moat, or on the far end of the moat from the bonobos (the visitors side). The disadvantage of having the electricity on the animals' side of the moat, is that if an animal jumps or falls over the wire into the moat, it may drown as it will be afraid to pass the wire to go back [de Jongh et al., 2006].

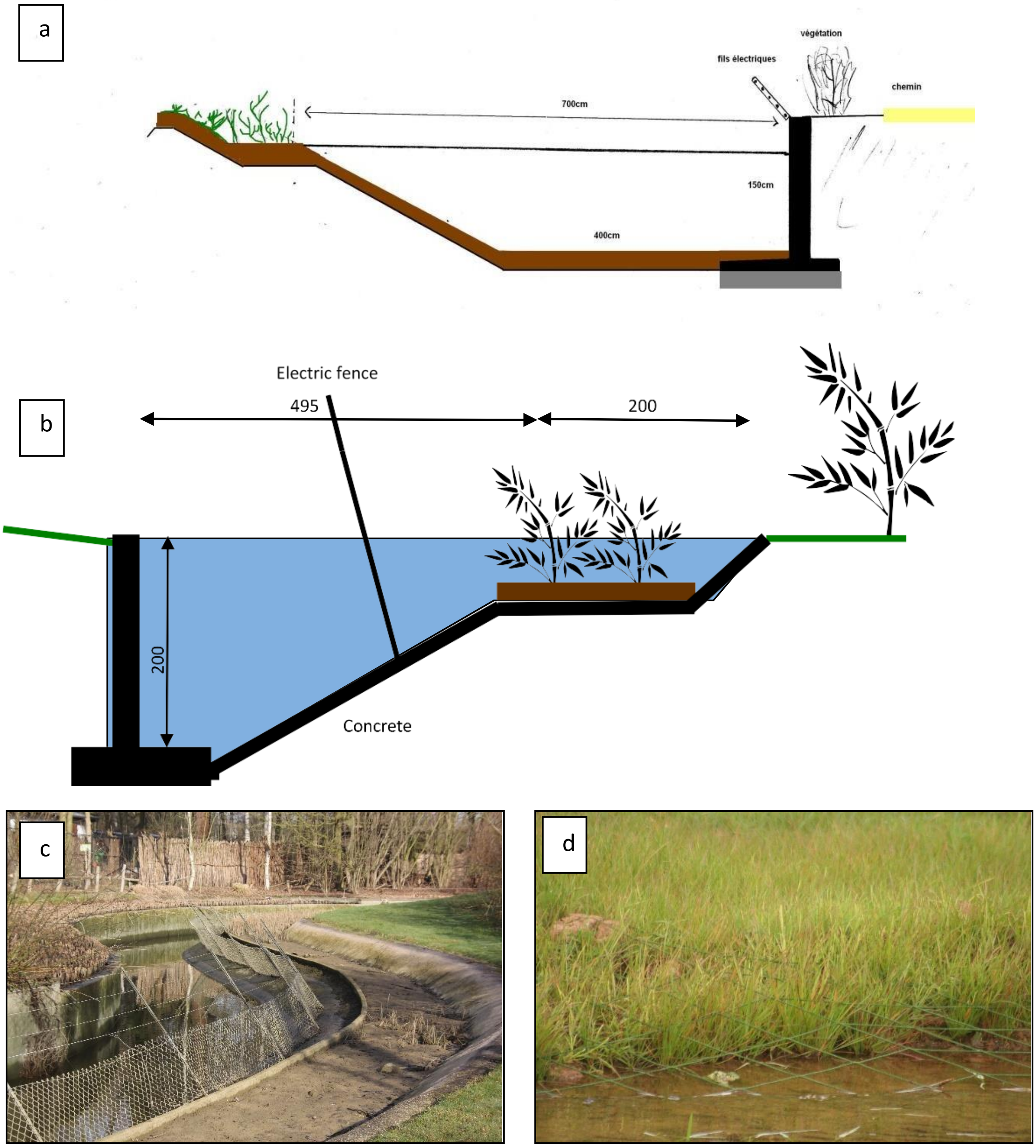


Figure 21: Various design of moats in bonobo enclosures. a: schematic view of the moat design in La Vallée des Singes; b: schematic design in Planckendael; c: Partially drained moat in Zoo Planckendael (Jeroen Stevens); d: nets used to prevent drowing (La Valée des Singes – Jeroen Stevens).

Glass walls and windows

Glass walls, panels or windows allow a clear and close-up view for visitors without the risks of direct physical contact, disease transmission or throwing food/objects in or out the enclosure; but the disadvantage is that they are expensive, and require regular cleaning. For glass panel strength, the bonobos physical power should be considered. In other ape species it has been estimated that on average **42 mm thickness** of tempered, laminated glass seems reliable. When broken, the break generally stays limited to a single layer, and the connecting foil keeps the glass in place [Becker et al., 2017; de Jongh et al., 2017]. This also is sufficient for bonobos. Because any thickness of glass is potentially breakable, consideration must be given to ease of replacement. Acrylic panels are less breakable, but scratch easily, therefore they are not the best option. Static calculations must always be done by glass specialists, based on the size of the openings and assumed loads [Becker et al., 2017].

When placing windows high in the enclosure, it may be important to provide safe ways for keepers to clean these. To avoid unwanted reflection, it can be useful to tilt the glass sheets a little bit towards the animals or to put a shading overhang above the visitors or to plant thick vegetation behind the public, which eliminates not only the reflection, but provides a more naturalistic environment as well. Another slight disadvantage of glass windows in indoor enclosures can be condensation on the side of the bonobos, given the required high humidity in the enclosure. Such condensation typically arises when temperatures in the enclosure are higher than on the other side of the glass. Some institutions have used close-to-invisible electric wires inside the glass to heat the windows 1° C above the temperature in the animal enclosure to prevent windows in the inside enclosure from steaming up [e.g., Jens, 1998], but raising temperatures in the area on the other side of the glass can also help. The use of glass walls should be limited to one or two sides of the enclosure, so the bonobos can have some areas where they can be out of the view of the public. When using glass windows outside, the collision of birds with the glass need to be considered carefully.

Fences: Mesh and bars

Several EEP institutes have created large netted outside enclosures for bonobos, which provide them with plenty of opportunities to climb, brachiate and make nests, up to 16 metres high (see Figure 22). The distance from visitors to the wire mesh should be large enough to prevent direct physical contact or feeding, and care should be undertaken with placing the wire mesh because bonobos have been known to spit, throw faeces or urinate on bypassing visitors. Several types of mesh are available [after de Jongh et al., 2006]:

Figure 22: Example of mesh netting that can be used for climbing and brachiating by bonobos [Cologne Zoo – Jeroen Stevens].

- **Welded steel mesh** (Figure 23a) : Mesh width ca 50 mm x 50-100 mm, steel thickness 6- 10 mm, welded in a frame of rectangular steel tubes. This has the disadvantage that the welds can break under the impact from heavy blows. A wire mesh of 50 x 50 mm is considered as practical as it allows good visual access, but prevents adult bonobos from reaching through. Care should still be undertaken as infants may reach their hand through, and adults can also still scratch and or use sticks and other objects to poke through at a close distance;
- **Steel crimped mesh**: Difficult to obtain in a sufficiently heavy quality (6 mm), but is a very suitable product. Recommended dimensions for this type of mesh: 6 x 50 x 50 mm. 5 x 50 x 50 mm is also suitable, but requires a denser support frame;
- **Wave mesh** (Figure 23b): Similar to steel crimped mesh. The waved strands could with sufficient force be more easily stretched, and the mesh deformed. The space in between the steel profiles can be filled with epoxy to prevent dirt and debris from collecting there;
- **Woven mesh** from stainless steel cables (Figure 23c): An expensive but visually pleasing material. Available in two types, one in which the cables are attached with soft metal rings that are clamped; and one in which the cables are interwoven at the attachment points (see pictures). Unfortunately, a few individual great apes from several institutions have so far developed skills to destroy this type of mesh locally and escape. To my knowledge this has never happened with bonobos so far. It is important to check the mesh routinely, keep an eye on what bonobos are doing with it, and interfere before the individual has improved its skills and passed this on to exhibit mates;
- **Steel bars** (Figure 23d): This has the advantage that steel bars are very strong when set in a heavy framework. Recommended dimensions for orangutans [Becker et al., 2017] would certainly work for bonobos, too: Solid steel bars 15 – 16 mm in diameter, centre distance 30 - 56 mm, distance between transversal bars (flattened steel or rectangular tubes) 440 – 700 mm.The disadvantages are that bars may hinder the visibility of animals inside the enclosure, especially under certain angles; and when bonobos put sticks through the bars they can swing these up and down in large moves; also bonobos with slender arms and wrists can sometimes reach through far, which can be dangerous for keepers. It is better not to use this type for this reason;

- **Chain link mesh** (Figure 23e): Generally not recommended for great apes, because it is less resistant to the destructive skills of apes [de Jongh et al., 2017; Becker et al., 2017]. For bonobos some institutions have used it, but would not recommend because it needs frequent repairing and fixing and constant monitoring.

Figure 23: Types of mesh used for bonobo enclosures. a: Welded mesh (La Vallée des Singes – Jeroen Stevens); b: Wave mesh (Cincinnati Zoo – Jeroen Stevens); c: Woven mesh with metal clips (Cologne Zoo – Jeroen Stevens); d: Steel bars NOT RECOMMENDED- showing how individuals can reach through (Planckendael – Jeroen Stevens); e: Chain-link mesh – NOT RECOMMENDED (Milwaukee Zoo – Jeroen Stevens).

Electric fences

Electric or "hot" wires should never be used as primary barriers, as there are several examples of bonobos that have learned to cross electric fences, especially during serious conflicts and fear. As secondary barrier (in combination with walls of adequate height, or with water moats) or to protect vegetation inside the outside enclosures, electric wires and/or so-called "hot grass" or "hot lianas" have been used successfully to deter bonobos.

In some institutions, newly arrived bonobos are trained to experience electric wire that is marked with plastic ribbons before they have access to outside enclosures. When these new arrivals then are released in the outside enclosure, all electric wires are marked with the same plastic ribbons to indicate to the bonobos were the boundaries of their enclosure are.

Doors

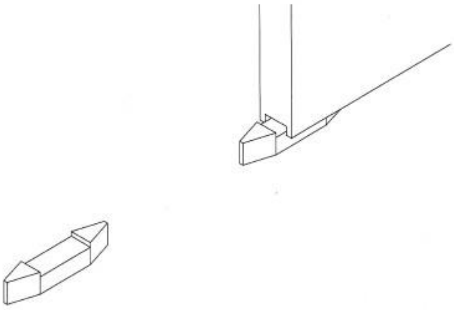
All doors connecting two animal enclosures should be large enough to allow easy access for a bonobo to walk through on all fours, including females that have infants “jockeying” on their back. Often doors of 80 cm wide and 100 cm high are used. Doors can be either on ground level, or raised above the ground. The latter helps to prevent the blocking of doors by bedding material or bark from biofloors, but may also constrain easy passing for bonobos, especially older or handicapped individuals. In the latter case, ladders or additional support should be provided.

Doors that slide down in a vertical plane (“guillotine” doors – Figure 24a) are commonly used, but may have the disadvantage that bonobos will try harder to slide under them head first. Doors that slide sideways in a horizontal plane (Figure 24b), seem to avoid this problem of ‘diving under’ them, but usually allow bonobos to sit in the doorway more easily. They should preferentially move away from the keeper when being opened. To connect enclosures that are situated on top of each other, horizontal sliding door in the floor/ceiling have been used successfully in institutions housing bonobos [e.g. Jens, 1998 - Figure 24c].

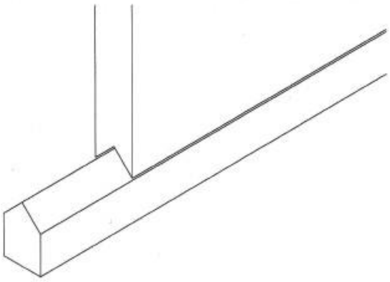
Figure 24: Different sliding doors in bonobo exhibits. a:door that slides in a vertical plain (guillotine door) (Milwaukee Zoo - Jeroen Stevens): b: door sliding in a horizontal plane (Cologne Zoo - Jeroen Stevens); c: sliding door in the ceiling connecting enclosures that are on top of each other (Leipzig Zoo – Jeroen Stevens).

All doors between enclosures should have an extra **security mechanism** to prevent the bonobos from opening the doors themselves. It should be kept in mind that bonobos might move the door with great force while a keeper is opening or closing the door. In some designs, parts of the mechanism might hit the keepers and injure them. In particular, doors sliding horizontally include this risk. They should preferably move away from the keeper when being opened. Ideally a door should have a mechanism that allows it to be fixed at intervals. When bonobos then block the doors, they cannot throw it back or break it, and keepers can give them a time out more easily to avoid “power struggles” over who controls the door. Several mechanisms exist (see

Figure 25).

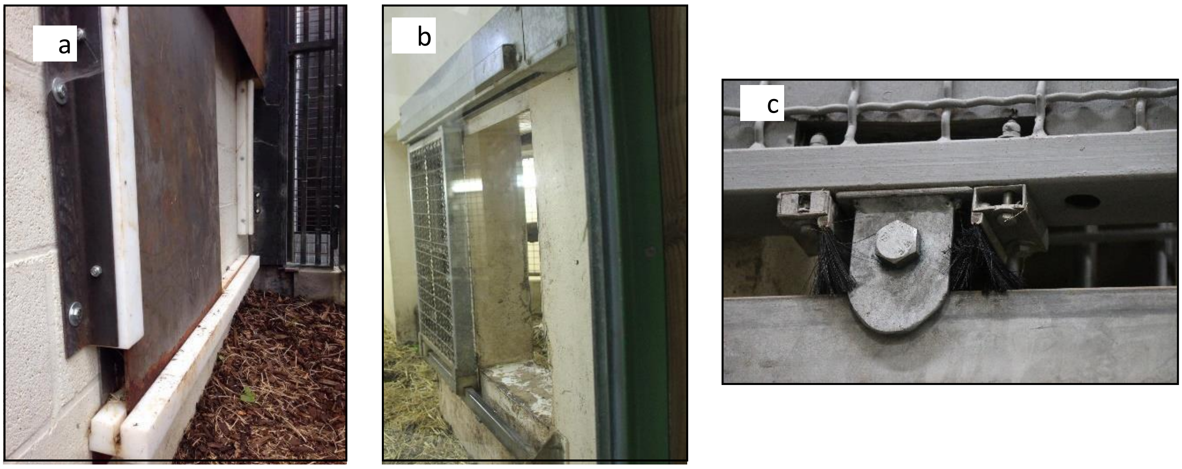


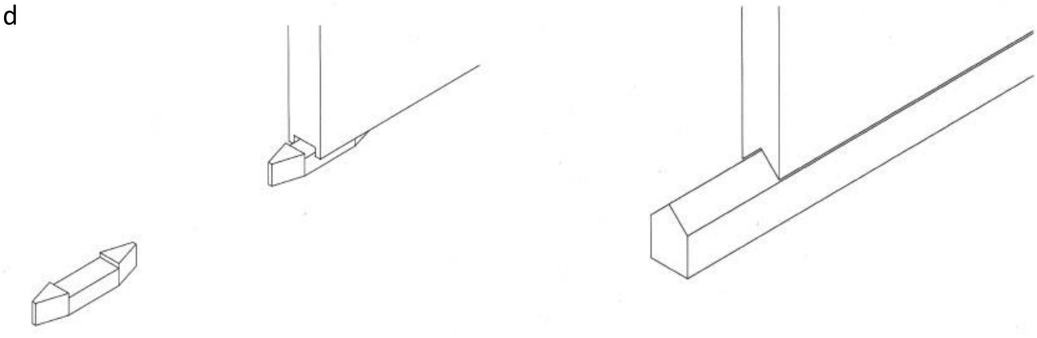
Sliding door with torpedo guides



Sliding door on a ridge

Figure 25: Mechanisms to prevent bonobos from pushing slides back open. a: Horizontal, grated bar with pins and holes to block slides (Columbus Zoo - Jeroen Stevens); b: wheel and chain principle with stick and hole mechanism to block the doors (Columbus Zoo – Jeroen Stevens); c: the horizontal bars can be made with a hinge so that they hang vertically when the slides are not used (Leipzig Zoo – Jeroen Stevens).





Sliding door with torpedo guides

Sliding door on a ridge

Figure 26: Different mechanisms to prevent bedding material blocking the doors. A: thin metal slides in a plastic guiding rail (Zoo Planckendael – Jeroen Stevens); b: slides hanging from the top rail and guided by a bottom rail (gorilla enclosure La Vallée des Singes – Jeroen Stevens); c: brushes preventing dirt to enter the wheel (chimpanzee enclosure La Vallée des Singes – Jeroen Stevens; d: sliding door with torpedo guides and sliding door on a ridge [de Jongh et al., 2006].

One disadvantage of doors sliding in the horizontal plane can be the accumulation of woodwool, biofloor in railings; several mechanisms have been used, like thin slides (Figure 26a), slides on railings or ridges, sometimes with a small broom attached (Figure 26b,c) and sliding doors with so-called torpedo guides (Figure 26 b-d).

Keepers must always have a **complete view of the full opening** of the door when opening or closing it. Before keepers open a door that gives access to some service area adjoining bonobo enclosures, they should have the means to visually check through a small window or mesh that this service area is safe to enter.

Cables, which are often used for vertically moving sliding doors, should be well protected. The condition of the cables should be checked frequently, similarly with other moving parts and attachments like bolts and nuts.

Hydraulic, pneumatic or electric doors have been used successfully in bonobo enclosures. The design of the doors should be such that the movement of the door stops instantly when the keeper lets go of the control button. It is also necessary to provide a manual override of the control mechanism, so that the doors can be used and locked even when the system fails. The speed of doors is also critical: they should be fast enough without risking injuries to the bonobos [after Becker et al., 2017].

It is recommended to design doors that allow **conversion from solid-surface doors to mesh doors** permitting airflow and opportunity for visual and minimized physical contact to animals on both sides of doors (so called “howdy” doors). This can be accomplished with a removable plate covering the mesh and/or barred portion of the door, or it can be eliminated altogether by utilizing double doors. The latter can be accomplished by having a door with a mesh/barred opening mounted on one side of a separation wall and a solid door mounted on the other side of the separation wall. This design allows for “howdy” opportunities throughout the day at times when observations are convenient and complete separation at other times, without having to enter a cage to attach or remove a cover panel.

Doors between indoor and outdoor enclosures should contain **plastic sheets to prevent draughts**. By providing a tilted front, and flaps that are slightly larger than the entrance, a system can be devised that allows the plastic sheets to close relatively tight, and still allows the bonobos to go in and out (Figure 27a). To prevent dirt accumulating in this little “tunnel”, the floor can be angled (Figure 27b).

Figure 27: Designs for doors between indoor and outdoor enclosures. a: plastic sheet to prevent draught with system to close relatively tight (Frankfurt Zoo – Jeroen Stevens); b: Slightly angled tunnel to prevent dirt accumulating in the tunnel (La Vallée des Singes – Jeroen Stevens).

It is recommended to provide at least one door that gives out directly to a service area for arrival of new individuals. Several designs have been developed so that transport crates with new arrivals can be safely fixed to this door before releasing the animals.

(Overhead) chutes or tunnels

To connect enclosures across a keepers’ corridor, many facilities use overhead tunnels or chutes, usually made of mesh, with sliding doors are at both ends of the tunnel. These tunnels have been proven useful and are a well-liked spot for bonobos, probably because it gives them a good overview of what happens in the different enclosures as well as in the keepers' corridor. Some institutions use these tunnels as wake up areas for bonobos after sedation, or a safe location to sedate the individuals without the risk of falling down, and have provided a door in the side to put the bonobos inside the tunnel. Care should be undertaken to prevent the accumulation of dirt, woodwool, etc. inside tunnels, especially when bonobos have permanent access to these tunnels. It can be difficult for keepers if they must climb inside the tunnel to clean it out. Some institutions use solid floors in the tunnels with a drainage system, but then bedding material such as woodwool can still accumulate. Other institutions use mesh bottoms, that can be cleaned out from underneath and which also have the advantage that keepers can more easily see who is inside the tunnel from below. Of courses there is the risk of bonobos urinating inside the tunnel, so keepers should be careful when standing under it, and providing drainage pits underneath, to prevent puddles of urine forming is a good idea. A hinged plastic sheet that can be opened when necessary is used in some institutions (Figure 28b). Some institutions also provide a small door in the bottom of these tunnels to allow ultrasound examinations of bonobos lying on their belly inside the tunnel [Teare et al., 1996; Drews et al., 2010 (Figure 28c)], or have lockable doors in the sides of the tunnel so that animals can be sedated in the tunnels and can easily be moved from the outside (Figure 28d).

Figure 28: Designs for overhead tunnels in bonobos. a: Solid bottom tunnel with water drainage (Planckendael – Jeroen Stevens); b: Wire bottom tunnel with plastic sheet protection (Apenheul – Jeroen Stevens); c: Small door in tunnel bottom for ultrasound inspections (Milwaukee Zoo – Jeroen Stevens); d) Side doors to be able to remove sedated bonobos from the tunnel (Milwaukee Zoo – Jeroen Stevens).

2.1.5. Substrate

Substrate for indoor enclosures

In indoor enclosures, hard and easy-to-clean substrates such as ceramic tiles and epoxy-covered concrete are often used for hygienic and practical considerations. However, if enrichment value and comfort are taken into account, this type of substrate is not ideal for bonobos, even if nesting-material is permanently available. When used, concrete substrates should be augmented with elevated surfaces of varied textures/materials. For the purpose of easy cleaning, concrete or epoxy floors should preferably be sloped 2 to 4%. Drains should preferably be placed outside the actual enclosure and can be used as urine collector. To allow for good cleaning and disinfection, the use of special coatings should be considered, but care should be taken in making the right choice. Coatings can either make a floor too smooth, forcing the inhabitants to move about in a careful, cramped gait, or too abrasive [de Jongh et al., 2006].

Deep litter floors, sometimes also referred to as ‘biofloor’ provide a good and comfortable alternative for smooth surface floors, and have now been used for more than a decade in several institutions housing bonobos (e.g. Apenheul, Frankfurt, Leipzig, Stuttgart, Romagne, Planckendael [Bakker, 1999a,b; Jens, 1998; Holtkötter, 2007; Vermeer 2012] – Figure 29) as well as in other great ape species. Deep bedding of bark creates a comfortable floor surface for the inhabitants, and can break falls during fights or play. It helps to increase the levels of humidity in the enclosure and provides enrichment when combined with scattered food. Biofloors also improve the quality of the air by removing bad smells [de Jongh et al., 2006] and dampen loud noises and reduce echo effects. Maintenance of these substrates include watering the surface to prevent it drying out (dusting), turning over the top layer to keep it fresh, and supplementing the mulch as it gets packed down. Faeces should be pick-cleaned daily, but urine flows through to the drains beneath Usually the underlying smooth surface floor is slanted towards drainage points. On top of the floor, a drainage mat is placed, sometimes protected by mesh wire to prevent digging bonobos from tearing up the mats. Above the drainage mats a layer of 30 - 60 cm of bark is placed. More information about the use and design of biofloors can be found in Bloks [2000]. Holtkötter [2007] conducted a survey in European institutions and made the following recommendations:

- Loosening up the top layer one time per day to one time per month, for better drainage;
- Doors and sliding doors should be placed high enough above biofloor level to work properly
- Bringing in and removing biofloor substrate should be technically easy (corridors and access to enclosure for tractors, ramp, possibility to blow substrate in, etc.)
- It should be possible to remove the biofloor completely within a relatively short time in case of diseases

- A good drainage system is needed (to avoid dust, raise humidity, and control pests, you must water the biofloor regularly!)
- Biofloors can attract pest species (rodents, cockroaches, crickets and ants), so pest control methods are needed. These may include the use of predators (cats, meerkats, civets, etc. although in the case of bonobos co-housing is not recommended, so these predators can only be used when bonobos are not in the enclosure); allowing the enclosure to flood by blocking the drainage and fill the floor with a layer of water deep enough to have water standing above the biofloor level (some institutions report that mice and rats will simply climb up the fences and climbing structures to avoid drowning).

Figure 29: a) Deep litter biofloor gives bonobos the opportunity to forage longer for scattered food, including natural foraging behaviours like digging (Zoo Planckendael – Jeroen Stevens).b) Drainage mat detail (Zoo Planckendael – Jeroen

Stevens).; c) drainage mat installation before biofloor is put in (Zoo Planckendael – Jeroen Stevens).; d) fixation points for trees installed above the drainage mat (Zoo Planckendael – Jeroen Stevens).

It is recommended to keep at least some part of the enclosure (e.g. some of the holding rooms) without biofloor, and use ceramic tiles or epoxy as substrate, for collecting urine samples, isolating ill bonobos etc.

Substrate for outdoor enclosures

For outdoor enclosures, natural substrate can provide more enrichment than easy to clean hard surface floors of epoxy or ceramic tiles. Outdoor enclosures can offer a variety of natural substrates, including sand, soil, shallow water, and grass, which provides opportunities for exploration, foraging for hidden items, digging, and play behaviour.

2.1.6. Furnishing and maintenance

Every effort should be made to create a complex and stimulating environment and to encourage bonobos to use all **three dimensions of both indoor and outdoor enclosures**, by providing them with a combination of horizontal and vertical climbing opportunities, so that they can display all five types of arboreal locomotion seen in the wild (palmigrade and knuckle-walking quadrupedalism; quadrumanous climbing and scrambling; bimanual suspension; leaping and diving; bipedalism [Doran & Hunt, 1994; Susman et al., 1980;] – see paragraph 1.8.2). his can be achieved through the installation of **fixed climbing structures** such as climbing frames, horizontal platforms and nesting platforms, in combination with more **flexible items** such as ropes, cargo nets, hammocks, etc.. By providing a large number of attachment-points, such as eyehooks, on walls, ceiling and furniture, the volume and flexibility of the design can be further increased. These eyehooks can also be used to change enrichment devices regularly (see below).

All **fixed climbing structures** should be easy to maintain and clean. Sharp edges should be avoided in the design. Materials should be of durable design that can withstand regular cleaning and disinfection, as well as rough handling by the apes. Fixed climbing structures can be constructed from a variety of materials, ranging from PVC or steel over naturalistic branches, or wooden poles. In the latter case, it is recommended not to use toxic paints. Water-logged wood or chestnut poles have been used successfully in several zoos. Entrance to the enclosure should facilitate maintenance on or replacement of the climbing structures. Consideration should be given to make climbing structures, nest sites, overhead tunnels etc. available to elderly and disabled bonobos, by adding fixed ladders etc. In outside enclosures, bonobos can be encouraged to use platforms in climbing frames by adding shade by for example, providing large platforms in multiple layers. The use of multiple platforms, and horizontal areas (e.g. horizontal poles), ideally on varying heights, allows bonobos to sit, rest, groom, etc. in elevated spaces. Horizontal beams stimulate natural modes of locomotion (suspensory locomotion). This mimic their arboreal lifestyle in the wild. Platforms that are large enough for several bonobos to use at the same time, provide interesting spots for bonobos to have social interactions, and for zoo visitors to see the bonobos. This means a climbing structure should not just consist of vertical beams with some ropes connecting them.

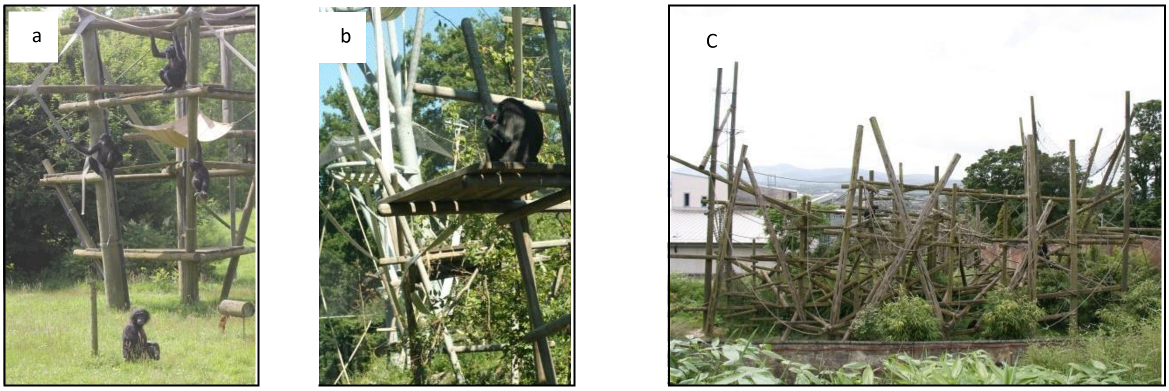
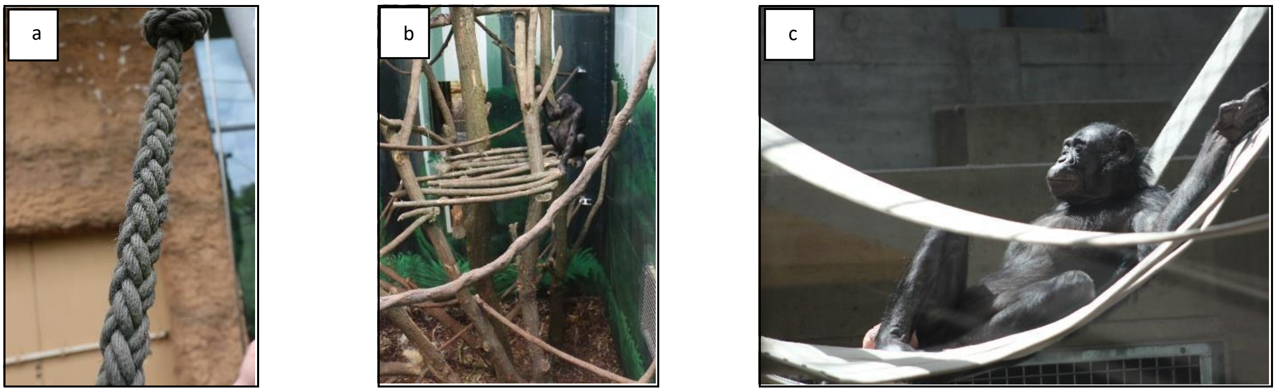


Figure 30: Examples of climbing structures. a: Zoo Planckendael – Jeroen Stevens; b: Wilhelma Zoo Stuttgart – Jeroen Stevens; c: Edinburgh Zoo (for chimpanzees) – Jeroen Stevens).

In addition to fixed climbing frames, **more flexible items** are also recommended. Ropes, artificial vines, firehoses, cargo nets, hammocks, swings have all successfully been used. Ropes and fire hoses can also be used to connect several fixed climbing frames, making an impressive network (Figure 23). To stimulate exploratory behaviour, it is recommended to regularly alter the environment by rearranging at least the flexible items (see section 2.5.3. Structural or Physical Enrichment). When using **ropes**, every care should be taken to prevent that bonobos strangle themselves! Bonobos and other apes have been known to hang themselves when they are caught in long loops of narrow ropes, or in ropes with lose ends, or when the braiding of ropes comes loose [Clyde, 2011]. Frayed ropes should be avoided at all times! Braided ropes are much harder to untwist than twisted ropes. The coating on certain types of rope deteriorate under UV light, creating dangerous flakes. For young bonobos, thick ropes may be difficult to manipulate, or may be hung too high from the ground floor. Therefore, cargo nets can offer a more stable climbing environment for little bonobos.



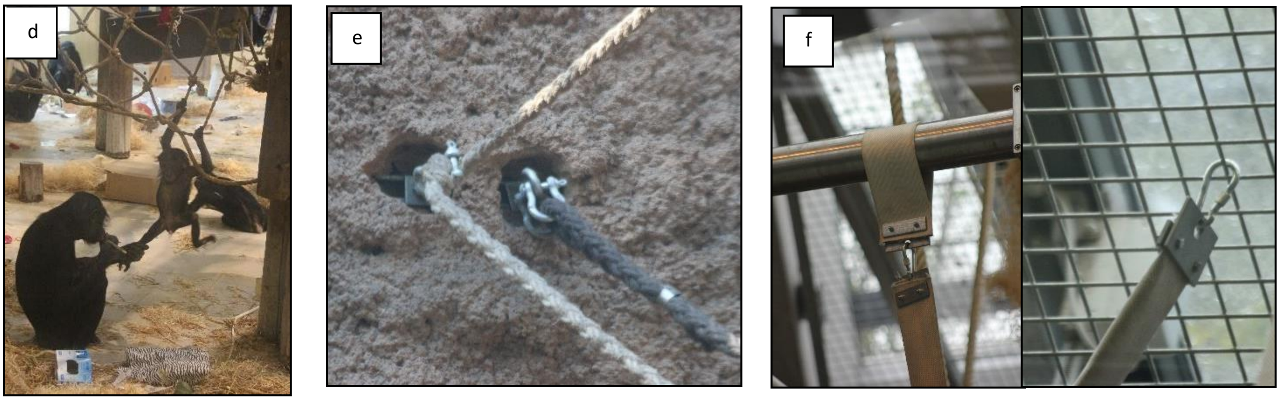


Figure 31: Examples of flexibile furnishing in bonobo enclosures; a: Braided ropes (Frankfurt Zoo – Jeroen Stevens); b: Artificial lianas (Zoo Planckendael – Jeroen Stevens); c: Firehoses (Wilhelma Zoo Stuttgart – Jeroen Stevens); d: Cargo netting (Zoo Planckendael – Jeroen Stevens); e: Flexible anchor points in the walls of the enclosure (Frankfurt Zoo – Jeroen Stevens); f: sFlexible eye hooks (Wilhelma Zoo Stuttgart – Jeroen Stevens).

Within an enclosure, **visual barriers** and hiding places can be created by adding corners, shelves, topography, burlap sacks, nets, solid walls, rock formations, etc. Visual barriers are important to block constant view from visitors or conspecifics, and allow victims of aggression to escape Outdoor shelters, such as artificial rockwork banks, can also be provided and can incorporate both heating and cooling mechanisms. Design of such shelters should consider prevailing wind direction, solar orientation and local seasonal sun angles [Coe et al., 2001] as well as viewing angles for the public, enclosure visibility for keepers, and monopolisation by dominant individuals, or entrapment of low-ranking bonobos during conflicts should be prevented.

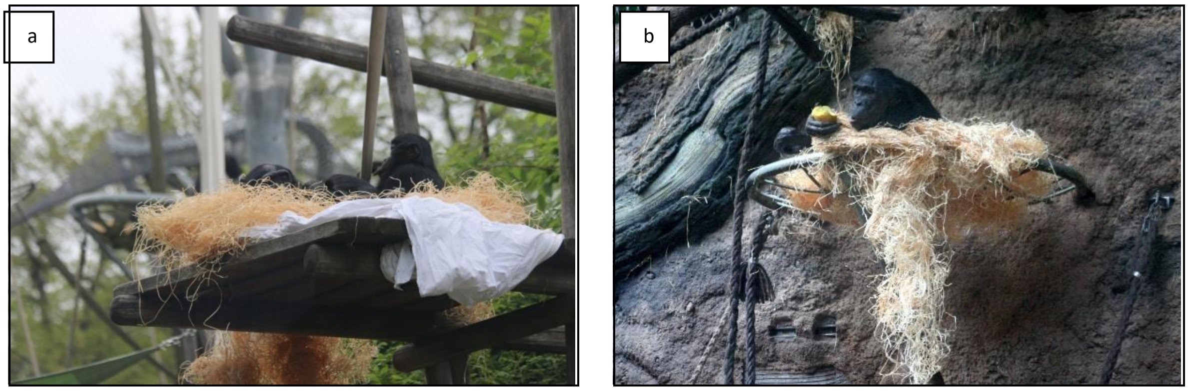


Figure 32: Examples of nesting places for bonobos. a: Wooden platform (Wilhelma Zoo Stuttgart – Jeroen Stevens); b: Nesting basket (Frankfurt Zoo – Jeroen Stevens); c: Burlap hammock (La Vallée des Singes – Jeroen Stevens); d: Firehose hammock (Wilhelma Zoo Stuttgart – Jeroen Stevens); e: Combination fire hose and metal ring (Wilhelma Zoo Stuttgart – Jeroen Stevens); f: Woven fire hoses (La Vallée des Singes – Jeroen Stevens).

Nesting platforms, nesting baskets, or hammocks should be provided at different heights for resting and sleeping (Figure 32). It is recommended to have at least one nesting platform for each adult or adolescent individual, and provide some extras to allow bonobos to choose their nesting location. Research on zoo-housed bonobos has shown that females prefer the highest nesting locations, and males like to build nests below them [Berle et al., 1995]. Although adult bonobos usually make individual nests to rest in, they occasionally share nests. Also, platforms are often used by bonobos during daytime to form social grooming groups, and therefore, should not be too small. The recommended size for these platforms is 100 by 70 cm. Nesting baskets have the advantage over platforms that the former can be more easily cleaned from below, and waste falls through without difficulty. Hammocks made from hessian sacks, cargo nets or woven fire hoses are also commonly appreciated by bonobos.

Bedding material should be provided daily for bonobos to make nests and stimulate natural nest-building behaviour, also when the main substrate in the enclosure is deep litter bark. Since bonobos make nests during the day as well as for sleeping at night, it is recommended to provide also bedding material during the day. Bedding material should be removed regularly. Woodwool, hay and straw are most commonly used, but some zoos have experienced allergies associated with straw. Paper, clothes, branches or banana frond leaves are also sometimes used. Occasionally, it has been observed that bonobos ingest bedding material, so excessive ingestion of certain materials should be monitored.

If the enclosure is sufficiently large, providing access to natural, non-toxic **vegetation** is highly recommended (Figure 33). Free access to natural vegetation, including entire trees, has been provided in several institutions and it seems that bonobos are less destructive than some other species of apes. Stevens et al. [2003] provide a list of 79 species of plants that were planted on the outdoor enclosure or that colonised the island themselves including 22 speciesthat were consumed by the bonobos at Planckendael during a one-month study in the summer. Ten years after this study, many of these plants still survive on the island, but most of the willow (*Salix sp.*) bushes have been depleted by the bonobos. Hotwire can be used to ward off bonobos during a plant's early growing period. *Berberis sp.* bushes have been used successfully in Apenheul to prevent bonobos from demolishing vegetation.

Poisonous plants have to be removed and controlled on a regular basis. For details about the suitable vegetation please refer to the EAZA primate plant compatibility database, developed by Sergio Pacinotti for the EAZA Zoo Horticultural Group. This database can be found on the https://www.zooplants.net/index.php/Main_Page (developed by the EZG, BIAZA Plant WG, ZSL, and ZooLex).

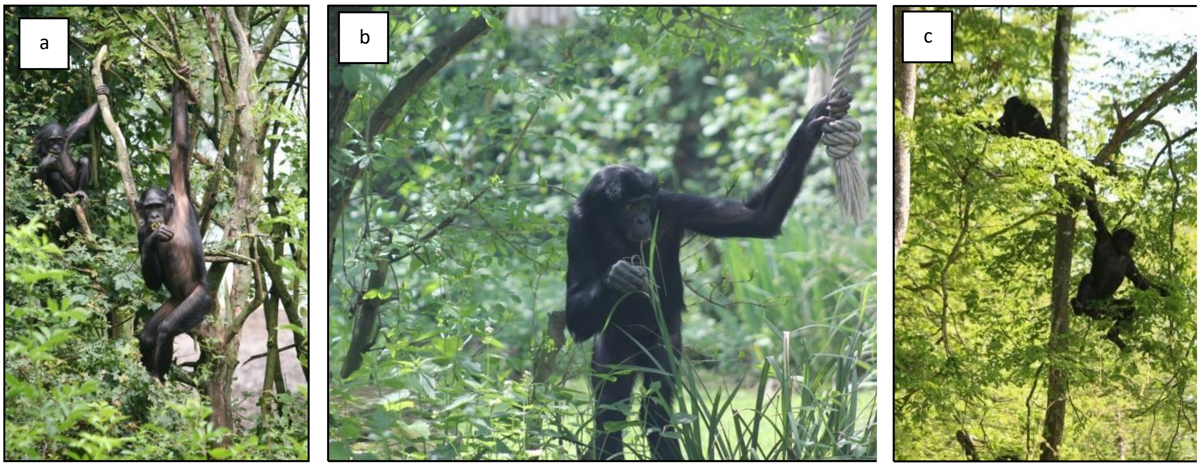


Figure 33: Examples of bonobos using vegetation in EEP zoos. a: Zoo Planckendael – Jeroen Stevens ; b: Cologne Zoo – Jeroen Stevens; c: La Vallée des Singes – Jeroen Stevens.

Maintenance

The frequency of cleaning will depend on the size and design of the exhibit and the number of animals. Natural indoor or outdoor enclosures with dirt, biofloor or other absorbent surfaces should be spot cleaned on a daily basis. This will ensure that the bonobos can avoid contact with faeces and food waste, which reduces the number of pathogens and pests. The use of biofloors will help control bacteria levels. Enclosures with hard floors should be cleaned regularly. Porous materials such as rope, fire hose, or burlap should be frequently replaced or steam cleaned.

It is recommended to provide a **safe environment for staff** to clean the enclosures, including climbing frames. This can be done by providing hooks and handles, to attach safety lines, as well as permanent ladders and safety rails (Figure 34). Please consult local legislation regarding health and safety for staff.

Pest control should be considered as an important factor during exhibit design. Cockroaches seek tight dark areas. Small openings, such as between steel cage frames and masonry walls or penetrations into tubular steel frames should be sealed. Mounting counters, cabinets or shelves away from walls, as well as maintaining open space around furnishings, gives the roaches nowhere to hide. The use of open shelving made of wire mesh also limits hiding places. Drain covers with tight fitting mesh drain baskets can help prevent movement of insects and rodents through the sewer systems. Rodents can pass on contagious diseases which may be lethal for bonobos. Many features contribute to the creation of a suitable rodent habitat, both indoors and outdoors. Food availability is probably the most critical factor. Since rodents are nocturnal by nature, removing food scraps at the end of the day should help limit rodent problems.

Figure 34: a: Safety stairs, barriers and b: safety hooks and handles (right) for easier staff access to climbing frames in bonobo inside enclosure (La Vallée des Singes – Jeroen Stevens); c: safety measures in large outdoor netted enclosures (Wilhelma Zoo Stuttgart – Jeroen Stevens).

2.1.7. Environment

Temperature:

Air temperature in indoor areas should be 18-22° C. Although temperatures in the bonobos' natural habitat vary between 20-30° C, zoo-housed bonobos in temperate regions have to be acclimated to colder conditions so that they can go outdoors as much as possible. Therefore, it is not recommended to keep the indoor temperature much higher than 20° C, except in case of illness, the presence of new-borns, or when outdoor temperatures are well over 20° C. Bonobos should always be given access to 'warm-up' spots (20° -22 °C) if the indoor temperature goes below 20° C, and nesting-material should always be available (see section 1.4.5).

Bonobos can cope well with **maximum temperatures** up to 40° C, but during hot and sunny weather they must be able to shelter from the sun within their indoor and outdoor areas [Van Puijenbroeck & De Bois, 1997], and sufficient air ventilation should be provided. Shade can be provided by shelters (Figure 35), vegetation, and to a lesser degree by landscaping such as hills and rocky outcrops. Water features such as shallow pools, sprinklers and misters can also be used to reduce temperatures. To avoid monopolisation of shady places by dominant individuals, it is recommended to provide several shady areas especially in areas where hot weather is common.

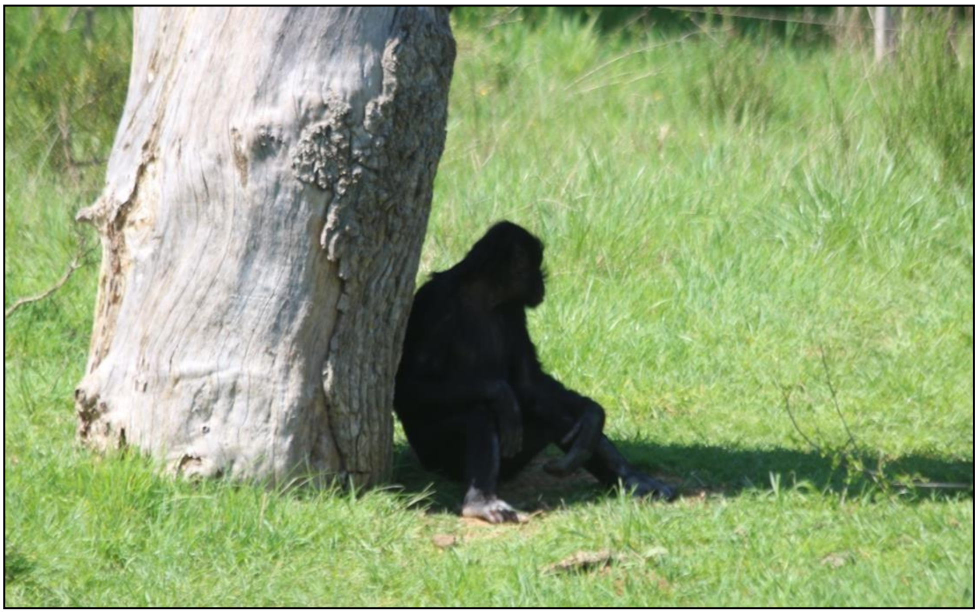


Figure 35: Shade is very important for bonobos (La Vallée des Singes – Jeroen Stevens)

Institutions vary in the **minimum temperature** they allow bonobos access to outdoor enclosures, ranging from 7° C to 16° C [Van Puijenbroeck & De Bois, 1997]. On rainy, windy and cloudy days with low temperatures, bonobos should not stay outside for long periods of time, and when temperatures are below 10° C, access to a heated enclosure (with minimum temperature of 18°C) should be provided at all times. During colder seasons, health of bonobos should be carefully monitored, as respiratory problems are common in bonobos and can be fatal. Twycross Zoo allows bonobos, as part of the general animal housing procedures, to choose where they want to be, giving free access to outdoor and indoor enclosures in a 24/7 schedule. Only in rare occasions, when weather is rough (temps falling below 0° C) or for enclosure management, animals will be locked in [Liptowsky, pers. comm.]. Milwaukee Zoo has let their bonobos outside in the snow for brief periods [Brookmire, 2012].

Standard forced-air **heating** systems are suitable heat sources for indoor facilities, but humidity levels should be monitored when these systems are used. Relative humidity should be kept between 50 - 60% (see below), utilizing misting or a humidifier when necessary. Floor heating has been used successfully in various institutions, but are not compatible with biofloor substrates. It has also been suggested that a negative side effect of floor-heating is that bonobos may spend more time sitting on the ground.

Humidity

The **minimum indoor humidity** must be maintained at 50 - 60%. When humidity is increased, the temperature should also be raised to keep the bonobos comfortable [Van Puijenbroeck & De Bois, 1997]. A deep bedding of pine bark (see 2.1.2) can help to increase the humidity in indoor areas [de Jongh et al., 2006]. Misters and/or sprinklers can also be used, but care should be taken to avoid bacterial infection (e.g. Legionella). Dry, scaly skin is regularly reported in bonobos and there are indications that this condition is linked with low environmental humidity. Also, air sacculitis has been associated with low humidity (see section 2.7.2.).

Lighting

Bonobos are equatorial animals, and a **12-hour light-dark cycle** should be appropriate in most cases, but no detrimental effects have been noted when bonobos are kept under 9-14 hours of lighted conditions per day, a condition that can occur when bonobos are kept in indoor facilities in winter in northern climates. Providing a gradient of light intensity in their enclosures is recommended, as bonobos in the wild would also encounter spatial variation in light levels. A choice between light (550 lux or more on ground level) and shaded (circa 300 lux on ground level) places might be beneficial to them. A colour temperature of 5000-6500 K is most similar to the colour temperature of sunlight [de Jongh et al., 2006; Becker et al., 2017].

The **primary light source** in the indoor area should be natural daylight, backed up by artificial light. Skylights are ideal light-sources, and when they can be opened up during appropriate weather, they provide fresh air without drafts, as well as UVB light. Windows are not only an excellent light-source, they are also highly appreciated by the bonobos as look-outs to observe activities of visitors, keepers, and of other animals (Figure 34). When skylights and windows are within reaching distance of the bonobos, they should be appropriately protected to avoid broken glass falling into the enclosure (also be aware of bonobos using sticks to reach further). Different options of UV-absorbing or UVB-transmitting materials are available (see below).

Figure 36: Natural light is enjoyed by bonobos also to look outside (a: Apenheul – Jeroen Stevens); and often groups will gather in natural light for grooming activities (b: Zoo Planckendael – Jeroen Stevens).

Additional artificial light is necessary in most regions. Full spectrum High Frequency fluorescent lights or halogen HQI lights are recommended [de Jongh et al., 2006]. LED lights have also been used without seemingly bad effects. Lighting fixtures should be mounted outside of enclosures and far enough away from the bonobos to avoid being broken. Where appropriate, fixtures should be waterproof and shatterproof. Variable and programmable timers on lighting systems can be used to provide longer periods of light during winter in northern hemisphere. It may be recommendable in some areas to provide additional lighting to allow caretakers to clean the facility effectively and view animals in all areas of the enclosure.

For animals held indoors seasonally or year-round, consideration should be given to use of **UVB-transmitting material** in skylights or windows to prevent the development of metabolic bone disease such as vitamin D3 deficiency. These materials have been in use only recently and there are few published data on their impact on circulating vitamin D levels in primates. UV-transmitting materials will still block many UVB rays from being transmitted, and will become increasingly less effective at transmitting UVB over time. Light bulbs generating UVB wavelengths also have a limited range (often within 45 cm), and shelf life (6-12 months). Both for UVB-transmitting skylights and UVB generating light bulbs, perching should be placed as close to the UVB source as possible, and should be large enough for all animals to use at the same time, preventing monopolisation by dominant animals. Still they provide only a fraction of the UVB provided by sunlight, and outside areas with wire-mesh ceilings are therefore recommended as important elements of primate exhibits [McLaughlin et al., 2007].

Special attention is needed for **new-born offspring** suckling from mothers housed within indoor exhibits. Vitamin D molecules are too large to pass into milk, and so are not provided to offspring from their mothers. Hypovitaminose D has caused death in infant bonobos kept indoors [Van Elsacker et al., 1993; Stevens et al., 2003]. It is recommended that infants receive a daily full-spectrum artificial light bath when they do not have access to direct sunlight for a long period of time. In the absence of sunlight (or other UVB sources), there may be a need to supplement infants with vitamin D through injections, or oral medication [McLaughlin et al., 2007].

Ventilation

Ventilation is often overlooked when designing primate enclosures [Lewis & Rietschel, 2004]. When an enclosure consists of several rooms, air flow and ventilation in each of them should be guaranteed also when the slides and doors between the enclosures are closed (Figure 35). A rate of ca 40 m³ per individual per hour is suggested [de Jongh et al., 2006]. Apart from refreshing the air, the flow of air can also help to improve the even distribution of temperature within the building; however, draughts should always be avoided [de Jongh et al., 2006]. Draughts have been reported as extremely problematic for bonobos, given their tendencies to develop colds quickly and often with big consequences. Therefore, the position of doors for keepers, the public and apes that connect to the outside, should all be studied carefully.

Figure 37: Air vent installed to allow air circulation between adjacent enclosures also when the full slides between the enclosures are closed off (Apenheul – Jeroen Stevens).

Sound and vibrations

Although bonobos can be very noisy themselves, they can be sensitive to loud noises and care should be taken to **avoid stress through overstimulation by loud sounds**. The hard surfaces of (indoor) enclosures may result in loud acoustic environments. Biofloor (see 2.1.5 “substrate”) can help to reduce noise levels. Similarly, wooden ceilings may dampen sounds, and noise absorbing, cleanable materials such as polypropylene, polycarbonate (lexan) and nylon can be used to furnish the environment to reduce excessive noise [Ross et al., 2009].

People working with the bonobos can be a considerable source of noise. Caregivers may not always be aware of how much noise they make when for example cleaning the enclosure, and they should be made aware. Bonobos seem to respond positively to humans that do not speak loud, and will produce less noise themselves. **Staff should be encouraged to remain calm** when working with the bonobos, even when the animals themselves are quite loud. Slamming of doors, yelling and loud talking or very loud music can easily be eliminated and this seems to have a positive, calming influence on the bonobos.

Construction and maintenance work of the enclosure should preferably be scheduled so that bonobos experience least stress, for example by scheduling necessary indoor construction or maintenance during spring and summer, when bonobos have access to the outdoor enclosures.

Zoo visitors can also be a source of noise. The design of a bonobo exhibit should prevent visitors encircle to the bonobos. In indoor glassed enclosures, visitors should be discouraged to tap or bang on the windows. Bonobo groups experiencing environmental or psychological stressors may exhibit greater rates of male displays, more frequent agonistic behaviours, and/or stereotypies (e.g., pacing, self-plucking, etc.). Individuals under stress within the group may appear timid and paranoid, and transfer through doorways very cautiously, or even refuse to transfer with their group at all.

2.1.8. Dimensions

While size matters, is it only one important aspect of the quality of an enclosure. It is therefore difficult to give specific recommendations. Much depends on how the enclosures are structured. Table 3 gives an overview of some recently built enclosures within the EEP and gives an idea about appropriate enclosure sizes.

Table 3: Enclosure size for four recently built enclosures in the EEP, with specifications for number and surface of inside enclosures, holding enclosures and outside enclosures

	Indoor	Holding	Outdoor	Intended group size
La Vallée des Singes, Romagne	Two rooms 100 + 100 m² [Total 200 m²]	Eight rooms between 16 – 35 m² Total of 200m²	Two moated enclosures 3500 + 8000 m² [Total 11500 m²]	25 individuals
Wilhelma Zoo Stuttgart	Three rooms 160 + 80 + 80 m² [Total 320 m²] Max height 6.7 m	14 rooms Total of 100 m²	Two netted enclosures, [total of 1220 m²] Max height 15.8 m	12 adults + offspring
Frankfurt Zoo	Two rooms 147 + 99 m² [Total 246 m²] Max height 8 m	Six rooms Total of 55 m²	Two netted enclosures 715 m² + 407 m³ = 1122 m²	9 adults + offspring
Zoo Planckendael	Four rooms; 100 + 50 + 50 + 78 m² [Total 278 m²]	8 rooms, between 9,6 and 33 m² [total of 143,87 m²]	One moated enclosure of 3000 m² + roof of largest indoor can open for 50%	16 adults + offspring

2.2. Feeding

Figure 38: Bonobo feeding on browse (Zoo Planckendael – Jeroen Stevens)

2.2.1. Basic diet

The diet of bonobos in zoos should be developed with reference to the diets of free-ranging bonobos (see section 1.6), but choice of food items should be based on their nutrient contents rather than their preference by the animals. The total amount of food types recorded for free-ranging bonobos rises above 110 for the longest studied populations [Badrian & Malenky, 1984; Kano, 1992; Kano & Mulavwa, 1984] and wild bonobos may eat up to ten different food types per day, and 40 different food types per month [Kano & Mulavwa, 1984]. Given this large variety in wild bonobo's diet, it is recommended to also provide a varied diet in zoos, which can be achieved through the diversity of foods offered, their quantity, their colour, size, texture, and taste, and the manipulative characteristics certain foods offer. Seasonal availability of some items can contribute to variability. It is critical that variety be provided within the context of maintaining nutritional standards and variation throughout the week is preferred to giving a large variety of items each day. In general, bonobos should be fed a dietthat includes a mixture of vegetables, fruits, grains, browse, and nutritionally complete dry food. Items can be presented in raw form, either whole or cut up. All food items should be fedin a manner that promotes species-appropriate foraging behaviours, requires manipulation, processing, and/or search by the bonobos.

2.2.2. Nutritional requirements

Energy requirements have not yet been experimentally determined for bonobos. Equations for the basal metabolic rate (BMR) for eutherian mammals in captivity have been estimated at BMR = 70 (body weight in kg)* 0.75[Kleiber 1961; Robbins 1993]. Alternatively, the regression for zoo-housed primate by Hayssen & Lacy [1976] resulted in an equation of BMR = 0.31 (body weight in grams)* 0.755. BMR values must be multiplied by a field metabolic rate (FMR) factor, which allows energy for behaviours, digestion, thermoregulation etc. [Evans & Miller, 1968]. Applying an FMR of two for moderate activity, and commonly reported weights for bonobos of 31.8-50 to these equations, gives an estimation of daily maintenance energy needs of **1876-2632 or 1617-2275 kcal/day**. This range fits well within the range of dietary energy fed across SSP institutions (1584-3803 kcals/day offered; average of 2721 kcals/day offered). These equations are a good place to start. However close monitoring of weights, body condition and behaviour of individuals will be necessary to develop ideal food requirements depending on the group, enclosure size, activity levels and climate.

In estimating dietary energy needs for maintenance, the **activity level** of the animal must be considered. The above formula assumes an activity factor of 2 x BMR, which is indicative of moderate activity [Scott, 1986]. Activity factors of 1.27-1.5 x BMR have been suggested for minimal to mild activity levels in humans and a range of animals in a zoo setting [FAO/WHO/UNU, 1985; Scott, 1986; Payne & Waterlow, 1971], while a factor of 3 x BMR has been suggested to meet the needs of highly active omnivores, of which would only be realisable for free ranging animals and very rarely in zoos [Scott, 1986].

The Primate NRC provides estimated **target nutrient** ranges for various life stages of non-human primates. In the absence of information specifically for bonobos, the "estimated adequate nutrient concentrations" for post-weaning non-human primates (Table 4) appear reasonable for this species. Estimated nutrient needs for humans (Daily Reference Intakes) may also be considered when planning diets.

Table 4: Target nutrient ranges for bonobos on a dry matter basis

Nutrient	Target [a]
Protein, %	15-22[b]
Essential n-3 Fatty Acids, %	0.5
Essential n-6 Fatty Acids, %	2
NDF, %	10-30[c]
ADF, %	5-15[c]
Vitamin A, IU/g	8
Vitamin D, IU/g	2.5[d]
Vitamin E, mg/kg	50-100
Thiamin, mg/kg	3
Riboflavin, mg/kg	4
Niacin, mg/kg	25
Pyridoxine, mg/kg	4
Folacin, mg/kg	4
Biotin, mg/kg	0.11-0.2
Vitamin B12, mg/kg	0.01-0.03
Pantothenic acid, mg/kg	12
Choline, mg/kg	750
Vitamin C, mg/kg	200[e]
Calcium, %	0.5-0.8
Phosphorus, %	0.4-0.6[f]
Magnesium, %	0.08
Potassium, %	0.4
Sodium, %	0.2
Iron, mg/kg	100
Zinc, mg/kg	20-100
Copper, mg/kg	12-20
Manganese, mg/kg	20
Iodine, mg/kg	0.35
Selenium, mg/kg	0.11-0.3

a Probable requirements are based on NRC 2003

b Lactation and growing young –Required concentrations are greatly affected by protein quality (amounts and proportions of essential amino acids), and this issue must be considered. Taurine appears to be a dietary essential for some primates through the first postnatal year.

c Although not nutrients, NDF and ADF when used at the concentrations shown for model species were positively related to gastrointestinal health.

d Exposure to natural sunlight and or artificial UV radiation should be considered as a contributing source for the requirement.

e Ascorbyl-2-polyphosphate is a source of vitamin C that is biologically active and relatively stable during extrusion and storage.

f Much of the phytate phosphorus found in soybean meal and some cereals appears to be of limited bioavailability.

Dietary sodium is known to influence blood pressure in human and non-human primates, with excess intakes frequently associated with increased blood pressure and hypertension. Given the association between high blood pressure and cardiovascular disease in primates, it is advisable to limit dietary sodium intake to levels deemed adequate to meet physiological needs. The Primate NRC provides a range of sodium intake (0.25-0.65% dry matter) that appears to support maintenance of non-human primates, but cautions that this range likely exceeds minimum needs. Recently, revised dietary sodium recommendations for humans recommend no more than 2300 mg//d (0.46% dry matter) for healthy individuals for disease prevention, and a stricter limit of 1500 mg/d (0.30% dry matter) for sodium-sensitive populations and those with hypertension, diabetes, or chronic kidney disease [IOM FNB Dietary Guidelines for Americans, 2010]. Comparing this range to that provided by the NRC for general primate maintenance (0.2% dry matter) finds the NRC recommendation to be lower than that set for disease prevention and management in humans, which suggests it, may be an appropriate target for minimizing contribution of this nutrient to cardiovascular disease in bonobos while still meeting their needs.

Factors Affecting Nutrient Needs

Age: For infant bonobos, **breast-feeding** is recommended whenever possible. If an infant appears underweight, attempts should be made to stimulate the amount or quality of the dam's milk through appropriate social settings that avoid interruption of lactation (last milk produced in each bout of nursing has highest fat content), and diet modifications that include adding high-fat items to the dam such as avocado, flax oil, or flax seed. It should also be considered that in some instances, it may take time for a dam's milk to fully come in, so adequate time should be given for the dam to increase production, provided the infant appears to be healthy and thriving. Supplemental food should be provided to the infant only if the first approach does not work, because supplemental feeding of the infant will reduce its attempts at nursing, which will have a negative effect on dam's quality and quantity of milk, thus lessening the mother-infant bond.

Bonobo groups containing actively growing animals should be monitored for necessary increases in diet amounts. **If diets are quickly and completely consumed, an increase is likely to be necessary.**

In **geriatric apes**, a diet low in fat, sodium and caloric content may reduce obesity and associated cardiovascular diseases [Lee & Guhad 2001]. Protein should become a larger proportion of the diet. Vitamin A, E, calcium and omega 3 fatty acid supplements should also be increased in the diet. These supplements should be given to these individuals separately.

Reproductive Status: It is important to assess the complete diet to determine if individuals require additional supplementation. Any vitamin and/or mineral supplementation should be overseen by a nutritionist or veterinarian.

Pregnant bonobos receiving nutritionally-complete diets with large amounts of fresh vegetables and nutritionally-complete biscuits should not require additional supplementation, other than a slight **increase in the amount of food** offered in later pregnancy. However, pregnant females are generally offered prenatal vitamins and monitored more closely for reduction in body condition. Diet increases are often provided during pregnancy and lactation, especially for lower-ranking females.

Females may also require diet increases from the last trimester of pregnancy through weaning, with the greatest requirement coinciding with peak lactation [NRC, 2003]. Lactation is the most energy demanding process a body will encounter. For humans, an additional 500 kcal ME per day is recommended for the first six months of lactation [FAO/WHO/UNU Expert Consultation, 1985]. Based on the average body weight of bonobos, an **additional 250 kcal ME per day** is likely sufficient. Biscuits and a variety of feed items, including green leafy vegetables, will often contain adequate nutrient levels to support females in any reproductive state and diets can simply be increased or decreased to account for changes in energy requirements. Body weight and condition should be monitored to allow for dietary modifications depending on life stage (growing, maintenance, and senescence), activity level and reproductive status (pregnancy, lactation).

Seasonal changes: Many facilities provide diets that vary on a seasonal basis (e.g., with varied access to produce and natural browse). Any benefit of significantly altering sources of food, based on season, for bonobos in zoos has not yet been researched. Many primates are adapted to a natural environment with periods of abundant high-energy, low-protein feeds (such as fruit) when they deposit fat, and low-energy, high-protein (Terrestrial Herbaceous Vegetation) periods when they metabolise fat [Raubenheimer & Rothman, 2012]. If bonobos follow this pattern, continuous access to excessive fruit and other high-calorie food items in zoos may predispose them to obesity.

Seasonal changes **in body condition** might occur in conjunction with reduced activity and consequent weight gain in temperate climate zoos that may restrict access to larger, outdoor yards during cooler months. In zoos, bonobos are generally housed in enclosures that allow them to maintain thermo-neutrality year-round. Energy requirements increase outside the thermoneutral zone due to processes to regulate body temperature, such as panting, sweating, and shivering [NRC, 2003]. Temperature extremes may also suppress appetite further, leaving individuals in a negative energy balance. Therefore, it may be difficult to sustain adequate feed intake and maintain body condition if exposed to extreme temperatures for extended periods of time In zoos, bonobos, fed a nutritionally complete diet, should be maintained at a body weight and condition to maintain optimal health year- round.

2.2.3. Diets

Although bonobos are known to be mainly frugivorous in the wild (see section 1.6), care should be taken when designing a zoo diet. The cultivated fruits that we as humans eat and often feed to our apes are generally richer in simple sugars and moisture, and lower in protein, vitamins, minerals and fibre than the fruits they would encounter in the wild [Popovich & Dierenfeld, undated; Ross & McNary, 2009]. Therefore, it is advisable to have a high proportion of vegetable, and lower proportion of cultivated fruits in the bonobos' diet. Since the diets of bonobos in the wild contain high concentrations of fibre (averages at 25%), several strategies can be used to increase fibre in the zoo diet [Ross & McNary, 2009], including:

- Offering all fruits raw and unpeeled, as fibre is often localised in peels;
- Replacing soft fruits (e.g. bananas, grapes, citrus fruits) which contain low fibre levels, with vegetables (e.g. yams, sweet potatoes, squash, turnip, beetroot, bean pods, broccoli etc.) which contain relatively more fibre. Overall, the fibre content of fresh produce is low. The most efficient way to increase fibre intake is to feed a high fibre biscuit;
- Increasing green produce and adding browse on a daily basis; provision of hay, beet pulp, corn husks, and/or banana leaves.

A guideline for diet development would include a total intake of approximately 2000-4000g of food, on an 'as fed' basis, per healthy, active, adult bonobo per day, divided approximately as follows:

Table 5: Suggested diet composition for zoo-housed bonobos, on an 'as fed' basis

Diet item	Percentage (%)
Nutritionally complete foods	5-10
Vegetable	20-40
Leafy green	10-25
Starch vegetable	5-15
Other food enrichment to vary	0-2
Fruits	10-20
Browse	> 5

Nutritionally-Complete Foods:

Nutritionally-complete feeds, such as primate biscuits or pellets, are an efficient means to ensure that zoo-housed primates meet their estimated (micro-)nutrient needs. Any complete feeds offered should be high in fibre (15% ADF, minimum), and low in fat and starch, and formulated to meet the needs of primates. Because primate biscuits are fortified in vitamins and minerals, when included in the diet at appropriate levels, additional nutrient supplementation should not be necessary. Inclusion of these feeds at 5-10% of the diet (as-fed), appears sufficient to meet their dietary fibre and other nutrient needs.

Although providing pellets makes the diet easier to assemble for non-nutritionists and provides difficult to obtain vitamins and minerals, pellets are not an essential part of the diet. The disadvantage of pellets is that they are highly concentrated in energy and are quickly eaten, reducing total feeding time. Primate pellets may also contain high amounts of sugars, including apple syrup etc. It has been noted in Planckendael that pellets increased regurgitation behaviour [Stevens et al., in prep]. Leaf eater pellets, offered by some manufactures have also successfully been fed to bonobos, and are generally higher in fibre than other types of pellets. In general, pellets can be replaced by other energetically dense, high protein food items such as beans, lentils, legume hays, germinated seeds, insects etc. but it is recommended to assemble diets without pellets with the advice of a nutritionist.

Vegetables

The bulk of the diet should consist of vegetables. To provide variability in the diet, exchange lists can be used for each category. The following table (Table 6) lists suitable exchanges:

Table 6: Dietary food exchanges for bonobos

Food category	Exchanges
Vegetables (common)	Broccoli, Brussel sprouts, green cabbage, red cabbage, cauliflower, celery, corn, cucumber, mushrooms, peppers, radishes, tomato.
Vegetables (leafy greens)	Beet tops, swiss chard, chicory greens, collard greens, dandelion greens, endive, kale, romaine lettuce, mustard greens, parsley, spinach, turnip greens.
Vegetables (bean/legume)	Lima beans, snap peas, kidney beans, chickpea (garbanzo beans), green peas, lentils.
Vegetables (tubers/squash)	Beets, carrots, onions, potato, pumpkin, acorn squash, butternut squash, summer squash, spaghetti squash, zucchini, sweet potato, turnips, parsnip.

Fruits*	Apple, apricots, banana, sweet cherry, cranberry, grapes, cantaloupe, honeydew melon, papaya, peach, pear, pineapple, plum, strawberry.

* Citrus fruits should be limited in quantity due to the ability of the acid in the fruit to increase absorption of iron from the diet, but can include grapefruit, lemon, lime, or orange.

Browse / Roughage

Browse is an important component of bonobo diets. Providing browse year-round is recommended, and is possible even in temperate climates where browse can be harvested in the summer and stored frozen or, better yet, silaged. Some types of browse trees can also be cut during the winter and “forced” to flower or leaf in water filled tubs placed in well-lit indoor locations. The addition of browse encourages processing and consumption of food. The addition of browse increased foraging time from 3-17%, and resulted in a drastic decline in coprophagy in bonobos [Daman, 1990] and has also been shown to reduce regurgitation & reingestion behaviour [Stevens et al., in prep]. In addition to its value to the diet of bonobos, browse is also an item that is manipulated and utilized for displays, especially by males.

See **Appendix 3** for a list of browses that has been reported suitable for bonobos in zoos [e.g., McLaughlin et al., Rafert et al., 1997; 2007; Stevens et al., 2003]. Obviously, there are regional differences in the availability of browse. Even though bonobos are not typical browse feeders, it is not recommended to feed one particular species of browse for prolonged periods, but to provide variation by offering different species of browse [Nijboer & Huisman, 2010].

Forage / scatter food

In addition to the normal diet, zoos will offer small food items that can be scattered in substrate to increase foraging. Items given by scattered feeding should be considered as part of the animal’s daily diet, and as such they should be "subtracted" from the rest of the daily diet, not given in addition [McLaughlin et al., 2007]. Typically, scatter feeds consist of nuts and seeds who are nutritionally very rich, due to their high fat content, unless they are shelled which requires more amount of work to open them.

Table 7: List of common feeds used as enrichment in bonobo diets. It is recommended to focus on providing items that are low in sugars and fats, and high in fibre. Some possible forage foods include soaked beans (lentils, chickpeas (garbanzos), lima, pinto, others), finely diced vegetables (pumpkin, carrot, rutabaga, turnip, sweet potato, celery, fennel, celeriac root, others), or small pieces of a complete diet such as commercially available enrichment pellets.

Table 7: List of common feeds used as enrichment in bonobo diets.

Food Item	Quantity	Kcal/Quantity
Almond	10 nuts	75
Apple sauce, no sugar added	1 cup	104
Cereal, puffed rice	1 cup	114
Cereal, puffed wheat	1 cup	100
Hazelnut	10 nuts	100
Honey	1 tbsp	64
Jam, no sugar added	1 tbsp	10
Juice	1 cup	110
Mustard, prepared	1 tsp	5
Oatmeal	1 cup	145
Pasta, whole wheat, cooked	1 cup	174
Peanuts, no shell	¼ cup	210
Peanuts, with shell	10 nuts	120
Peanut butter	2 tbsp	188
Pecans	5 nuts	105
Popcorn, air popped	1 cup	31
Raisins	¼ cup	109
Rice, cooked	½ cup	100
Salad dressing, low fat	1 tbsp	32
Seed and grain mix, various	½ cup	200
Spices and herbs, dried	1 tbsp	10
Spices and herbs, fresh	1 cup	5
Vegetables, frozen, mixed	½ cup	53
Walnut	5 nuts	190

Animal matter

Given the recent findings that bonobos in some wild populations consume **animal protein** regularly, it may not seem a bad idea to occasionally feed bonobos some form of animal protein. It is, however, hard to estimate how much animal protein an average wild bonobo consumes on an average day. Nitrogen isotope values from bonobo hair samples indicate plants are the major source of protein in the diet for this species [Oelze et al., 2011]. The amount of animal protein that zoos include in their bonobo diet varies. Some zoos will feed yoghurt, curd cheese, eggs, hardboiled eggs or small quantities of lean meat [Rafert et al., 1997]. It is not recommended to feed raw animal protein to bonobos due to risks of bacteria induced gastrointestinal infections (e.g., salmonella). In general bonobos in zoos do not seem keen on consuming insect matter, but insects may be a source of enrichment (see Section 2.5. Behavioural enrichment). Non-fermented milk products may cause problems of lactose intolerance in adult bonobos, although this has never been proven clinically. Yoghurt can be used as food-based enrichment to stimulate extractive foraging, but quantities should be limited.

2.2.4. Methods of feeding

Food is usually given to the **entire group** to stimulate social dynamics, but occasionally lower ranking individuals may have to be fed separately, or highly priced food items can be given to the individuals separately. This also allows for administering medicine or additional nutrients when needed.

Since feeding makes up the majority of the activity budget of bonobos in the wild, every effort should be made to stimulate foraging behaviour in zoos, and to increase time spent on foraging and feeding. Most zoos will feed between two and six times per day. A **minimum of two feedings** seems recommendable, as wild bonobos mostly feed in the morning and late afternoon. It is recommended to give bonobos the first major feeding in the morning, between 06:00 and 09:00 h and the second feeding late in the afternoon, between 15:00 and 17:00 h to mimic the two peaks seen in feeding behaviour of wild bonobos [Badrian et al., 1981 – see 1.6.2.]. Additional feedings will stimulate the animals throughout the day, and will keep them occupied. Some zoos chose to offer within each feeding a mixture of different food items, others choose to offer one kind of food item per feeding, to reduce competition for priced food items, and to increase the chance that all individuals including the lower ranking ones get access to food. It is recommended to use enrichment devices to increase foraging and feeding time further, and to make bonobos 'work for their food'. There may be special cases where this is not appropriate (e.g., ill animals, or animals that are new members of a group), but most apes should have such opportunities (see section 2.5 for more details on enrichment).

Introducing **variation** throughout the week, rather than offering a wide variety of food items daily, has many benefits. Food items may have a greater novelty value when offered less frequently which helps to maintain interest in less preferred food items and stimulate investigation. It prevents more dominant individuals eating only their preferred items daily, ensuring a more balanced diet for the group. It also allows for more options of presentation as some feeding methods, such as hanging whole bunches of greens or skewering produce, may require larger amounts of a food item to be most effective. Apes living in social groups should generally be fed in several locations to increase access by subordinate individuals. Variation and novelty can be introduced by simply varying where food is placed in ape enclosures [AZA Guidelines for bonobos].

In a study on zoo housed bonobos, it was found that stress (measured by salivary cortisol) increased when food was presented in a clumped way that could easily be monopolised, versus when **food was scattered** in the enclosure [Hohmann et al., 2009]. However, this depends on the type of food included in the clumping: highly prized food items such as fruits are more likely to elicit dominant behaviours [Baxter & Plowan, 2009]. The best way to avoid monopolisation by dominant individuals, as well as to stimulate foraging behaviour, is to spread the food throughout the enclosure, and reduce amounts of highly salient food items such as fruits and animal products. Food can be scattered around on the floor and where possible also include climbing structures as food sites. To further increase foraging time, food should be hidden in boxes, bags, or puzzle feeders etc. to increase foraging time (see also Section 2.5. Behavioural enrichment).

2.2.5. Water

Water should be available to all individuals 24 hours per day, as bonobos have been observed to drink during the night, especially pregnant and lactating females. It is recommended to provide running water from drinkers or "Lixit" devices (Figure 37d), which are nipple-like water-flow regulators that release water only when an animal places pressure on the regulator while drinking. Some zoos have used motion detectors fountains (Figure 37a-b), which function fine but with new arrivals it should be checked that new individuals know or learn how to use them. Drinking devices should be installed on several locations to prevent monopolisation by dominant animals. For young individuals, the height of the drinking devices may be a problem, so care should be taken that they can also reach these. Water from moats or pools is sometimes drunk by bonobos (Figure 37c), but water quality has to be checked and pools and moats should be cleaned on a regular basis to ensure that they contain water that is safe to drink. The frequency of cleaning may depend on animal usage and algae growth. Any chemicals used to disinfect pools and moats should be approved by the veterinary staff for animal safety and effectiveness. Some zoos offer herbal tea as (additional) drink [Rafert et al., 1997]. Flavouring the tea with (too much) sugar may lead to tooth decay. Using steviol glycosides ("stevia") based table top sweeteners instead of sugar have been used successfully in apes, when flavouring liquids. Milk is not recommended as drink to adult bonobos.

Figure 39: Sources of water - ape controlled water fountains (a:Wuppertal Zoo – Jeroen Stevens) ; b: drinking from a moat (Apenheul – Jeroen Stevens); and c: from a Lixit device (Columbus Zoo – Jeroen Stevens).

2.3. Social Management

Figure 40: Females grooming and juveniles playing (Apenheul – Jeroen Stevens).

Bonobos should be kept in **multi-male, multi-female social groups**, preferably including individuals of different age categories. In 2019, the median group size in the EEP was thirteen individuals (range: 4-21 individuals, including infants and juveniles). Likewise, SSP median group size equalled eleven individuals (range: 7-20 individuals), which is a respective increase in group size by five and six individuals since the 1990s, when the zoo population was a lot smaller [Ono-Vineberg, 1997]. For new groups it is recommended to build enclosures for a minimum of ten adult bonobos, and allow fission-fusion (see Section 2.1 Enclosure).

2.3.1. Managed fission-fusion

Wild bonobos live in a complex and fluid fission-fusion society (see Section 1.8.4 Social Behaviour). It is recommended to build enclosures that allow for this species-specific social organisation (see Section 2.1. Enclosure). Ideally, **bonobos would always be free to choose** their own social partners, or to spend time on their own, avoid certain individuals, etc.. In some instances, however, it can be useful to split up existing groups, and several institutions are managing their bonobo groups now under "managed fission-fusion". Some institutions regroup animals several times during the day, depending on interpretations of keepers on what is indicated by the bonobos; others will regroup once every 24 hours; or once every few days. There are several potential reasons for temporarily splitting up groups. It is, however, recommended to avoid the formation of long-term, stable small subgroups, as the goal of the EEP is to keep bonobos in larger, socially dynamic groups. A comparison of the behaviour of bonobos living in two stable groups (Planckendael Zoo and Cologne Zoo) with that of one group of bonobos living in a large group with managed fission-fusion (Frankfurt Zoo) showed that the behaviour in the managed fission-fusion group was more dynamic and varied, which was interpreted as positive for the individuals' welfare [Classen et al., 2016; Kieβling, 2008]. Moscovice et al. [2015] studied behavioural and endocrinological changes in female bonobos at Frankfurt Zoo after reunions (fusions) and found no differences in urinary cortisol, or grooming; mild increase in aggression, and significant increase in socio-sexual interactions among the females.

Keeping bonobos in managed fission-fusion may be demanding on keeper time and experienced keepers who can correctly interpret bonobo behaviour are required. Often their knowledge is difficult to pass on to others, as there is a lot of "gut feeling" involved, and few objective criteria can be used in deciding when or how to split up groups. By "over-managing" bonobo groups, we risk going back to effective very small subgroup sizes. It is not recommended to use managed fission-fusion if it results in long-term subgroups of less than five adult bonobos. Below, I list some reasons for keeping bonobos in a managed fission-fusion system, and their practical implications.

Managed fission-fusion for breeding recommendations

If a certain female can **only breed with one male, based on recommendations** by the EEP species coordinators, it is suggested to build a small subgroup around this pair for as long as the female is in the fertile phase of her reproductive cycle (see Section 2.4 Breeding). This subgroup should only include the recommended breeding male(s) and none of the other fertile males (aged six years or older), except adult sons of the breeding female, if it has been confirmed that no mother-son breeding occurs. The subgroup can be further complemented by other females that have a breeding recommendation with the same male(s), and/or by lactating or pregnant females, and by immature offspring of the females in the subgroup. Depending on the overall group size, the breeding group can be of considerable size. The composition of other subgroups should however also be monitored carefully. The breeding subgroup can join other individuals when the female is not ovulating, or as soon as she is pregnant. Managing this type of fission-fusion requires regular ovulation tests to determine when the female is expected to ovulate. Experience in Columbus Zoo indicates that although timing of the ovulation within a cycle varies between females, it is very consistent within females across cycles. That is: some females will ovulate a few days prior to detumescence of the swelling, while others will ovulate after the swelling has deflated. Keeping bonobos in managed fission-fusion for breeding thus requires good knowledge on when females are likely to ovulate, which can be determined by ovulation tests. A period of ten days around the ovulation (five days before, five days after ovulation) is believed to be enough to make sure only the recommended males can breed.

Managed fission-fusion for housing bonobos with fewer social skills

Several bonobos in the current zoo population have come from private institutions where they may have **grown up without learning the appropriate social skills** to cope with the complex dynamics of living in large groups. Similarly, zoo-born hand-reared individuals, especially males, sometimes fail to react appropriately to other individuals. There may be learned responses to aggressive attacks; some bonobos may actually learn that when they cry loudly, they are likely to be “rescued” by the keepers, and may be separated. Likewise, some bonobos may learn that they get attention from keepers when they bully or victimise a bonobo. Therefore, keepers should not react too quickly or interfere too soon. However, experience has taught us that some bonobos cannot cope well with the complexities of living in large social groups. For those individuals with fewer social skills managed fission-fusion can be a solution, e.g., by forming a smaller subgroup around this (these) individual(s). Care should be taken to rotate the other bonobos in the subgroup(s), to avoid that they are “stuck” with these individuals.

Note that very good results have been obtained using a combination of antidepressant and anti-psychotic **drugs and behavioural therapy** through positive conditioning, and carefully managed fission-fusion in individuals that were very anxious. For example, a male bonobo in Milwaukee Zoo came as a depressed and nervous individual, and finally rose to be the alpha male in his group [Sandin, 2005, 2006]. See Prosen & Bell [2001] and Wallace et al. [1998] for more details about specifics on behavioural therapy and drugs used.

During the **introduction of hand-reared infants or juveniles** back into the group, it is recommended not to change group composition too quickly, and start by introducing the hand-reared juvenile into smaller groups first, and do a stepwise introduction where the infant can establish good relationships with a few individuals before new individuals are added (see section 2.4.8 for more details). However, it is not recommended to split up the group permanently for longer periods during the whole introduction process.

Managed fission-fusion to mimic social organisation in the wild

Wild bonobos live in a fission-fusion society where changes in party composition can occur every 1 hr and 40 minutes on average [White, 1988]. Individuals gather in larger parties at night, split up during the day and party size increases again in the late afternoon [Fruth, 1995]. It is suggested that in the bonobos in Wamba form more cohesive parties than chimpanzees, divide less often into fewer parties and especially female bonobos are more cohesive than chimpanzees [Furuichi, 2009]. This fission-fusion system can be difficult to mimic in a zoo setting. It is recommended to provide large enclosures where bonobos can choose themselves how to group during the day, according to their needs. Some zoos that use managed fission-fusion, split and regroup multiple times during the day, while others regroup at night and split again in the morning or after a number of days. Especially the first method requires a lot of staff time, training and experience to correctly interpret the behaviour and needs of the bonobos.

Managed fission-fusion for aggression management

For zoo management, it is important to realise that **aggression is an integral part of everyday bonobo social life** [see section 1.8.4]. Aggressive interactions per se are not a reason to separate individuals or remove individuals out of the group. Especially when individuals reconcile with former opponents, or receive consolation from group member and recover well from the aggression, there is often no reason to intervene. After cases of serious aggression, a brief time-out can be used to separate victims and to check and if necessary, treat wounds, but the longer the victims are separated from the group, the higher the risk that reconciliation will be prevented, and tensions may accumulate. So, the quicker wounded animals can go back into the group, the better. Often wounded bonobos will receive much attention from their previous attackers who will inspect, groom and clean the wounds they inflicted. These processes are believed to strengthen relationships [de Waal, 2000]. Bonobos can be easily trained to allow minor wounds to be treated with disinfectant spray. Too frequent human interventions risk making the complex social environment more confusing for bonobos. Exceptions may be males that for various reasons were hand-reared, and who seem to be less able to cope with group dynamics (see above).

Occasional pairing of males by themselves, or creating **'all-male parties'**, for short periods of time is thought to provide some relief from the stress of being in the presence of dominant females. In such groups, males may give a more relaxed and playful appearance. Long-term all-male groups are not recommended, however, so this can only be considered a temporary measure. Older, fully adult males may also provide needed examples of social skills to younger males and therefore should not be separated for longer times from other males.

In conclusion, the Bonobo EEP sees managed fission-fusion as a means to manage certain individuals or situations, but not as a goal in itself. The goal should be to create large, naturalistic groups in large enclosures that allow the animals to create subgroups and regroup according to their own needs. For specific reasons and needs of individuals the groups can be managed and temporarily split up.

2.3.2. Transfers and introductions

Transfers between groups

When animals are transferred, please fill out the "Bonobo (*Pan paniscus*) behavioural information sheet" (see Appendix 4) and send one copy to the receiving institution and one copy to the EEP coordinators.

For all medical advise on medical procedures around bonobo transfers, please see the EAZA GREAT APE TAG VETERINARY GUIDELINES (July 2019) [Liptowsky et al., 2019, section 2.2.8.].

Since 1991, the EEP has focused **on leaving males with their mother** and transferring females out of their natal group as would happen in nature [de Bois, 1995; Van Elsacker, 1991]. When males have to be transferred, ideally, they are accompanied by their mother. Hand-reared males that don not rely on their mother, or males whose mother has died, can be considered an exception and may be candidates for transfer between groups. Whenever possible, these males will be accompanied by other familiar individuals from their original group, which seems to facilitate their integration. Experience shows that males often have a harder time adjusting to their new environment, especially when they have been hand-reared, and a successful transfer and introduction of these males in a new group will depend on the personalities of the male and other bonobos involved.

Females should not be transferred too young. In the past, several females that were labelled as "problematic", because they showed quasi-aggressive behaviour as adolescents, have been moved to other zoos at the age of 5.5-6 years. Experience has shown that this may result in insecure females who do not know how to behave appropriately in their new group. It is especially useful if young females learn in their natal group that there are boundaries and that dominance relationships should be respected. It is typical for juvenile females to get away with everything, but eventually they will learn in adolescence that not all privileges come for free. It is now recommended to leave females in their natal group as an adolescent, and only transfer them at the age of 7-9 years, when they have an established swelling cycle and are independent of from their mother. In addition, there are some indications that female bonobo who left their group without experiencing access to younger siblings, show reduced maternal skills. Ideally, young females will also have observed their mothers giving birth before leaving and have been able to practice their maternal skills on younger siblings.

Introducing new animals

Here we deal with the introduction of mature individuals. The introduction of (hand-reared) infants is described in section 2.4.8.. Compared to other species of great apes, bonobo introductions are **relatively easy** [e.g. Rieches, 1997]. Initially, introductions involve a lot of sexual activity, often quickly followed by grooming interactions and usually there is very little aggression [Gold, 2001; Hol & Van Elsacker, 1990; Pfalzer & Ehret, 1995; Rieches, 1997; J. Stevens pers. obs.]. It is, however, not unusual for more complex behaviours, including aggression, coalition formation etc. to start a few months after the introduction. These changes should also be monitored to evaluate the long-term success of an introduction.

New individuals can either be introduced new individuals **to the whole group in one go, or in a more gradual manner,** depending on background of the individuals, the size and the complexity of relationships within the group, and facility design. Especially in more complex groups, or when introducing a male into an existing group, a more stepwise introduction may be preferred. If aggression from a resident bonobo to the newcomer persists, it has been helpful in some cases to have these two individuals introduced to each other separate from the rest of the group to create a bond after which the two of them can be reintroduced back into the group [McLaughlin et al., 2007; Sexton & Gallagher, 1997].

The introductions of **adolescent females,** between seven and ten years old are generally not difficult. As reported for wild bonobos [Idani, 1991b], these females will quickly associate with a “Specific Senior Female” and form a bond with her [Pfalzer & Ehret, 1995; J. Stevens pers. obs.]. Resident infants and juvenile bonobos usually contact immigrants and can help to facilitate integration in the group [Pfalzer & Ehret, 1995; J. Stevens pers. obs.]. If **males** are to be transferred, it is suggested to be more careful, and to do introductions more gradually. Especially in the case of males without a mother, it may be wise to have the new male bond to one or more members of the new group, before introducing him to strong coalitions of females. For (re-)introductions of hand-reared infants, see section 2.4.7.

It is recommended to give bonobos **visual and tactile access** to on another prior to introductions. This may be necessary for only a few hours or up to several days depending on the age, sex, and psychological condition of the individual being introduced. If the composition of the subgroups is often changed (fission-fusion), it is important that the new bonobo(s) are allowed to observe all individuals in various combinations. This will allow the new bonobo to have a better understanding of the inter-individual relationships in all likely social settings.

Prolonged visual access without opportunities to interact may cause stress and therefore the duration of this period should be closely monitored.

Newcomer bonobos should be given **an opportunity to explore** the enclosure where the introduction will take place, before to the actual introduction process. This allows them to become familiar with escape routes in case stress or aggression become a problem as the introduction proceeds.

The introduction process should always be **closely monitored** to determine when each next step can be taken. The pace of the process should be geared to the animals' reactions and therefore the bonobos should be closely watched for signs of stress, and their physical and psychological status must be assessed at each stage of the introduction process.

It is recommended to give the bonobos **enough space** during an introduction, and avoid dead corners where animals can be entrapped. However, doing the initial introduction in too large areas is not advisable as individuals may then avoid each other continuously, and it may be more difficult for zoo staff to exert control in large areas, if necessary. Therefore, most institutions will do an introduction in the inside enclosure and/or in the holding facilities, where interventions are easier [e.g., Sexton & Gallagher, 1997]. When the newly arrived individual is well integrated in the group, is relaxed and has shown positive behaviour to several resident individuals, and aggression is minimal, introduction into the outside enclosure can start [Sexton & Gallagher, 1997]. The exact timing depends on factors such as the character of the individuals, design of the enclosure etc. It is usually preferable to give the new individual access to the outdoor enclosure in the presence of (a) conspecific(s) who is (are) familiar with the exhibit and management routines (e.g., entering and exiting the inside enclosure, etc.). New individuals who are introduced by themselves in an outside enclosure may not want, or know how to, get back inside, and this may hinder the introduction process [Sexton & Gallagher, 1997]. Individuals that are not used to designs such as water moats and/or electric fences should be monitored when they explore the outside enclosure for the first time. Some institutions train the bonobos and expose them to electricity and or water in the inside enclosure. It is also useful to know if new individuals have had (visual) experience with other (large) species if these are housed in the vicinity of the new enclosure, to prevent new bonobos from panicking when they encounter these “strange” other species.

The presence of large **amounts of food during an introduction** can be helpful in creating a relaxed atmosphere, but sometimes this leads to tensions. Much depends also on the character of the individuals, and on the kind of food that is offered. Offering (only) low quality food and/or food that is difficult to monopolise, such as browse, scattered seeds, non-preferred vegetables may provide distraction to the animals. Offering very valuable food, such as large pieces of preferred fruits, and/or food or enrichment items that can be easily monopolised can create extra tension and should be avoided during the first phases of the introduction.

Reintroducing adults after absence

Since bonobos are a fission-fusion species, and have developed a long-term recognition of former group-members, it usually is not a problem to reintroduce an animal if it has been absent for up to a few weeks, because of illness or wounds. When a male has to be separated for wound treatment after an aggression, it is recommended to give him some company of familiar individuals, also when he tries to avoid making contact initially. The advantage of such a companion is also that when the male is reintroduced into the group, the group's attention will be divided between him and his companion(s), making the reintroduction less stressful.

Reintroducing infants after absence

In some cases, zoos have taken infants away from their mother for medical treatment (usually in case of respiratory disease). Even very young infants of three weeks old have been taken from their mother, treated for a period of ten days up to a few weeks, and then could be given back to the mother. When such long-term separation is needed, the critical matter is than to keep the mother from losing her milk. This seemed not to be a problem in a number of cases. Sometimes the female will drink from her own breasts, sometimes older infants or even adult group members keep the milk flowing.

On the moment where the infant is returned to the mother, the following rules are advised:

- If the mother has been anaesthesised to provide medical care for the infant, but the infant does not have to stay in prolonged separation from the mother (e.g., a single shot of antibiotics is given, or when individuals are transferred), always WAIT until the mother is fully recovered before giving her access to the infant. When the baby is put on the mother's breast while she is sedated, there is a chance it will suckle and get some of the sedative in, falls asleep and does not respond when the mother is awake again. However, Chapman et al. [2017] report no negative effects from the sedation of the mother for medical surgery on an infant bonobo. Let the mother awaken in a separate enclosure next to the infant. Do not proceed further until she seems awake and alert.
- If the mother has not been anaesthesised, separate the mother from other individuals who are likely to interfere with the infant (rough adolescents, more dominant females, etc.)
- Put the infant in an enclosure adjacent to the mother, on a blanket or some woodwool
- Open the slide and give the mother the time to get used to her baby again. Monitor closely for nursing. Give them some time before introducing them back into the group.

2.3.3. Sharing enclosure with other species

Some wild bonobo populations have been seen to ignore guenons (*Cercopithecus ascanius; C. wolfi*) [Ihobe, 1997]; in other cases, bonobos were groomed by male red colobus (*Procolobus badius*) [Ihobe, 1990] or the bonobos themselves even showed affiliative behaviour to other species, such as play towards guenons and Angolan colobus monkeys (*Colobus angolensis*) [Sabater-Pi et al., 1993] or apparent concern towards a duiker trapped in a snare [Hayashi et al., 2012]. In zoos, co-housing of bonobos with patas monkeys (*Erythrocebus patas*) and red-tailed monkeys has been attempted without problems, but was abandoned when the monkeys aged, died and were not replaced[5]. Co-housing with bushpigs (*Potamochoerus pictus*) has been successful at one institution, but pigs were separated with electric fence when piglets were expected, to prevent the bonobos from taking the piglets [A Meinelt, pers. comm.]. Ingmanson & Neary [1987] observed bonobos in SanDiego Zoo interacting with local wildlife, and found that interactions were driven by curiosity rather than food acquisition.

However, since 1) zoo-housed bonobos have been observed to use sticks as clubs to kill a peahen [Gold, 2002] and a study by Ross et al. [2009] noted that all AZA zoos that kept bonobos stated that the bonobos behaved aggressively towards native wildlife in their enclosure and 2) at least some wild bonobo populations hunt, and kill small antelopes, rodents and monkeys, and consume these while they are still alive (see section 1.6.1. diet and 1.8.3. predation).

In conclusion co-housing bonobos with other species is not recommended. Co-housing bonobos with other great ape species, which was not uncommon in the past [e.g., Becker 1983, 1984; Carmo, 2005], is also not recommended.

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[5] Several of the bonobos housed with the monkeys were nursery raised, often alongside other species such as François langurs, which may have influenced their attitude towards monkeys!

2.4. Breeding

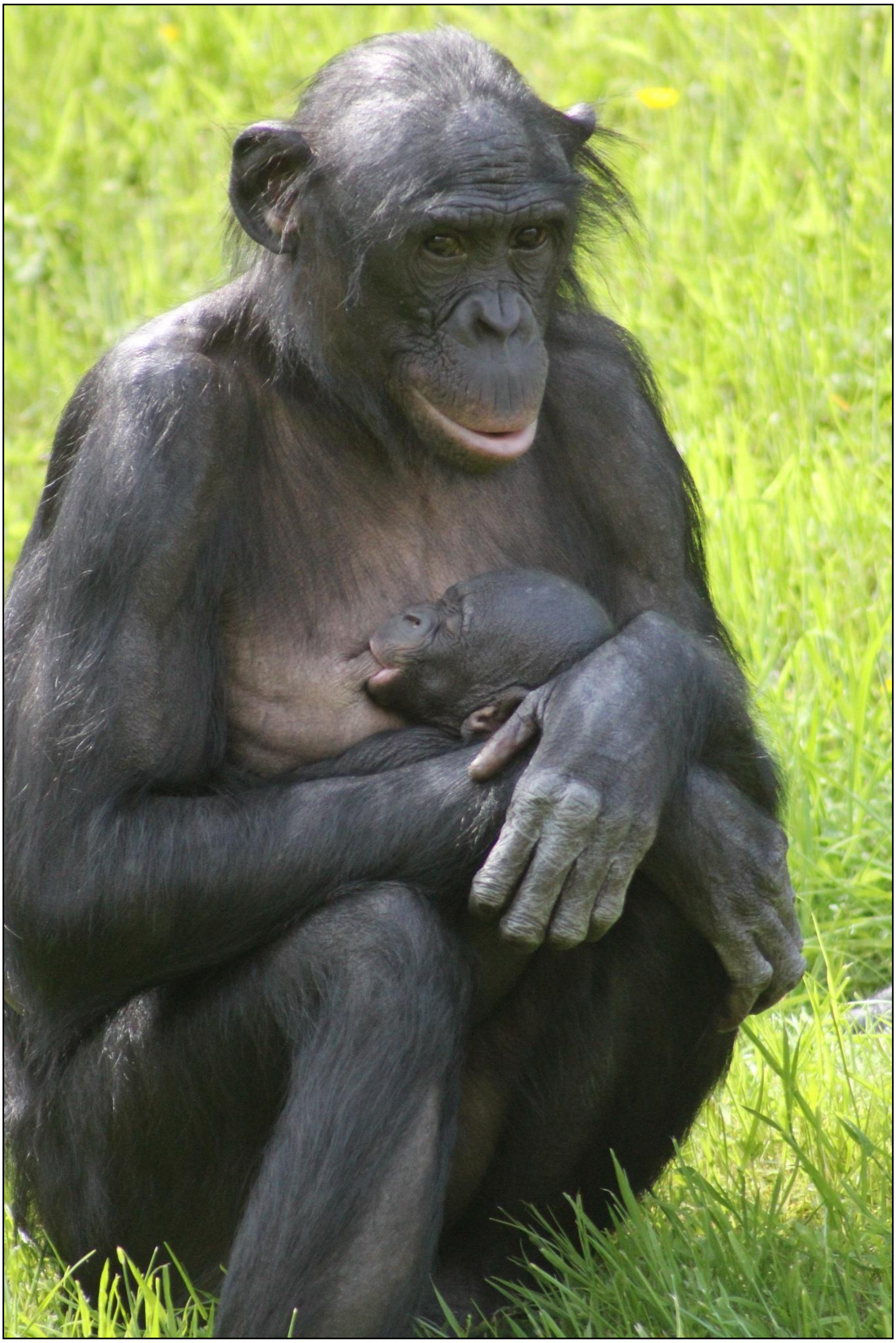


Figure 41: The Bonobo EEP recommends maternal rearing (Zoo Planckendael – Jeroen Stevens).

For EEP institutions it is not mandatory to produce a birth management plan for each bonobo. However, the SSP document “Bonobo Birth Management/Surrogate/Hand-rearing Packet” contains interesting information, as well as DVDs showing footage of births, ultrasound training, and hand-rearing. EEP institutions are encouraged to consult this document (available on request from the EEP coordinator) when in doubt about breeding problems associated with the bonobos in their care. The recommendations below are based on this document, as well as on various other sources.

2.4.1. Paternity diagnosis

Paternity diagnoses are vital for managing the zoo populations, as inbreeding may have deleterious effects on infant survival [Van Coillie et al., 2008] and for making appropriate transfer recommendations based on accurate pedigree information. When bonobos are kept in multi-male groups, any male from the age of six on should be considered a potential father of offspring, even when the group has been in managed fission-fusion. Therefore, it is recommended to take DNA samples of infants as soon as possible. When taking DNA samples, always wear gloves when taking the hair samples or cheek swabs to avoid contamination of human DNA with bonobo DNA. Change gloves if you sample different individuals to avoid contamination between individuals. Usually hair is pulled from individuals, which does not seem too harmful to adults. When sampling infants, be careful about the reaction of the mothers. A minimum of ten pulled hairs per sample is recommended. Samples must contain hair roots. Infant hairs are noted to be difficult to take, and may break off easily – so please make sure that the roots are attached. If the bonobos are trained to open their mouths, using cheek swaps can also be useful for DNA sampling, instead of hair samples.

See Appendix 5 for more details on how to collect hair samples. Send samples in a closed envelope (one envelope per individual) to EEP coordinators for analyses.

2.4.2. Mating

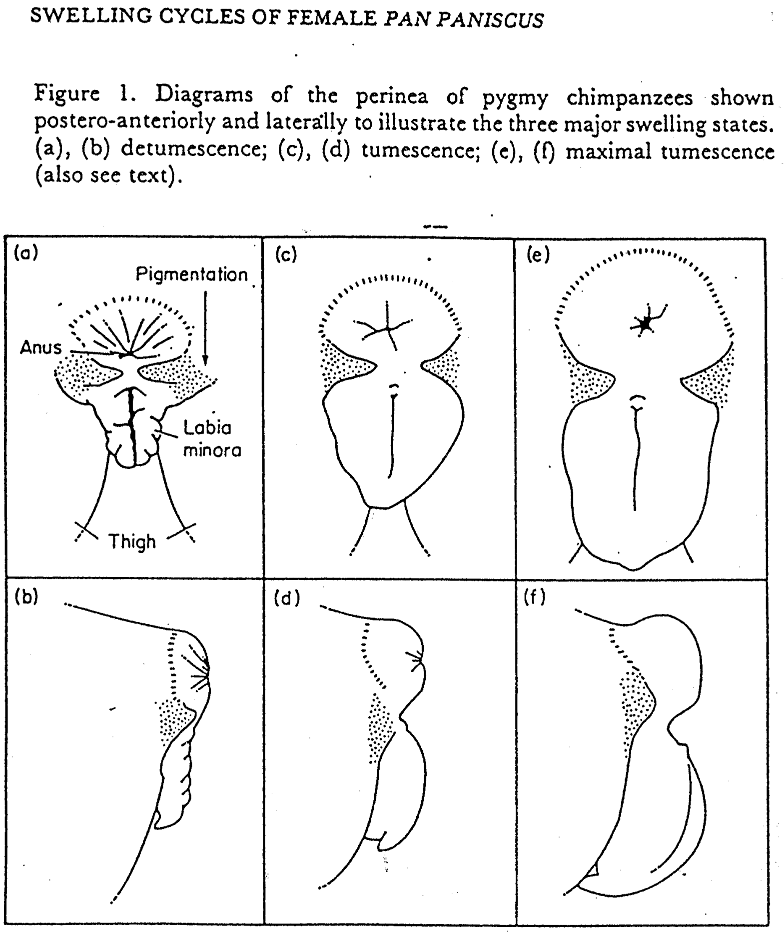
Each breeding group of bonobos should contain at least two adult males to allow for female mate choice and naturalistic group composition. Males as young as six years can be potential fathers. When multi-male groups are kept, paternity is hard to control. Nonetheless specific breeding recommendations to allow only certain male(s) to breed with certain female(s) can be made by the EEP coordinators. Then every effort should be made to allow for these breeding combinations, without hindering the welfare of the individual bonobos involved. Managed fission-fusion has been used successfully in these cases (see section 2.3.2).

2.4.3. Female swelling cycle

It is recommended that each zoo keeps track of the swelling cycles of the females. See Appendix 6 for a swelling score sheet.

For further details about anatomy of the swelling (Figure 42), the duration of swelling cycles etc., see section 1.7.1. Because no two females' swellings look exactly alike, it is recommended that you take photographs of each of your females during the different stages of their cycle to use in training/consistency of the keeper staff.

- Stage 1: No Swelling: the sexual skin is greatly wrinkled and sways when walking.
- Stage 2: Tumescent / detumescent: the sexual skin is rather turgid, but small wrinkles are visible on its surface.
- Stage 3: Maximum: the sexual skin seems quite firm, being lustrous without wrinkles.
- Stage 4: Super-maximum: the sexual skin is quite firm, without wrinkles and a clear gloss or shine on the sides.



SWELLING CYCLES OF FEMALE *PAN PANISCUS*

Figure 1. Diagrams of the perinea of pygmy chimpanzees shown postero-anteriorly and laterally to illustrate the three major swelling states. (a), (b) detumescence; (c), (d) tumescence; (e), (f) maximal tumescence (also see text).

Figure 42: Schematic overview of swelling phase 1 to 3 [Dahl, 1990].

Because swellings in bonobos are not reliable indicators of the period of ovulation, hormones can be used to test when females ovulate. Heistermann et al. [1996] found that the measurement of oestrogens and Progesterone metabolites in both urine and faeces are reliable methods for assessing reproductive function in this species. Jurke et al. [2000] noted that "*oestrogens that are found in urine are a good indicator for ovarian cyclicity, however, in faeces, oestrogen measurement did not yield any meaningful results […] It appears that the estrone in faeces is to some degree masked by other components in the extractant and can therefore not be reliably monitored using this technique*".

Human ovulation tests have been used successfully for bonobos by some institutions, to narrow down the window when pregnancy is likely to occur. To do this, urine must be collected from a clean surface. Training the females for urine collection will make this processless time consuming. First morning urine is recommended, but is not required for the test. This test detects the luteinising hormone (LH) surge. When the test is positive, it indicates thatovulation should occur within the next 24 to 36 hours. The use of ovulation tests is not necessary; rather it is just one of the tools that is available [Meinelt et al., 2007].

2.4.4. Pregnancy

Because bonobo females are known to continue to copulate during pregnancy [e.g. Bolser & Savage Rumbaugh 1989; Dahl, 1987; Furuichi 1992], the last observed copulations are usually not reliable indicators for determining pregnancy duration (Figure 43). **Pregnancy duration** can be calculated either from the last menses, or from the last maximal swelling. Because menses can be difficult to detect, the latter method is probably more practical [Meinelt, 2011]. Also, in the wild, pregnant adolescent females may only show shrinkage of swellings two months prior to parturituin [Kano, 1989]. When measured from the last menses to parturition, the entire follicular phase of the menstrual cycle is included, which can range from 17 to 34 days [Heistermann et al., 1996] and pregnancy duration is about 245 days on average [Thompson-Handler (1990): 246 days ± 4.1 SE (range: 227-277), N = 11; Bolser & Savage-Rumbaugh 1989: 244 and 245 days]. When measured from the last day of maximum swelling, Thompson-Handler [1990] found an average pregnancy of 235.6 ± 1.9 SE (N=3; range 230-241 days), and Van Elsacker et al. [1993] report pregnancies of 235 and 238 days. In a subsequent pregnancy the same female also had a pregnancy of 235 days.. See Appendix 7 for a list of individual pregnancy durations.

Behavioural indicators of pregnancy can include decreased appetite in some [Bolser & Savage-Rumbaugh, 1989] but not all females [Van Elsacker et al., 1993]. Increased thirst [Bolser & Savage-Rumbaugh, 1989; Van Elsacker et al., 1993], reduced activity [Bolser & Savage-Rumbaugh 1989; Van Elsacker et al., 1993; Behringer et al., 2009] and manipulation of nipples [Bolser & Savage-Rumbaugh, 1989; Van Elsacker et al., 1993]. Typically, swelling cycles become erratic during pregnancy, without reaching full tumescent size, but swelling events during pregnancy differ greatly between females [Bolser & Savage-Rumbaugh, 1989; Van Elsacker et al., 1993, 1997a; Vervaecke, 1999], but females generally continue to be sexually active [Kano, 1992; Van Elsacker et al., 1997a]. Post-conceptive vaginal bleeding has been recorded in some bonobos, and can be mistaken for menses, making estimates of pregnancy duration sometimes difficult [Meinelt et al., 2007; Van Elsacker et al., 1993; Vervaecke, 1999]. In bonobos observed at the Columbus Zoo, the female swelling has become shrivelled upon conception, indicating pregnancy, prior to positive confirmation from urine tests. This shrivelled state lasts for as short as two days and then returns to normal. The same shrivelled swelling appears again late in the pregnancy, and remains for up to a year following birth [Meinelt et al., 2007].

The use of human pregnancy tests is recommended for confirming a pregnancy. These tests are based on the detection of a human pregnancy hormone, Human Chorionic Gonadotrophin (HCG), in the urine. Various brands have been used at bonobo institutions with good result. It is best if the test is performed using fresh morning urine and the sample should not be contaminated with foreign materials or other bodily fluids. Usually these tests don't work in the first two weeks after conception, and their ability to detect pregnancies also diminishes agter the 5th month of pregnancy.

Methods used for detecting pregnancy include [Meinelt, 2011]:

- ClearBlue test kits (Frankfurt Zoo, Leipzig Zoo, Planckendael Zoo and Wuppertal)
- ClearBlue One Step (Unipath) tests (Frankfurt Zoo, Twycross Zoo)
- Urine EPT tests (San Diego)
- UCG-BETA STAT 1-hour passive hemaglutination inhibition tests (Milwaukee)
- Abbott Test Pack Plus hCG urine test (Columbus)
- QuickVue hCG urine test & HCG-S pregnancy test stip (Verify diagnostics) were used to monitor pregnancy in a wild bonobo female, and yielded positive results in all three trimesters of pregnancy [Douglas, 2014].

In some institutions females are trained to participate in **ultrasound monitoring** of pregnancies. This can be helpful to determine the stage of pregnancy, predict parturition dates and monitor health of mother and infant [Clyde et al., 2002b; Drews et al., 2010].

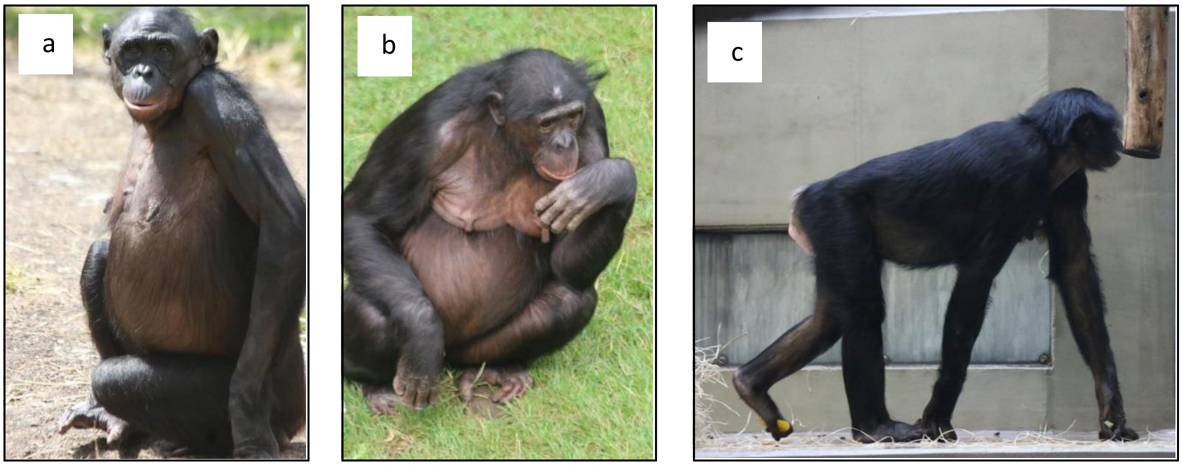


Figure 43: Examples of pregnant bonobos a: Djanoa six days before parturition (Zoo Planckendael – Jeroen Stevens)]; b: Yasa, four days before parturition (Leipzig Zoo- Jeroen Stevens); c: Huenda, four days before parturition (Wilhelma Zoo Stuttgart – Jeroen Stevens).

2.4.5. Contraception possibilities

It should be noted that contraception is currently not recommended for bonobos in the EEP. Nevertheless, the information below is provided for completeness, and for cases where contraception is necessary or advised. The information below was collected by the Bonobo SSP, AZA RMC and the EAZA Reproductive Management Group. For additional information, see the EAZA Reproductive Management Group (EAZA RMG) website http://www.egzac.org or contact contraception@chesterzoo.org.

EEP Institutions that have a recommendation to change the reproductive status of a bonobo must report every change (putting an individual on or off contraception) to the EAZA Reproductive Monitoring Group and fill in the EGZAC questionnaires.

Males

Vasectomy by surgical removal of a segment of the *vas deferens* is a practical and effective method of male contraception.

Vas ligation using a metal clip for vas occlusion without severing the *vas deferens* has been performed in five bonobos in the SSP population as a possibly reversible technique. No reversals have been attempted in any of these animals. With vas ligation (as with all vasectomy techniques), there is a risk of spontaneous reversal because of recanalization of the *vas deferens*. One such reversal was observed in a bonobo within a year after vas ligation. The reversal was detected due to the return of an opaque appearance to the ejaculate, which turns translucent after successful vasectomy. The spontaneous reversal necessitated the application of a second set of metal clips to the *vas deferens* of the affected animal. Monitoring semen quality from contracepted males over time is necessary to detect spontaneous reversal, which is identified by the presence of sperm in the semen. This follow-up analysis should be done at frequent intervals to guard against failure. Risks associated withthe vas ligation procedure must be predetermined, and the possibility of infection must be evaluated. An institution should endeavour to enlist the assistance of human medical specialists before undertaking this procedure.

Females

It should be emphasized that contraception for bonobo females is appropriate **only as a last resort**, in a case when relocation for suitable breeding is not possible, and when relocation to a reproductively appropriate situation (e.g., with aged, non-cycling female; or to an all-male group) is not practical. Special consideration must be taken with potential social implications of preventing oestrus swellings. Descriptions and additional recommendations are provided below. Keller et al. [2010] noted breakthrough bleeding while on lower oestrogen dose oral birth control pills.

Oral birth control pills (various brands): The use of birth control pills in apes is compromised by the difficulty in ensuring an animal's complete compliance with accepting and retaining the proper dose. Human birth control pills are available in different formulations of combined synthetic oestrogen and progestin. The human regimen for most formulations is 21 days of hormone treatment and seven days of placebo, which results in withdrawal bleeding similar to menstruation. Most apes contracepted with oral birth control pills have followed the same regimen. However, many bonobos have a longer cycle than 28 days, and some bonobos have received hormone for 28 or 35 successive days rather than 21, to more closely match their normal cycle. If oestrus behaviour is not desired, the placebo can be skipped for up to 12-16 weeks. If you start oral birth control pills, remember that it can take two to four weeks before the animal is contracepted, so you still have to separate the female from the males, if breeding is not allowed. Keller et al. [2010] noted breakthrough bleeding while on lower oestrogen dose oral birth control pills. Please see Agnew et al. [2016] for a review of oral birth control pill use in the bonobo SSP.

Etonogestrel (Implanon/Nexplanon) Intramuscular or subcutaneous implant: 1 rod is recommended, depending on the weight of the individual. Nexplanon in primates usually lasts between 2-3 years, however, this varies from individual to individual. There may be a low level of follicle production whilst on Nexplanon which can stimulate sexual behaviour or signs of oestrus such as skin swelling. Nexplanon will also thicken cervical mucus so even if ovulation does occur, sperm is inhibited. The first problem is knowing if the female has a sufficient dose of progestin to keep her effectively contracepted. There have been cases in various species where females showed oestrus, and may have even copulated but didn't conceive. If the implant is not in place or if the implant has been in for a minimum of two years then replace it with a new one.

Medroxyprogesterone acetate (DepoProvera) Intra-muscular injection formulation: Administration of this synthetic progestin is by injection, which may involve the use of darts to administer the drug or an anaesthetic event. The recommended dose is 2.5-5mg/kg body weight every 2-3 months respectively. Care must be taken to ensure administration of the full dose [Perkins 1995]. Latency to effectiveness is approximately 1-3 days, however, it is recommended that sexes should be separated for one week or the first bout must be supplemented with additional contraception for seven days. DepoProvera is designed to be fully reversible and time to reversal varies greatly among females and can be as long as two years. As DepoProvera is not an implant it needs time until the drug to clear from the individuals' system and this length of time can vary between individuals is unpredictable in some cases. The effects of long-term administration of DepoProvera are not completely known. It may be best used as an interim contraceptive method. As recommended by the AZA Orangutan SSP, DepoProvera is best considered if females are at risk of becoming pregnant if there are delays in obtaining or administering another contraceptive method [Perkins 1995]. A side effect of DepoProvera is that females may develop male secondary sex characteristics and there may also be an increase in aggression. There may also be a deleterious effect on the endometrium following prolonged use.

Intrauterine device (IUD): Physical considerations suggest the use of an IUD recommended for use in the human nulliparous female (i.e., the smallest size). Use of an IUD is complicated by the potential for removal of the device by the animal, a possibility countered by shortening of the removal strand. This, in turn, makes removal of the device when desired more difficult. Further, there is potential for complications should pregnancy be initiated in the presence of the device. Limited experience suggests a failure rate of approximately 5% (not dissimilar to the rate for human females) [Nadler et al., 1994; Porteous et al., 1994].

Gonadotrophin Releasing Hormone (GnRH) agonists: GnRH agonists, such as deslorelin (Suprelorin; guideline below) or leuprolide acetate (Lupron), reversibly suppress the reproductive endocrine system, preventing production of pituitary hormones ((FSH and LH) and gonadal hormones (estradiol and progesterone in females, testosterone in males). The observed effects are similar to those following either ovariectomy in females or castration in males, but are reversible. GnRH agonists first stimulate the reproductive system, which can result in oestrus and ovulation in females or temporary enhancement of testosterone and semen production in males. The stimulatory phase can be prevented in females by treatment with a progestin or oral birth control pills for 2-3 weeks. This method has not been used to date in bonobos and only limited experience with this method is available in nonhuman primates.

Deslorelin acetate (Suprelorin) Subcutaneous implant: 1x 4.7 mg is recommended for a minimum duration of six months and 1x 9.4 mg is recommended for a minimum of one year. Up to three implants have been used in some cases if sexual behaviour or characteristics are not fully suppressed. Due to the initial stimulation of the reproductive system, the first bout must also be supplemented with additional contraception e.g., oral megestrol acetate (Ovarid/Megace) daily seven days before and eight days after placing the implants, or by continuing to administer birth control pills after implant placement. Suprelorin is designed to be fully reversible. In order to increase the chances of a full reversal, place the implant in such a way that facilitates removal. The most common side effect of Suprelorin is weight gain.

Weight gain is a common side effect associated with synthetic progestins and GnRH agonists, but less so with combination oral birth control pills. Because obesity can have serious health consequences, weight should be carefully monitored and diet managed as necessary.

Extensive data from humans and limited data from the AZA Wildlife Contraceptive Centre database indicate that oral birth control pills and the synthetic progestin products should be reversible in apes.

2.4.6. Birth

It is not recommended to separate any pregnant female from the social group prior to parturition.

Based on a survey in 1994 [Fagan, 1997], most births in zoo-housed bonobos are reported to take place at night. Average labour time is 7.1 hours (N = 7). Birth weights are between 1.000 and 1.700 g [Hill, 1968; Kuroda, 1989; Neugebauer 1980, 1985].

In **the hours prior to parturition** observers have noted increased pacing/restlessness, increased nest building and re-building, posturing, including stiff postures that may indicate straining (21-9h prior to parturition), manipulation of the nipples and genitalia [Bolser & Savage-Rumbaugh, 1989: Coppola et al., 2011; McLaughlin et al., 2007; J. Stevens pers. obs.; Van Elsacker et al., 1993]. Visual ano-genital contractions can become apparent 120-60 minutes prior to birth; visual abdominal contractions 34 to 25 minutes prior to birth. Sometimes a white lump or mucous plug can be seen in the middle of the swelling prior to giving birth [Douglas, 2014; Van Elsacker et al., 1993].

During the birth process mothers typically use their hands (or feet) to manipulate the vulva, open the amniotic sac and draw the infant out [Bolser & Savage-Rumbaugh, 1989; Coppola et al., 2011; Kirchshofer, 1962a, 1963; Van Elsacker et al., 1993]. After birth, female bonobos will clean, inspect, cuddle and look at their new-born infants [Bolser & Savage-Rumbaugh, 1989; Coppola et al., 2011; Douglas, 2014; Kirchshofer 1962a; Van Elsacker et al., 1993].

The delivery of placenta can vary from 3 to 75 minutes post-partum [Bolser & Savage-Rumbaugh, 1989; Coppola et al., 2011; Halbwax et al., 2009; Kirchshofer, 1962a;]. Biting of the umbilical cord is observed in some [Coppola et al., 2011], but not all females (e.g., Douglas, 2014], and sometimes the umbilical cord will just dry up and break, usually within 24 to 26 hours after delivery [Bolser & Savage-Rumbaugh, 1989; Halbwax et al., 2009; Kirchshofer 1962a]. If the female does not sever the placenta immediately, close monitoring of the placement of the cord is necessary to ensure that it does not become wrapped around the neck of the infant or constrict the body in any way. If the cord is wrapped, but the mother is attending to it and keeping it from constricting around the infant, monitoring is warranted, but intervention may not be necessary. The female may continue to vaginally bleed for a few days [Meinelt, 2011]. **Placentophagy** (Figure 45) by the mother and even sharing of the placenta between other individuals is commonly observed [Bolser & Savage-Rumbaugh, 1989; Coppola et al., 2011; Douglas, 2014; Kirchshofer, 1963; Van Elsacker et al., 1993].

Figure 44: Placentophagy in bonobos (a: mother eats the placenta of her own newborn (Wilhelma Zoo Stuttgart - (c) Katharina Chaefler photography); b: adult male chews on placenta of a newborn in rhe group as an adolescent looks on (Planckendael Zoo – Peter De Ridder).

Nursing by the infant is usually seen within the first 24 hours in bonobos, although inexperienced mothers may take longer than 24 hours to begin nursing [Van Elsacker & Struyf, 1991]. Nursing sessions are short in duration, and seem to occur every one to three hours. Breast size varies between females. Small breasts are not an indicator of a lack of milk production. As the baby nurses, breasts tend to fill out a bit more. If the infant's health and general condition are good and there are no immediate threats, the mother and infant should be given as much time as possible to form a bond with one another before intervention [Meinelt, 2011]. If the infant's health and general condition is good, the mother should be allowed up to 72 hours to begin nursing [McLaughlin et al., 2007].

First time mothers' responses to new-borns may vary from fear and avoidance to completely competent maternal care. However, it should be recognized that experienced bonobo mothers can sometimes reject subsequent infants (Zoological Society of San Diego records). Adolescent females or future mothers may benefit from observing births and maternal care while housed in a social group. Van Elsacker & Struyf [1990] recommend that guidance be provided for inexperienced primiparous females, starting in the last quarter of the pregnancy (e.g., animal care staff can use a stuffed toy to demonstrate proper ways of holding an infant) [Figure 45a]. In one case an unexperienced mother observed such keeper demonstrations and afterwards reared her own offspring [Van Elsacker & Struyf, 1990].

Giving birth in group settings seems to have no negative effect, and some authors suggest that giving birth is a social event in bonobos [Coppola et al., 2011; Douglas, 2014; Ryu, 2017]. Therefore, it is not recommended to separate mother from the group, unless there is serious concern for maternal health or social problems in the group. Usually the other group members show curiosity [Fagan, 1997]. Other females can be interested in the birth, and may help to chase males away [Coppola et al., 2011; Demuru et al., 2018; Van Elsacker et al., 1993]. **Kidnapping** new-borns or young infants from their mothers has been reported occasionally, usually by more dominant females who take infants from younger inexperienced mothers, [Bakker, 1999; Hübsch, 1970; Bolser & Savage-Rumbaugh, 1989; Neugebauer, 1985; J. Stevens pers. Obs.; review: Vervaecke et al., 2003]. Usually mothers are capable of retrieving infants, or infants manage to return to their mother by themselves [Vervaecke et al., 2003]. In some cases, it has helped to separate mother and kidnapper in a smaller room to make it easier for the mother to retrieve her infant, but in some cases, it has been necessary to sedate the kidnapper to give back the infant to its mother. Permanent "adoption" of a newborn by a more dominant female has been successful when she was nursing her own 1-year old offspring [Leipzig Zoo, J. Stevens pers obs.- Fig 45b]. When infants get older, alloparenting is also common, but is usually less obtrusive, and it is not unusual for other group members, including adult males, to carry around infants and juveniles [Ingmanson, 1992; Kano, 1998; Patterson, 1979].

Figure 45: a: keeper demonstrating to an expecting first time mother how to hold an infant bonobo with a stuffed toy (Zoo Planckendael - from STruyf & Van Elsacker, 1990); b: adult female having adopted an additional infant 1 year after giving birth herself and rearing both simultaneously

2.4.7. Development and care of young

Female bonobos rear their own young and other individuals are not very involved in caring for the young. A case study showed that a three-year-old, unweaned infant whose mother died in a zoo and was kept in the natal group, did not develop a specific relationship with any of the adult group members, but was still not showing signs of depression and could cope with the new situation, without special interventions needed [de Lathouwers & Van Elsacker, 2007]. Subsequent similar cases have occurred within the EEP with equally good results, as long as the infant can feed independently and move around no special intervention seems necessary. In the wild, care of orphaned bonobos by adult males has also been reported [Hashimoto et al., 1996]. There is tremendous individual variation among infant bonobos and the highly interactive mother-infant relationship [Weaver, 1997; Johnson, 1997; de Lathouwers & Van Elsacker, 2004], and to date very little information has been published on infant development and care of young. The following information is therefore largely indicative.

Infant development (0 to 1 years)

Bonobos nurse about twice every hour in the natal period, three times per hour in from one to six months of age, and once every two hours thereafter [Weaver, 1997]. As in other species, there is a bias to suckling the left nipple [Hopkins & de Lathouwers, 2006; Weaver, 1997]. Mothers may sometimes direct the infants head to the nipple, a behaviour called ‘cupping’ [Weaver, 1997]. Although, it is sometimes reported that bonobo mothers will not refuse their infants to nurse [Kuroda, 1989; Kano, 1992; Weaver, 1997], it is not uncommon to see female bonobos refuse their infants access to the nipple, and in fact a comparative analysis showed that zoo-housed bonobo mothers rejected their infants more frequently than chimpanzee mothers did [de Lathouwers & Van Elsacker, 2006]. Wild bonobos are weaned at four to five years of age [Kuroda, 1989]. de Lathouwers & Van Elsacker [2006] found that four juvenile bonobos, observed at an age older than four years, were still not fully weaned; other anecdotal evidence reports that individuals were still sucking at age of six [Johnson, 1997; J. Stevens, pers. obs.]. While weaning in bonobos seems to be less stressful than in chimpanzees [Kuroda, 1989; de Lathouwers & Van Elsacker, 2006], temper tantrums in youngsters that are being weaned are common in zoo-housed bonobos, in contrast to reports from the wild [Kano, 1992; Kuroda, 1989]. It has been suggested that weaning may be more traumatic in male infant bonobos [Johnson, 1997]. Some mothers with short interbirth intervals have been observed to nurse the new-born as well as the previous offspring [J. Stevens, pers. obs. – figure 46a]. In some cases, females have adopted an additional infant one year after giving birth themselves, and were able to nurse both to good health. It is also not uncommon to see zoo-housed bonobo mothers drink milk from their own breasts (figure 46b). This does not seem to limit the milk uptake or growth of the infant.

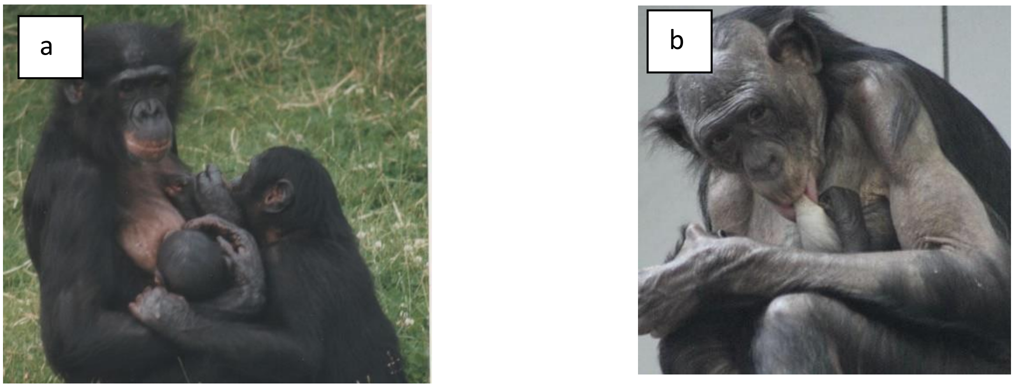


Figure 46: a female nursing her newborn as well as her previous offspring who is 3.5 years old (Zoo Planckendael – Peter De Ridder); b: Female drinks from her own breasts while nursing her own offspring (Wilhelma Zoo Stuttgart – Jeroen Stevens).

Hand-reared infants will turn their heads towards keepers in the first few days of life, earlier than in other ape species; vocalisations start in the first week; they can focus between four and six weeks; smile at five weeks; grasp at seven weeks; sit alone at three and a half months [Neugebauer, 1980]. Between the age of three and six months, bonobo infants begin to crawl around, dangle, climb and explore the environment [Fagan, 1997; Neugebauer, 1980; Weaver, 1997]. Frankfurt Zoo has reported three bonobos infants in human care between 0 and 120 days old; each of them started crawling at 45 days, and sit alone with 60 days [C Knott & M. Casares, pers comm.]. For the **development in a mother-reared** infant, approximately the same applied: in the first week, the infant can keep head up for very short periods, makes gripping movements with arms and kicking movements with legs during nursing and can cling on to mother from day one; in the second week, the infant can keep head up for a few seconds; in the third week, the infant shows visual orientation towards mothers face and it can pull its own body upwards with the arms; fourth to fifth week: infant starts to move around on mothers body, shows visual coordination when fixating on objects, rooting behaviour becomes weaker [Jordan, 1977]. The airplane game, where mothers dangle infantsin the air with their feet, has been observed from fourth to fifth week [Hübsch, 1970]. The firstdeciduous teeth appear between four and six weeks, and temporary dentition is complete atten months [Neugebauer, 1980]. Six to ten weeks: the infant pulls herself down from her mother's body and can sit upright lean against her mother's body, it shows gripping movements towards mesh, and starts gnawing on her own hands which may indicate breakthrough of the teeth; 11-15 weeks: the infant can sit upright and scoot around with herlower body touching the ground and arms stretched, it reaches out to food when her motheris eating; 16-20 weeks: the infant attempts to climb the mesh and begins to show coordinatedquadrupedal movement [Jordan, 1977]. Bonobo infants start feeding on solid food between three and eight months [Fagan, 1997; Hübsch, 1969; Jordan, 1977; Kano, 1992; Weaver, 1997],first picking up pieces of food with their mouth, later with their hands [Weaver, 1997]. Some infants start riding their mothers back around five to six months [Jordan, 1977], but this is veryindividualistic: some mothers always carry infants and juveniles on their belly. From six to seven months, infants may start to climb around, by seven to eight months an infant shows knuckle walking when moving on the floor [Jordan, 1977]. Bipedal locomotion starts to develop between 10 and 13 months of age [Jordan, 1977]. Nest building behaviour started to develop around eleven months of age [Jordan, 1977]. Around 12 months of age, infant bonobos begin to spend more and more time away from their mother, although this occurs later than in chimpanzees [de Lathouwers & Van Elsacker, 2004].

Weaver [1997] summarised the development of two mother-reared infants she observed as in Table 8:

Table 8: Development of behaviour in two mother reared bonobos observed by Weaver [1997].

Age (month)	General behavioural trends
First month: mostly immobile; behavioural units are recognizable but not performed completely or with control	- Constant ventral contact with mother - Grasp weak and intermittent - Mother moves carefully, provides full support and walks with hunched gait on three limbs - Mountaineer short distances over mother's body - Suckles from one nipple; changing nipples is unusual - Rooting behaviour; maternal assistance in finding nipple - Head off position brief and weak but improves by midmonth - Pushes rear end away to defecate off mom - No evidence of white tail tuft
Second month: Beginning of weak localised activity, associated with increasing strength	- First clinging without maternal support (45 days) - Head-off position less wobbly, changes from event to state - Arms used with some control, e.g. reach for an object - Maintains integrity of behavioural states - Facial expressions more defined - Visual acuity: look at, reach for and touch mother's face
Third month: Stage characterised by active localised activity called the fidgets, associated with increasing body and appendage strength	- Tooth eruption begins - Balance enhanced - 'elbow behaviour' - Rapid development of visual following and attentiveness - Ventral contact maintained now without maternal assistance - Reflexive grasping when mother moves - Chest-off clinging when mother walks
Fifth month: Active postural activity performed next to rather than on mother Increased locomotory skills and oral behaviour	- Only ventral contact when mother is stationary - Sit, crouch, bipedal stand next to mother (with ambidextrous grab) - Starting to stand and walk quadrupedally - Increasing interest in food evident - First observation of infant mouthing food - Visually vigilant and highly responsive to movement
Sixth month:	- Exhibits quadrupedal walk - Reduction of maternal contact with infant

Primary changes involve locomotion and feeding	- Few vocal complaints from infant at noncontact - Climbing: extends arm to mother for retrieval - Dangles upside down from shelf - Beginnings of social interaction with non-mother conspecifics - Development of white rear-end hairs - First laugh - Self-grooming with long adult-like scratches - Mother entices infant to walk to her - Mother holds food in front of infant's mouth - Mother stops keeping one hand on infant
Eight-nine months: Refinement of existing behavioural patterns rather than addition of new ones Increasing attention to social and non-social environment	- First observation of infant eating solid food in adult-like manner - Foraging - Dangling typical when mother is moving - Invited to play by juvenile; one or both mothers intervene and prevent - Receives extensive grooming from conspecifics - Leans against something when out of contact - Remains within 5 meters of mother - Frequent manipulation with both hands and feet - Mother shares masticated food with infant - Naps on ground next to mother - Rides jockey on occasion; doesn't always position correctly - Maternal vigilance high but tolerance increases for noncontact and interaction with older conspecifics

Juvenile development (2 to 6 years)

Much less research has been reported on the development of juvenile bonobos. By the age of two years, young bonobos start showing most of the adult behaviours. After 20 months of age, immature bonobos start to increase their time grooming conspecifics, [de Lathouwer & Van Elsacker, 2004], and other friendly interactions with group members, such as social play or sexual activities [Braem, 2015]. Also, in wild bonobos, it is observed that after the age of two, sexual contacts with group members increase, but drop again at the beginning of adolescence [Hashimoto & Furuichi, 2004]. In comparison to chimpanzees, juvenile bonobos seek more contact with their mother's nipples than chimpanzees [de Lathouwer & Van Elsacker, 2004]. By the age of seven years, wild bonobos are independent from mothers with regards to movement and alimentation, but will still keep close social proximity to their mothers [Kano, 1982a; Lee at al., 2020]. Males will continue to keep a close bond with their mother during adolescence and adulthood, females will usually become less dependent on their mothers and eventually migrate out.

2.4.8. Hand-rearing

Before any decision is being made on hand-rearing a bonobo, the Bonobo EEP coordinator should always be consulted first.

Although hand-rearing protocols are available (see below, and Appendix 8)**, hand-rearing is not recommended for bonobos in the EEP and should only be used in life-threatening situations for infant and/or mother**. Therefore every effort should be made 1) to give mothers the chance to rear their own infants, 2) to find surrogate parents. While common in the past, nursery rearing with conspecifics or with other species [e.g. Wolf 1990; Scharf, 2000] is no longer recommended for bonobos, as there is ample experience with placing the individual back in the group under the care of a surrogate parent. Also, experience has shown that **nursery-reared infants may be showing a lack of social initiative**, possibly because they are used to undergo activities (being put up, being fed, being put away) without exercising any control and this passive attitude can draw aggression from other individuals after reintroduction. Sexual contact, including patting, touching, rubbing and tickling genitals is also necessary for normal infant development [Johnson, 1997]. Especially male bonobos need their mother throughout their lives for support and social contact [Surbeck et al., 2010]. Hand-reared "orphan" male bonobos are more likely to lack some of the appropriate social skills males need.

If no surrogate parent can be found in the group where the infant is born, the EEP coordinator(s) will look for a suitable surrogate parent in other groups.

Decision process

The following text has been adapted from Bemment et al. [2006] ""EAZA Great Ape TAG guideline on the hand-rearing and early integration of infant apes":

It is strongly recommended to leave young apes with their mothers whenever possible.
The following circumstances are examples where the welfare of the individuals concerned demands that action of some sort is taken:

- When a mother gives birth to twins and cannot cope, and it is not possible to help with supplementary bottle feeding [6].
- When social conditions threaten infant survival.
- When a mother has died, is too ill or inexperienced to care for her young.
- When an infant is abandoned by its mother.
- When the baby is too ill or weak to suckle.

---

[6] Note that in bonobos, one mother successfully raised a set of twins, so twinning is not a reason per se to hand-rearing.

Under such circumstances one or more of the following actions should be considered to bring about natural rearing:

- Encouraging the mother vocally.
- Separating the mother and baby to give them some peace.
- Separating aggressive group members if it helps to calm the mother down.
- A trusted keeper showing the mother what she is supposed to do.
- Anaesthetising the mother and putting the baby in the right position to suckle.
- Supplementary feeding with the infant still being with its mother or another female of the same species willing to accept it.
- Surrogacy / foster rearing by another ape (maybe at another zoo).

In the event of a potential case of maternal neglect a mother should be given as long as possible (taking due account of the welfare of the baby and drawing upon the experience of colleagues) to try to suckle/rear her offspring. **At least 48 hours**[7] can usually be allowed to elapse before non-suckling becomes a concern as new-born apes can usually survive at least as long as this without having suckled. The ability to hold the head up, strength of clinging reflex and frequency of crying may give indications of the condition of infant and the degree of urgency to act in one of the ways mentioned above. Therefore, after the female gives birth, the situation should be watched closely by preferably only one person and at least for the first three to four days, especially, in the case of a primiparous female or a female who has shown a lack of maternal behaviour before. Care must be taken that the mother/group does not feel disturbed by being watched (with or without binoculars) or by the presence of video camera equipment.

In such situations of potential maternal neglect, it is strongly recommended that institutions contact the Bonobo EEP coordinator or other experienced colleagues to help them find the best solution and decide if hand-rearing is unavoidable and/or if early (re-)introduction or the transfer to a nursery is advisable.

An infant's long-term future should also be taken into account before finally deciding to hand-rear it i.e. its genetic value to the breeding programme and the likelihood of successful reintegration. If this is in doubt then euthanasia should be considered (if allowed under national laws) after consultation with the owner, the EEP coordinator, the zoo veterinry, and (depending on the zoo’s policy) the veterinary of the official authority.

Hand-rearing protocols

When all options have been exhausted in attempting to keep the infant with its mother and social group or in case of life-threatening situation, then a hand-rearing and re-socialization plan needs to be implemented. If the baby has to be taken away from the mother to save its life, initial care should preferably be given by an experienced zoo staff member and following

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[7] Killmar et al. [1997] state even 72h period might be necessary

methods which have proved to be successful. Accurate, consistent record keeping is an important part of the hand-rearing protocol.

Hand-rearing should always be done with **early reintroduction** to conspecifics in mind. The goal is to **return that individual to a social group as soon as possible**, with the self-confidence, physical abilities, communication skills, and social skills necessary to be a well-adjusted participant in the group, and ultimately a contributing member of the species. When the decision is made to hand-rear an infant, the caregiver should keep in mind that the methods used will have a lasting impact on the animal in all subsequent phases of its life. Prolonged isolation could result in social retardation, health problems, inability to raise infants, and aberrant behaviour. A lack of early social experience is a major setback in the infant's development, and can cause alienation from the group, which may never be overcome even in adulthood. Rearing should therefore occur alongside conspecifics as much as possible, and human caregivers should mimick adult bonobo behaviours such as quadrapedal motion, (including abrupt movements and speed changes), playing, discipline, vocalizations, and providing body contact around the clock.

It is recommended to start introducing the new-born to a surrogate parent as early as possible (see below). Prior to the actual introduction, however, the infant should **be exposed daily** to the sounds, smells and sights of other bonobos (Figure 47). Building up a relationship starts with carrying the infant to the group (as soon as its health is stable enough) and making contact through the wire-mesh for the initial months of life. The social integration should be finished (i.e., the infant being in the group all day) at 18 months of age. However, full integration may be possible much sooner.

Figure 47: Set-up where the bonobo infant is in visual and auditory contact with a group of bonobos during the day [Frankfurt Zoo – Jeroen Stevens].

Human **formulas of 20 to 24 Kcal** can be successfully used to bottle raise bonobos. The diet used for each individual should be chosen with the neonatologist's advice. Human infant formulas such as Enfamil, Similac and SMA have been successfully used to hand-rear bonobos at the San Diego Zoo [Kilmar et al., 1997]. The approximate amount of formula fed at the San Diego Zoo is determined by the infant's body weight. Two techniques can be used to assess total amount fed each day.

1) An amount of formula should be fed each day that is equal to approximately **20% of the infant's weight**. The formula mixture is usually 1:1 with water. If the infant is not maintaining its weight, the amount of formula can be increased, if the infant will take it. Alternatively, the concentration of the formula mixture can be increased to two parts formula to one part water. The richer the formula, the more likely that diarrhoea may occur. This must be treated quickly to prevent dehydration.
2) Determine the Kcal/kg body weight needed to meet daily energy needs. The calculation is: **120 to 150 Kcal/kg body weight/24 hours**. If, for example, SMA is the formula to be used, it offers 20 Kcal/30 ml (when mixed per label instructions). Calculations for a bonobo infant that weighs 2 kg would then be:
    - 2 kg (120 Kcal/kg) = 240 Kcals needed per day
    - 240 Kcals (30 ml/20 Kcal) = 360 ml/day to meet energy needs
    - For 12 feedings every 2 hours: 360 ml/12 = 30 ml per feeding.

The concentration of the formula can be increased slightly if the infant is not consuming the prescribed amount of Kcal nourishment in a 24-hour period [Kilmar et al., 1997]. Similac Special Care 24 Kcal has been used by Columbus Zoo and Aquarium to increase weight gain when it is desirable to do so without increasing the volume fed.

Lombardi et al. [2011] describe the following procedures for bottle feeding.

- For the first few months, disposable volufeeders and disposable nipples can be used for all liquids. 250 ml plastic bottles are used as volume increases. The nipple is determined by the infant's ability to suckle.
- Bottles under 20 ml, can be heated by immersing them in hot water, which gives more control of temperature for a limited volume. Before wrist testing the temperature, bottles should be shaken well.
- During feeding, the infant is held close to keeper's breast, simulating the ventro-ventral position in which bonobo females feed their young, and feeding slowly to prevent aspiration.
- For the first few days infants can be fed approximately 10 ml and then burped. As infant's sucking ability and volume of formula increases, larger amounts can be given between burps.

- From two months on, the infant can be trained to drink a bottle through the mesh, during the day. This will help the infant become comfortable with this type of feeding as this is the only way the infant can be fed after the introduction to the surrogate.
- For the first three months, the infant is bottle fed formula every two or three hours. If the infant becomes hungry between feedings, you may offer small amounts of oral electrolyte (e.g., Pedialyte), or water (about half of the volume of the formula.) As solid foods are added it is possible to stretch the feedings to once every four hours.
- Night bottles are discontinued before the introduction in the group. Depending on the age of the infant, bonobo keepers may stay to give an evening bottle after introduction.

Feeding frequency: A new infant should be fed **every two to three hours**, on a 24-hour schedule, at least for the first few weeks. The plan to reduce the number of feedings will depend on the infant's general health, and specifically on the infant's willingness or ability to consume more formula per feeding as the number of feedings are reduced. Generally, when it is determined desirable or necessary to discontinue the 24-hour schedule, one feeding can be discontinued per week until the desired schedule is achieved. The amounts of the remaining feedings are increased so that the total amount of formula consumed over a 24-hour period remains the same. Great care should be taken not to rush the infant. Only proceed with reducing the number of feedings if the infant's consumption and weight are maintained at acceptable levels. As an example, the schedule used by the Columbus Zoo and Aquarium on an infant is described in Table 9:

Table 9: Bottle feeding schedule used for a hand reared bonobo in Columbus Zoo

Time	Feeding schedule
1-3 months	Feeding every two hours, for a total of 12 bottles per 14 hours
3-6 months	Feedings every 3 hours, for a total of 8 bottles per 24 hours
6 months	One feeding was dropped
7 months	One feeding was dropped
8 months	One feeding was dropped
9 months	Infant was introduced to biological mother. Bottles were continued after reintroduction, although modifications to the schedule and amounts per feeding were made to lessen disturbance of the group

The introduction of solids should take place by the time the infant is mobile and/or teething, at about four months of age [Kilmar et al., 1997]. The infant may not consume the food items, but the presence of solid foods that the infant can manipulate, smell, and taste, is an important part of the learning process. Food items should be cut into pieces that are easy for the infant to pick up, but not of a size that can be choked on if consumed. It may be desirable initially to steam and soften root vegetables (carrots, yams, etc.). As the youngster increases its consumption of solids, the process of weaning it off of the formula can begin. The schedule and timing of the process should be determined by the overall consumption, weight gain, and general health of the animal [McLaughlin et al., 2007].

Providing a variety of stimuli and opportunities to develop motor skills is critical from a very early age. It is strongly recommended that the infant be held continuously in ventral contact with the keeper, and encouraged to cling much as it would if it were being mother-reared. The more close contact the better, and the infant should certainly not be left lying in one position for long periods of time. Even during the night, the bonobo should sleep on the keeper's chest / breast to relax by the heartbeat of the caregiver and as great apes do handle new born usually. The tactile stimulation and movement provide critically needed stimulus. Sexton & Herfel [1992] report on the use of fake fur vests that stimulate gripping muscles, which is also used successfully in Frankfurt Zoo. Assistance should be given to the infant to move or climb. A variety of opportunities for seeing, feeling, tasting, smelling should be provided. Audiotaped bonobo vocalizations, mirrors and grooming by keepers as beneficial stimuli [Sexton & Herfel, 1992]. However, it is important for the infant to maintain a sense of security; a familiar toy, blanket, or an individual can do much to reduce fears of new stimuli or experiences. The best stimuli are provided by keeping the bonobo infant, in the company of the caregiver, in close proximity to other bonobos, so the infant can familiarise itself with bonobos with all senses: seeing, hearing, smelling and if possible, touching.

Keeper-infant interactions: The keeper needs to treat the bonobo infants as much as bonobos do: constant ventral contact is recommended, but also the infant can be held in various positions, grooming the whole body, walking with different speed and making it used to unpredictable body moves, and different unpredictable sounds. Keeps should minimise the manual support of the infant, and should encouraged it to hang on to the keeper as much as possible on its own accord. Keepers can stimulate the infant to climb on different structures in different heights, and give the infant the chance to feel different kind of textures and materials to feel and to hold and grasp on. It is recommended that hand-reared bonobos be given every opportunity to "initiate" games and other interactions with keepers, so that they can develop a sense of their own efficacy. One marked feature of most nursery-reared infants is their lack of social initiative. Such passivity can often draw aggression from other animals after reintroduction. Hand-reared infants may be "taught" to behave this way in the nursery, since activities tend to be done to them (picked up, fed, put away) without their being able to exercise any control over their own fate. Success has been achieved in avoiding these developmental aberrations by having staff that understand and can mimic bonobo maternal behaviour care, and maintain tactile contact with their infant bonobo charges around the clock. Much of this time should be spent in a bonobo enclosure next to normally functioning bonobo social units. This results in a youngster that is not frightened unnecessarily by adult bonobos, and who has some understanding of acceptable bonobo behaviour in the context of bonobo society.

Keepers should watch other bonobos at play and attempt to both imitate and respond to the spontaneous appearance of relevant signals in their charges. One especially vital social lesson that young bonobos must learn is that sexual contact is a normal and important part of social interaction. Despite the potential uneasiness about this, it is crucial for nursery keepers to make regular, playful contact - such as patting, rubbing and tickling - with the young bonobo's genital area, and to allow - and even encourage - the young animal to initiate such genital contact. This behaviour can go a long way toward helping the juvenile react appropriately in later interactions with its own species. This type of stimulation from the caretaker can be avoided if the infant is introduced to a surrogate when it is still less than nine months of age, making early introductions even more attractive for keeper staff.

Social development: As the infant grows and develops, the enrichment opportunities should increase in complexity. This should most certainly include peer-rearing, if at all possible. Social experience should be provided by exposing infants to an intact social group by setting up the hand-rearing unit within the bonobo facility, as described above. Allowing the bonobo infant to experience the noise, smells, visual opportunities, and activity of the adults' environment will ensure the infant has a less traumatic acclimation, and an understanding of how to participate in bonobo social environments. Also, it helps to increase social interest of the bonobo group and make them eager to learn about the new bonobo.

(Re-)introduction in the group and foster rearing

The most beneficial alternative to maternal rearing is **adoption by an adult surrogate parent.** Introducing a rejected infant into a group of bonobos requires significant amounts of planning and expertise. An early reintroduction and socialisation mean that keepers have a different focus compared to the idea of keeping the baby for longer period and minimizing any kind of risks. Much of the description below is based on the experience of the Frankfurt Zoo and Columbus Zoo and Aquarium, but various other approaches can also be used effectively as well [e.g., see Akel, 2009; Brookmire 2001; Hawes, 2006; Kilmar et al., 1997].

Early (re-)introduction is only recommended if conditions seem promising. Conditions which are more likely to result in a successful early introduction include:

- A well-balanced, stable group
- An adult and socially experienced (female) group member that is:
  - Willing to take, keep and protect the baby
  - Allowed to do so by the other group members
  - Lactating, or trained to allow bottle-feeding of the baby
- Suitable facilities e.g. an enclosure which:
  - Allows visual, auditory and olfactory contact by the baby to the group.
  - Offers protected physical contact through wire mesh.

  - Has selective sliding doors through which only the infant can pass in order to be fed or to escape from aggression.
- Other (preferably mother-reared) infants in the group (whilst being mindful that juveniles may be aggressive towards a new infant).

The most promising **candidate surrogates** are bonobos who have shown caring behaviour toward infants and juveniles of the group. Lactating surrogates should be considered; such an adoption has been successful in Milwaukee Zoo, and spontaneous adoption of infants by lactating females other than the mother have been recorded [Kilmar et al., 1997; Stevens pers.obs]. However, non-lactating females or even males should also be considered as long as the surrogate parents can be trained to permit keepers to bottle-feed the infant [Kilmar et al., 1997]. In Milwaukee Zoo “a babysitting network” in which several individuals were involved, led to the successful reintroduction of a two-year-old male in the group [Brookmire, 2001]. The opportunity to have the infant raised by a surrogate mother located at another institution should also be considered. During the early phase of hand-rearing, a likely surrogate for the infant may become obvious by observing affiliative behaviours through the mesh separating the infant from the group. Group members who show signs of active interest and appropriate behaviour to the infant through the mesh (without aggressive responses) when the infant is in visual contact, may indicate the best individual to initially target as the surrogate.

The **appropriate time for reintroducing** the bonobo infant to a surrogate and later into the group can vary according to circumstances and reintroduction timelines have to be flexible, based on the infant’s development and the adult’s interest. Crucial is that the infant must be able to sleep all night long without additional feeding during the night, to avoid waking up the whole group during the night. There can be a late feeding and early feeding but no in the middle of the night. To train the infant, the amount of milk the infants gets by the bottle should be gradually increased to reduce the number of feedings. At Frankfurt Zoo, all three hand-reared infants started to sleep all night long (20:00 pm until 06:00 am) in the age of ten weeks. Introductions started when the infant could sleep through the night for two weeks every night.

As the infant requires continued bottle-feeding after physical introduction to the surrogate, both the infant and/or surrogate mother must be trained to approach the mesh for a bottle. This process can start during the first ten weeks already, by bottle-feeding the infant in front of the bonobos, so that the other bonobos witness that the infant relaxes when it is being bottle-fed. The surrogate can be provided with some positive distraction (e.g., receiving juice) while the youngster is taking the bottle.

The **actual physical introduction** to the adult should be carefully planned and monitored. As mentioned in section 2.3. bonobo introductions are relatively easy compared to other apes. Introductions of infants often are even more so, because bonobos are highly social and empathic animals. By allowing contact through the mesh before physical introduction, the other bonobos can familiarise themselves with the infant which helps in the process.

Nevertheless, even when keepers try to mimic as much as possible bonobo locomotion and social interactions, the separation of familiar human caregivers and the introduction to bonobos who will interact in different, intense ways with the infant (including probing the body, ears, eyes and nose, hair plucking, sexual interactions, etc.) is a major step in the life of an infant bonobo, but having a well-prepared introduction, preferably only one time, the whole process will be much less traumatic for all the involved animals.

Prior to the actual introduction, the infant should have had ample opportunity to become familiar with the introduction enclosure. It is recommended putting the infant into a holding enclosure, off exhibit to avoid influence of zoo visitors, and letting the surrogate parent enter in this enclosure. It may be useful to monitor the introduction process with remote cameras to prevent the infant from seeking too much contact with familiar humans, and to prevent that the surrogate is distracted. If the surrogate is not used to be separated in the holding enclosure, a small number of relaxed, older group members of either sex can be added, but the presence of young unexperienced females is not recommended as they sometimes play too rough with infants and may harm them. A door can be left partially opened to an empty enclosure that the infant can retreat to or be called to if separation becomes necessary [Kilmar et al., 1997]. However, the infant should not be given the choice of the female bonobo surrogate or its human caretakers, as this can be a distraction to the goal of the process. If overall the interactions are positive, the infant can remain with the surrogate even beginning the first day and not return to animal care staff. Unnecessarily removing the youngster and reintroducing it daily can have a confusing and agitating effect. However, this process must be closely monitored for the first few days, and even overnight via remote video. When the bond between infant and surrogate is certain, and the surrogate is consistently staying with the youngster or taking it with her when transferring, they can be gradually introduced to the larger group. The timeline for this should be dependent on surrogate/infant behaviour, and may take several days. As mentioned, it is important to have a well-established group that can provide a relatively low-stress environment for the infant.

If the introduction of an infant appears headed towards physically or emotionally harming the infant, the method of reintroduction needs to be reconsidered immediately. If no alternative method is possible at that time, other institutions with likely surrogates should be contacted for possible placement.

Only in the case that there is no realistic prospect for an early socialisation/reintegration into a group or when attempts to do so have failed, it is recommended to rear the baby together with conspecifics in an ape nursery. In such a nursery, contact to/socialisation with adult conspecifics is desirable to prepare the infant for the integration into a family group. **This practice has, however, not been used in the Bonobo EEP since two decades, since all rejected bonobo infants are now being reared by their mother or a foster-parent.**

2.4.9. Population management

The EEP population is managed globally, together with the SSP population. Based on the current population size, generation length, genetic diversity and an estimated current population growth rate of 4%, the EEP needs a population size of 219 individuals and the SSP 233 individuals to meet the program objective of retaining 90% Gene Diversity (GD) after 200 years. For the combined SSP and EEP a population size of 152 individuals is necessary to meet the genetic objectives [Pereboom et al., 2015].

2.4.10. Sperm preservation and artificial insemination

At present, **very little experience with Artificial Insemination (AI)** in bonobos exists. Sperm collection, freezing the semen in liquid nitrogen, intercontinental transfer of frozen sperm and attempts to inseminate female bonobos occurred as early as the 1970s and 1980s, but without success [Bader, 1983; Benirschke & Kumamoto, 1983; Campbell, 1978, 1980; Matern, 1983].

Three techniques to obtain sperm from great apes are 1) masturbation; 2) the use of an artificial vagina; 3) electro-ejaculation [Gould, 1990]. Sometimes, sperm can also be collected from the floor after a male has masturbated [Keller et al., 2012; Matern, 1983]. Electro-ejaculation has been performed in apes, including bonobos, but sometimes gives bad estimates of sperm quality [Benirschke & Kumamoto, 1983; Matern, 1983]. Two attempts to collect fresh sperm and inseminate females directly were made independently in Columbus Zoo and Milwaukee Zoo [Bell, 2003; Clyde 2000; Pohl, 2003;]. In Milwaukee Zoo, the seminal plug was inserted close to the cervix in the female which had been trained for vaginal AI and the female was then allowed to breed with other males which had previously been sterilized by the application of clips to their vas deferens [Clyde, 2000], which is believed to have stimulated the uptake of the sperm in the female reproductive tract [Bell, pers. comm.]. Both attempts eventually resulted in pregnancies and confirmed paternities, but since male and female were housed together continuously, it could not be excluded that there was normal sexual behaviour in addition to the AI. In 2012 the Bonobo SSP published a protocol for the analysis and cryopreservation of sperm [Keller et al., 2012]. Sperm preservation and AI. are one of the research priorities for zoo management of the species.

2.5. Behavioural enrichment

Figure 48: Bonobo using tools to extract food from a wooden log [Leipzig Zoo – Jeroen Stevens]

Like other apes, bonobos have high cognitive skills, both on a social and physical level [e.g., Clay & de Waal, 2013; Hare, 2009; Hermann et al., 2010]. Given their intelligence, it is necessary to implement a highly variable enrichment schedule to encourage bonobos to display their natural behaviours, increase feeding time and locomotor activities and can be used to reduce undesirable behaviours. Providing daily enrichment is essential, especially during periods of confinement indoors. Frequent rotation of enrichment items is recommended. It is recommended to have each enrichment device controlled by the institutions veterinarian.

While the overarching goal of enrichment is to increase general welfare, it can be useful to think about specific goals for enrichment [Buchanan-Smith, 2011]. The following list has been adapted from Young [2003] and Buchanan-Smith [2011]:

- Increase diversity and performance of normal (wild, desired) behaviours
- Increase positive utilisation of the environment
- Prevent abnormal behaviour developing
- Increase the ability to cope with challenges in a more normal way

Bloomsmith et al. [1991] distinguish the following five main categories of enrichment: (a) food-based; (b) occupational (including psychological ‘puzzles’ and physical exercise); (c) structural; (d) sensory (for example visual, auditory); and (e) social. See also Buchanan-Smith [2011]. Sometimes these categories overlap. It is recommended to provide daily enrichment from all categories, and vary often to avoid habituation to the enrichment items. When the same items are being offered daily, there is a risk of habituation. Unpredictable enrichment seems to increase interest. There is not much literature available specifically for enrichment in bonobos, therefore many references below refer to studies in other apes.

2.5.1. Food based enrichment

Much of the enrichment that zoos provide for bonobos is food based, including some of the occupational enrichment devices such as artificial termite mounds, hollow logs etc. (see below). Food is a great motivator for bonobos, and some preliminary research suggests that bonobos, like many other zoo-housed animals, prefer to “work” for their food, and when given the choice between freely available food, and food that requires manipulation before consumption, will choose the latter, a phenomenon known as “contra freeloading” [Wild, 1998].

Care should always be taken when providing too many extra foods, and **food based enrichment should be based on the daily diet** (see section 2.2), which is presented in a more challenging way, instead of adding extras such as nuts, or seeds which can cause obesity or other health issues. Rather than adding extras, variation in the presentation of daily diet can be made enriching by presenting it under different forms (e.g., whole versus chopped) and food can be presented in various ways. Putting food on wire ceilings or other high locations

Figure 49: Examples of food-based enrichment: Throwing a coconut against a wall (Zoo Planckendael – Jeroen Stevens) ;b: placing food in kong toys on a metal grid roof (Zoo Planckendael – Jeroen Stevens); c: Seeds in turning pipes (Zoo Planckendael – Jeroen Stevens); d: Horizontal food maze (La Vallée des Singes – Jeroen Stevens); e: Extractive foraging from a wooden log (Leipzig Zoo – Jeroen Stevens); f: Frozen yoghurt stick (Leipzig Zoo: Jeroen Stevens); g: Extractive foraging from a metal tube (Wilhelma Zoo Stuttgart – Jeroen Stevens); h: Extractive foraging from a termite mound (Columbus Zoo – Jeroen Stevens); i: Extractive foraging from a puzzle feeder (Wilhelma Zoo Stuttgart – Jeroen Stevens); j: Fishing for floating fruits in a platic box (Zoo Planckendael – Jeroen Stevens); k: Shaking seeds out of a barrel [Apenheul – Jeroen Stevens].

can stimulate arboreal feeding. Searching time and manipulation time can be increased by scattering food in hay, straw, wood-wool or other substrates; and/or hiding food in card board boxes, paper bags, wood sticks, pipes, tree-trunks, kong® toys, puzzle feeders, boomer balls and so on (see Figure 49). Foraging bins, with food hidden in wood shavings, or leaf litter can be very effective in keeping bonobos occupied. Food can be presented in difficult to reach locations, (e.g., animal needs to jump or cross unstable furniture to reach location). Also, changing the feeding schedule can have enriching effects. In chimpanzees, more species-specific behaviour was observed under an unpredictable feeding schedule (meals fed within 150-minute period) than under a predictable feeding schedules (always fed within 30-minute period) [Bloomsmith & Lambeth, 1995].

2.5.2. Occupational enrichment

This category includes devices that require manipulation and/or tool use, which can also extend feeding time. Since wild bonobos spend up the majority their active day time feeding and foraging, great efforts should be made to increase the amount of time bonobos in zoos in similar endeavors. Providing a variety of manipulable objects to apes both increases the amount of time spent in foraging-type activities (e.g., with food retrieval devices such as termite mounds), and presumably increases their well-being [Ross et al., 2009].

Although wild bonobos are poor tool users when compared to wild chimpanzees or orang-utans – for example, they do not show extractive foraging in the wild [Fruth et al., 1999; Furuichi et al., 2015; Ingmanson, 1996], they are very adept tool users in zoos [Bardo et al., 2016; Gold, 2002; Gruber et al., 2010; Jordan, 1977; 1982; Neufuss et al., 2016; Takeshita & Walraven 1996; Walraven et al., 1993] and can easily learn to extract food from artificial termite mounds [Boose et al., 2013]. Puzzle boxes and/or wooden blocks with holes can also be filled with food items to stimulate extractive foraging. Such devices must be well constructed due to the strength and intelligence of apes. Feeding devices like water barrels with floating fruit, piñatas, etc. can also be placed outside of the enclosure so that the apes use their digits or use tools through a barrier (e.g., wire, and bars) to access the foods. When using feeding devices of this nature, it is best to provide multiple sites for food acquisition, spaced apart in order to avoid competition and conflict and to allow subordinate animals the opportunity to have access to them. These can be different types of feeders to cater to individual task preference.

During the day, **non-fixed objects** that stimulate play, display, foraging, and exploratory behaviour (e.g., boxes, balls, barrels, paper, clothes, small food items) should always be available to the animals, and varied regularly. Bonobos like clothes and sheets to build nests and/or play blind man's bluff. It is recommended to remove zippers and buttons from clothing to prevent bonobos from choking. Csatadi et al. [2008] found that adding new enrichment items (Kong®toys filled with food) increased activity and reduced undesirable behaviour (infant abuse) in a group of six bonobos. Behringer [2011] evaluated the use of puzzle box

Figure 50: Examples of occupational enrichment a: blankets (Zoo Planckendael – Jeroen Stevens); b: Gift boxes wrapped in paper (Zoo Planckendael – Jeroen Stevens); c: Kong toys and plastic barrel (Twycross Zoo – Jeroen Stevens); d: Large plastic ball used for punching and play (Zoo Planckendael – Jeroen Stevens); e: Blankets for resting (Apenheul – Jeroen Stevens); f: Platic barrels used for male displays (Zoo Planckendael – Jeroen Stevens); g: Banana leaves for nestbuilding (Zoo Planckendael – Jeroen Stevens); h: Volleyball for play (Wilhelma Zoo Stuttgart- Jeroen Stevens]; i: Blankets and balls (Wilhelma Zoo Stuttgart – Jeroen Stevens).

feeders, tennis balls and firehoses all filled with food and found that all three enrichment devices were used to varying degree by different individuals, and found no negative effects on the salivary cortisol.

Sometimes this category is also referred to as **cognitive enrichment** – obviously puzzle feeders can present a cognitive challenge, especially in the beginning, but usually the apes learn solving strategies quickly and the cognitive challenges become limited. Modern technology, including touch screen computers can present bonobos and other apes with challenging cognitive tasks. Research has shown bonobos are very quick in learning to use computer technology, e.g. to communicate with humans [Savage-Rumbaugh et al., 1986, 1989] or psychological tests [Kret et al., 2016] but applications in zoos generally have been limited, and could be furthered explored.

Finally, **positive reinforcement training** is also seen as a form of occupational enrichment [Buchanan-Smith, 2011]. For more information on PRT in bonobos, see section 2.6.2. General handling/Training.

2.5.3. Structural or Physical enrichment

Structural enrichment usually refers to **changes in the zoo environment**. By providing a flexible enclosure, where changing the climbing structures is possible, a more enriching environment can be created, using hammocks, ropes, fire hoses and cargo nets for additional flexibility (see section 2.1.6. Furnishing and Maintenance). Diversity in itself is also a form of structural enrichment, and can refer to diversity in substrates, physical conditions such as shade, temperature, humidity, (see 2.1.7. Environment). Again, the concept of choice is crucial and by providing a diverse and flexible environment, bonobos can make their own choices.

As mentioned before, **water** can be an enriching aspect of bonobo enclosures (Figure 50b). Wild bonobos wade into pools and streams [Hohmann & Fruth, 2003a; Kano, 1992; Myers-Thompson, 2002] and especially immatures, have been seen to play in shallow water [Behncke, 2015; Bermejo et al., 1994; Myers-Thompson, 2002]. In zoos showers, water basins or small ponds in the enclosure, or the moats of outside enclosures can have stimulating effects [Jordan, 1977; Rafert et al., 1997]. Care should be taken to reduce risks of drowning, especially for young individuals. A pool of 50 centimetres deep is generally considered to be safe.

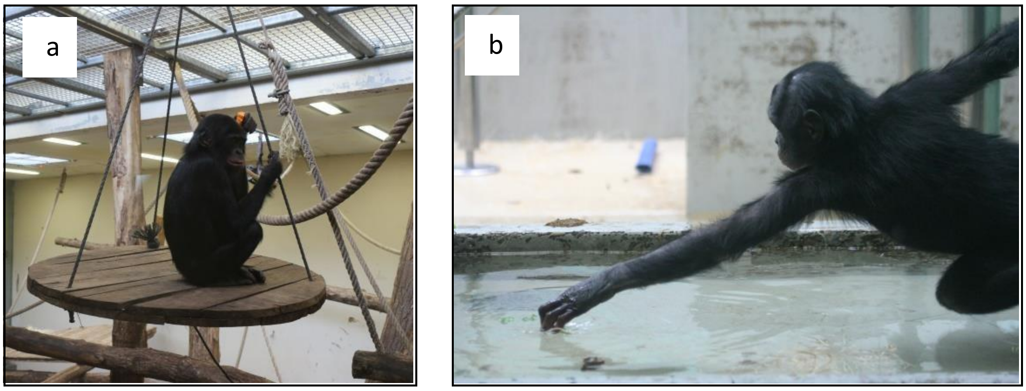

Figure 51: Structural enrichment a: Flexible platform (La Vallée des Singes – Jeroen Stevens); b: Water basin (Wilhelma Zoo, Stuttgart – Jeroen Stevens).

2.5.4. Sensory enrichment

There is not much research done on this kind of enrichment in bonobos specifically, but evidence from other ape species shows which forms of sensory enrichment can be used in bonobo management.

For **visual enrichment**, television screens and showing videos has been shown to be an effective means of enrichment in chimpanzees and gorillas [Bloomsmith et al., 1990; Bloomsmith & Lambeth, 2000; Maloney et al., 2011]. Several institutes have found that using **television** screens, showing various films such as cartoons or nature documentaries, can also be an interesting form of enrichment for bonobos (Figure 52a). In one institution, adding a tv-set was shown anecdotally to reduce auto-hairplucking behaviour in bonobos [minutes EEP meeting Frankfurt, 1997]. **Mirrors** have also been offered (Figure 52b), since bonobos like other apes, show evidence of recognising themselves in mirrors [Walraven et al., 1995; Westergaard & Hyatt, 1994], but the effectiveness of mirrors as enrichment device has not been assessed for bonobos. It was found that zoo-housed chimpanzees and gorillas preferred blue and green **coloured** stimuli to the same objects coloured red [Wells et al., 2008], and another study found that anxiety-related pacing was mitigated by green lighting in zoo-housed chimpanzees [Fritz et al., 1995]. **Windows** in inside enclosures provide the bonobos a view on their surroundings even when spending a lot of time indoors, e.g. during colder weather, and are a great way of providing visual enrichment.

Olfactory enrichment, by providing scents, herbs etc. is usually not very effective in apes, whose sense of smell is not extremely well developed; apes will sniff scented cloths briefly, but it has very little effect on overall behaviour [Ostrower & Brent, 2000; Wells et al., 2007]. To our knowledge, no published records of bonobos' reactions to scents exist, although several zoos include adding scents and perfumes to their enrichment schedule. Whilst olfactory stimulation should not be completely overlooked as a method of enhancing the environment of zoo-housed non- human primates, enrichment strategies that facilitate vision-driven goals (e.g. foraging, object manipulation, etc.) may be more appropriate for apes [Wells, 2009].

Auditory enrichment by playing music or naturalistic sounds etc., has yet again been investigated in chimpanzees and gorillas, where it was found to have mixed results [Brooker, 2016; Ogden et al., 1994; Robbins & Margulis, 2014; Wallace et al., 2017; Wells et al., 2006]. But to our knowledge no specific studies on bonobos exist.

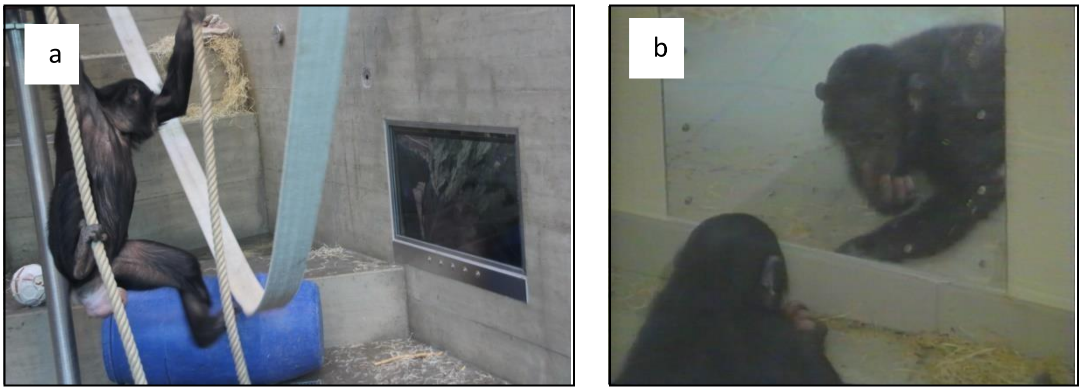

Figure 52: Examples of sensory enrichment; a: Television (Wilhelma Zoo Stuttgart); b: Mirror [Zoo Planckendael - archives]

2.5.5. *Social enrichment*

See section 2.3: Social structure for conspecific social enrichment; section 2.6.2. for contraspecific human social enrichment under form of handling/training; and 2.3.3 for contraspecific, non-human social enrichment, which is not recommended.

2.6. Handling

Figure 53: Bonobo keeper interaction through protected contact (Zoo Planckendael – Jeroen Stevens).

2.6.1. Identification and sexing

Bonobos can easily be identified based on individual characteristics and sexing is obvious. In new-borns, identifying the sex can be sometimes difficult as mothers keep infants in close contact, and it also takes some experience to discriminate between the genitals of a new-born male and a new-born female (Figure 54).

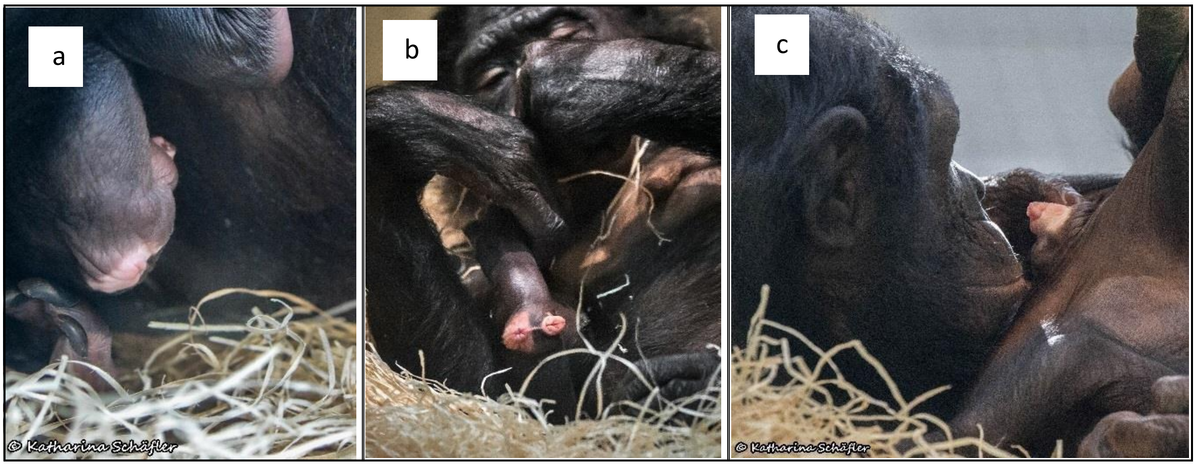

Figure 54: Genital areas of male (a: Wilhelma Zoo Stuttgart- Katharina Schäfler) and female (b: Planckendael – Jonas Verspeek; c; Wilhelma Zoo Stugttgart - Katharina Schäfler) new-borns can be hard to tell apart.

EEP zoos generally place microchips in the left shoulder of individual bonobos.

2.6.2. General handling

No quantitative measures are available on how strong bonobos are, but as all great apes, bonobos are extremely quick, powerful and muscular, and have long canines, thus should always be **considered as dangerous animals**. Manual restraint is ineffective and unsafe, even with mobile youngsters. Direct contact is not recommended, especially not between humans and adults. Access behind barriers (“protected contact”) should be the rule at all times, and the use of operant conditioning is recommended.

Training

Positive reinforcement training (PRT) has been very successful in zoo-housed bonobos, and can be an important part of every bonobo husbandry programme, although the goals and behaviours trained may vary from facility to facility. Desired behaviours can be rewarded by primary reinforcers, such as desirable food items, such as juices, cereal, and special fruits (all food offered should be calculated as part of a nutritionally balanced diet). Secondary reinforcers, such as new toys, verbal praise, and tactile contact from caregivers, have also been effective in the training process. Clickers have been successfully used as a training bridge(i.e., a stimulus which connects the time span between completion of a desired behaviour andits reinforcement [Bell & Ballmann, 1997], although bonobos unfamiliar with clickers may initially be startled by the sound. Verbal praise is an important secondary reinforcer that, through training, becomes a primary reinforcer. Giving an animal a “time out” (a brief period in which the trainer simply ignores an animal by walking or looking away from it) is one training tool that can be effectively used to communicate to an animal that it responded incorrectly, and is the only recommended type of punishment [McLaughlin et al., 2007].

By rewarding positive behaviours and ignoring negative ones, PRT can be used to introduce simple procedures such as name recognition, targeting, stationing, separations, proper shifting [Bell & Kahn, 2001]. PRT can also be used to perform various veterinary procedures without anaesthesia, including examination of eyes, mouth, ear, digits, etc. [Bell & Ballmann, 1997], follow up of wounding or surgical recovery [Chapman et al., 2017]. Furthermore, PRT can also be used to perform more complex investigations without the need of anaesthesia, and can allow the use equipment such as rectal or tympanic temperature [Bell & Ballmann, 1997], obstetrical ultrasound measurements of foetal growth [Clyde et al., 2002a,b; Bell & Kahn, 2001; Drews et al., 2010; Teare et al., 1996;], cardiac ultrasounds [Bell & Kahn, 2001; Clyde et al., 2001, 2002a,b], blood drawing [Bell & Kahn, 2001; Clyde et al., 2001; 2002], hand injections [Loehe, 1995; Bell & Khan, 2001], X-rays [Bell & Kahn, 2001; Kitchen, 2009], urine collection [Loehe, 1995; Drews et al., 2010], saliva collection [Behringer et al., 2009]); or semen collection and artificial insemination attempts [Bell, 2003; Bell et al., 2001; Pohl, 2003; Yoshida, 1997]. Finally, bonobos can also be trained to enter a shipping crate to reduce the need for tranquilisation (see section 2.6.3. Catching/restraining and 2.6.4. Transportation). Apart from making medical and management manipulations less stressful, PRT also helps to improve the bonobos' attitudes to keepers and reduce negative behaviour such as aggression, spitting or urinating [Bell & Ballmann, 1997; Bell & Kahn, 2001; Loehe, 1995;], which makes the work environment safer. Introducing strangers in a positive manner to bonobos can help facilitating access to medical staff [Bell & Khan, 2001]. study of salivary cortisol showed that PRT does not induce stress in bonobos [Behringer et al., 2014b]. The number and timing of training sessions can vary greatly between institutions, as can the range of behaviours that are trained, the methods used etc. There is no universal way, as training depends on staff ability, motivation as well as on infrastructure. However, even without any dedicated infrastructure, basic PRT can be achieved, as bonobos are inquisitive learners. For an exampleof how a training programme was set up, we refer to Bell & Ballmann [1997].

Practical equipment

Several institutions have implemented "training walls" in their holding facilities (Figure 55). When 50 x 50 cm mesh is used, it can be difficult to do some training tasks. By providing 'windows' in the mesh, where for example ultrasound probes can be pushed through, or where blood sleeves can be fitted (below), a more flexible training environment can be provided. Another option used by some institutions is to install a "training cage", which can be attached to holding rooms, and which can be used to transport the apes within the same facility (e.g. between buildings, to veterinary station, etc.) without sedation.

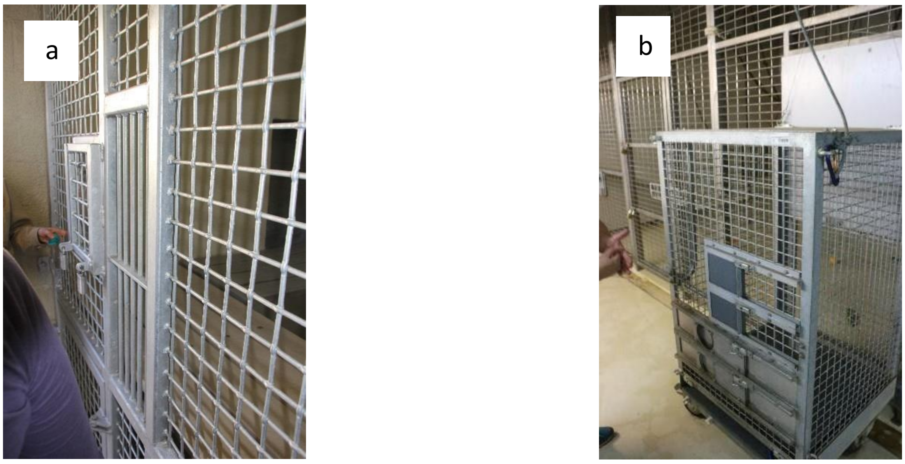

Figure 55. Training equipment a: Training wal with a built in 'training window' (San Diego Safari – Jeroen Stevens). b: Moveable training cage with possibility to attach blood sleeve (Frankfurt Zoo – Jeroen Stevens).

Several institutions have installed a PVC blood sleeve to enable the easy collection of blood samples after proper training (Figure 56). For more details, building instructions which have been used in Columbus Zoo can be found in Appendix 10.

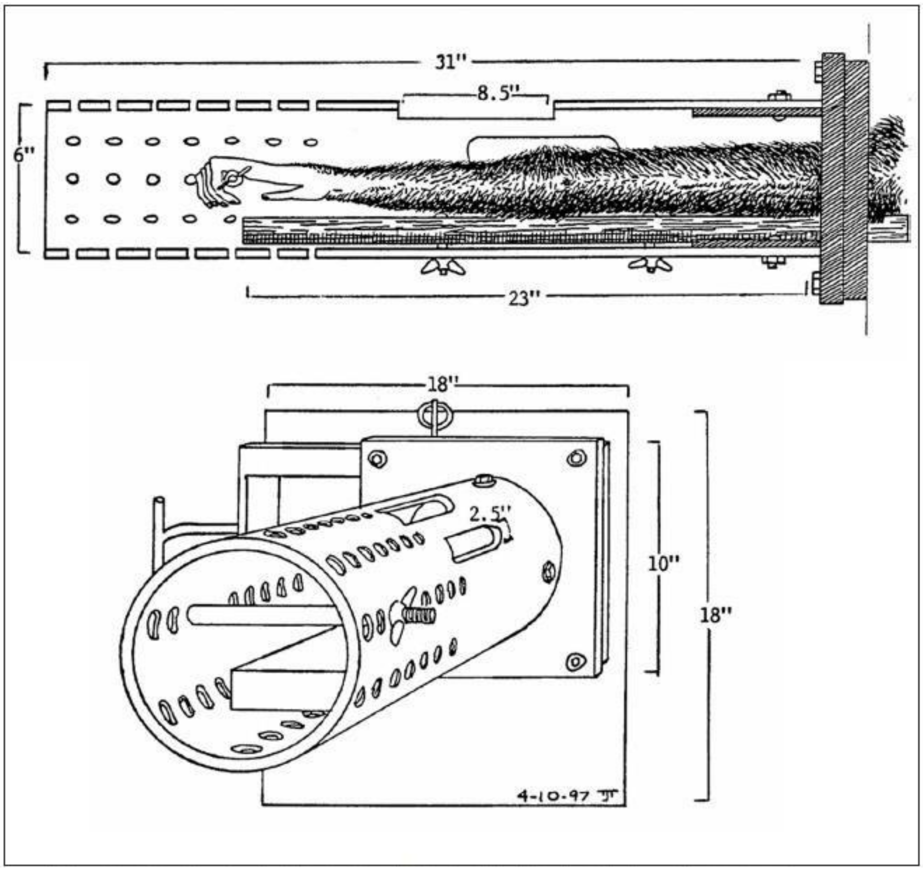

Figure 56: Illustration of a bloodsleeve at Milwaukee County Zoo. Courtesy of Milwaukee County Zoo

When building a bonobo facility, it is recommended that a permanent scale be installed within the exhibit to assist staff with weight monitoring. This also helps keepers to determine when diet increases are necessary to ensure continued growth and development of infant and juvenile animals. Several types of scales are used in various institutions. Also, removable scales may be practical in use (see Figure 57).

Figure 57: Different models of weighing devices used for bonobos: a: Table model (Columbus Zoo – Jeroen Stevens); b: Integrated in sleeping platform (Leipzig Zoo – Jeroen Stevens); c: A hanging cage in which the bonobos climb and sit (Wuppertal Zoo – Jeroen Stevens).

2.6.3. Catching/restraining

Manual restraint is not recommended for bonobos older than three years. Squeeze cages are not recommended, and are unlikely to ever be used. Bonobos can be trained to enter transport crates voluntarily by positive conditioning [Bell & Khan, 2001]. For this a transport crate can be securely attached to a door of a separated holding room, and conditioning the bonobo to get some food in the crate. Some institutions provide a removable chute, through which the individuals walk in normal everyday management, but which can be closed off and wheeled out when bonobos need to be transported. Enough time should be provided for the bonobo to be trained, and animals should not be rushed or trapped, as this will be counter productive. When sedation is necessary, bonobos can be trained to allow hand injections, which has been shown in chimpanzees to be less stressful than when they are darted[Lambeth et al., 2006]. If the options mentioned above are not possible, a bonobo can be anaesthetized by darting with a blowpipe by a trained veterinarian.

2.6.4. Transportation

Within Europe, bonobos are usually transported in a crate by car or truck (via the institution's vehicle, rented truck, or by an experienced exotic animal transporter) and rarely by airplane (commercial carrier or freight carriers). For intercontinental transfers, bonobos aretransferred by airplane in a crate (Figure 48). Each independent bonobo should be crated individually, except for mothers with young infants who can share a crate together. In the latter cases, some zoos have had good experience with transporting mothers with infants up to 2.5 years in (large) crates. An infant of three months old was shipped with her mother in one crate on a long intercontinental flight from DRC to Belgium, and further by car to the Netherlands without any negative results. An intermediate solution to diminish the risk of injuries to infants, can be to construct a large crate with a strong mesh panel in the middle so that mother and infant are physically separated, but they can interact for comfort. Young hand-reared infant bonobos have been transported without a crate.

There are several factors that determine the best mode and time of transportation, such as the age of the animal, or the climate in both the sending and receiving institution. Enough time should be calculated for unforeseen delays as weather conditions, vehicle or mechanical failure, or traffic delays.

If immobilization for shipment is necessary, it is better to fast the animal to avoid complications with anaesthesia. The bonobo should be given enough time to recover inside the crate, and the condition of the animal should be checked inside the crate before the journey begins.

It is recommended that a person who is familiar with the bonobo - preferably the ape keeper - accompanies the animal during transport. The presence of a familiar keeper will contribute to the animal's welfare by alleviating some of the stress associated with the transport. In addition, the keeper can provide the receiving institution with direct information about the animal's behaviour and personality. Ideally, the keeper should stay in the new institution for a few days until the animal is well adapted to its new home [Abelló et al., 2006].

During the whole shipment the correct temperature of 18 to 25° C and adequate ventilation must be always guaranteed [Abelló et al., 2006]. Crates with bonobos should only be transported in a closed truck or vehicle, with climate control. For transportation by aircraft we refer to the IATA Live Animals Regulations, which are applicable to members of the International Air Transport Association according to the provisions of *Cargo Services Conference Resolution 620* and to airlines being parties to the IATA Multilateral Interline Traffic Agreement-Cargo [IATA, 2014].

The IATA Live Animals Regulations are accepted by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the Office International des Epizooties (OIE) as guidelines in respect to transportation of animals by air. These regulations have been used by the Council of Europe as a basis for its code of conduct for the international transport of farm animals. The European Union has adopted the IATA Live Animals Regulations as the minimum standard for transporting animals in containers, pens and stalls. As an increasing number of countries adopted or accepted these regulations as a part of their national legislation, shippers are warned that shipping live animals in violation of the regulations may constitute a breach of the applicable law and may be subject to legal penalties.

The IATA Live Animals Regulations *Container Requirement 34* concerns adult apes; *Container Requirement 33* concerns young and sub-adult apes. We use these requirements as mandatory for air transportation, and as recommendations for transport by cars or trucks. Many institutions now have well designed crates and it is not uncommon for EAZA zoos to borrow transport crates for transportation of bonobos, instead of constructing new ones.

Crate design and dimensions

The crate must be made of high-quality materials which can adequately contain the animal. The crate must meet the size criteria for the animal and the limitation of the carrier [Abelló et al., 2006]. Handling bars must be provided on three sides of the crate. Documents accompanying the shipment should be attached in an easily accessible manner to the outside of the crate plus information about the animal, feeding and watering instructions.

Container dimensions depend on the size of the animal that is being transported, and may also be under government regulations of the countries from and to which bonobos are exported. "*The dimensions must allow the animal to turn around completely and easily. The height of the container must allow the animal to stand upright completely with its head extended and the length of the container must allow it to lie down in the fully prone position*" [IATA, 2014].

Container materials that can be used for young/sub-adult great apes include wood, metal, wire mesh or other light material. For adult great apes these materials include hard wood, metal, welded mesh and muslin or other light material [IATA, 2014].

The **container frame** for young/sub-adult great apes should be made of solid wood or metal that is bolted or screwed together; for adult great apes, welded metal lined with smooth wood or other similar material of a minimum thickness of 1.2 cm (1/2") is recommended. Additional strengthening braces must be present on the sides of the container when the total weight is more than 60 kilograms (132 pounds) [IATA, 2014].

Sides and front: The sides of the container for young/sub-adult great ape should be wood or metal. The front must consist of 2.5 cm (1") weld or chain link that must be attached to the frame with a steal strip (staples must not be used). Behind the mesh 2 cm (4/5") bore steel tubes must be sunk into the top and bottom of the frame to a depth of approximately 2.5 cm (1") at a distance of 7.5 cm (3") apart centre to centre. The distance between bars and mesh must be such that the animal cannot poke its fingers outside the container. A 2/3 solid panel with 1/3 mesh wire at its lower portion and two 10 cm (4") observation openings in the upper part must be placed in front of the weld mesh/ chain link. The other three sides must be solid with ventilation openings [IATA, 2014]. For adult great apes, solid wood or lined metal. The front must consist of iron bars spaced in such a manner that the animals cannot push its arms through the bars. The bars must have a sheet of welded mesh fixed at a distance of 7.5 cm (3") in front of them. A wooden shutter with slots or holes for ventilation must cover the whole front in order to reduce the amount of light inside the container, as well as to reduce the disturbance to the animal and to protect the handling personnel. The other three sides, one of which is the door, must be solid with ventilation openings [IATA, 2014].

Handling: For all apes, handling and spacer bars must be provided on three sides of the container [IATA, 2014].

Floor: For all apes, the base of the container must be solid and leak proof. A grill can be securely fixed and placed over a leak proof droppings tray in order that the excreta falls onto it.

Roof: For all apes, the roof of the container should be solid but with mesh ventilation openings [IATA, 2014].

Door: For young/sub-adult great apes, access into the container must be by a vertical sliding door at the back that extends the whole height of the container. It must be fastened with tamper proof fasteners or bolted shut after loading. A centre batten must be provided across the whole width of the container, including the door, which is put in place after the door is closed. For adult great apes, a sliding door the same height and made of the same material as the container must be placed in the rear of the container. It must have strong and secure means of fastening that cannot be opened accidentally [IATA, 2014].

Ventilation: For sub-adult great apes, mesh ventilation openings approximately 2.5 cm (1") in diameter must be provided along the base, in the upper 1/3 of the sides and rear and on the top of the container. Whenever openings are covered by mesh, care must be taken that there are no sharp edges present within the container, and all edges must be covered with smooth material that is tamper proof. A muslin, or similar material, curtain must cover all ventilation openings including the front. For adult great apes, mesh ventilation openings, approximately 2.5 cm (1") in diameter must be provided at heights that will give good ventilation at all levels but particularly when the animal is in a prone position. Openings must cover the sides, rear and top, as well as the sliding shutter. All openings can have exterior mesh screening. A muslin, or similar material, curtain must cover all ventilation openings including the front [IATA, 2014].

Forklift extrusions must be provided when the total weight of the container plus animal weighs more than 60kg (132lb) [IATA, 2014].

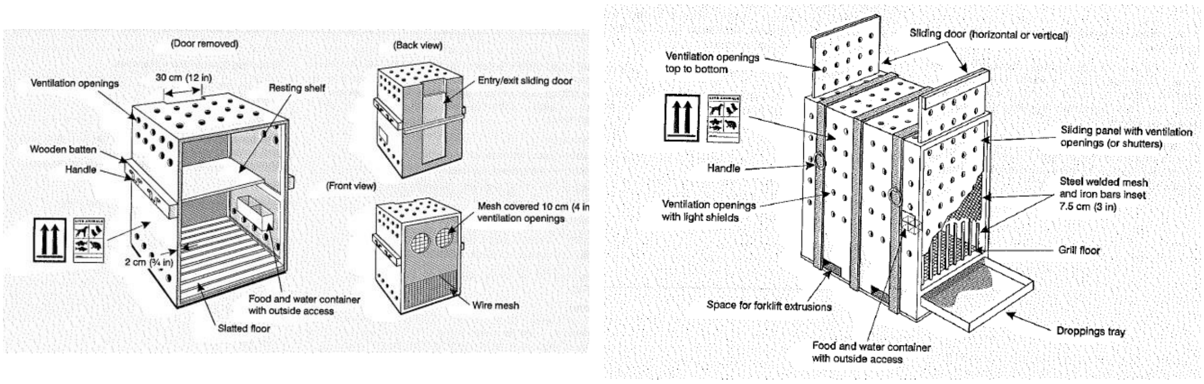

Figure 58: Illustration of transportation containers a: Container for subadult apes (IATA, 2014); b: Container for adult apes (IATA, 2014); c: Photograph of a container (Apenheul – Jeroen Stevens); d: Cargo sticker (Jeroen Stevens).

Feed and water containers: Separate food and water containers must be provided, either revolving or fixed. If fixed inside the container they must be placed at a height that does not allow the animal to sit upon it and there must be outside access for filling and emptying which does not allow the animal any chance of escape. Water containers should only be filled to demand and must be emptied after each use so animals do not splash themselves and become wet and chilled. These containers must have rounded edges and be made of non-toxic material suitable for the species. Feeding and watering instructions must be affixed to the container and a copy must accompany the documents. Any food or water given must be recorded on the container instructions with the date and time of supply. Food must be provided by the shipper but it must be checked that it does not contravene any regulations of the country(ies) of transit or importation. IATA regulations state that animals do not normallyrequire additional feeding or watering during 24 hours following the time of dispatch. If feeding is required due to an unforeseen delay, portions of the bonobos' normal diet can be fed sparingly to prevent a build-up of uneaten food in the container and avoid gastrointestinaltract discomfort. Ideally, this should be done by the attendant accompanying the shipment.

2.6.5. Safety

It is recommended to have **only protected contact** with bonobos, i.e. from behind appropriate safety barriers (see above), with the exception of hand-reared infants. Bonobos are highly intelligent, agile and several times stronger than humans. Bonobo attacks on humans have happened and severe injuries can occur. Direct interaction of caregivers with apes should be undertaken with caution, even when protected contact is utilized. The caregiver's experience level and knowledge of the specific animals they will be working with should be taken into consideration when interacting with apes.

Bonobo-staff barriers should allow some interaction between staff and animals (e.g., for individual feedings, treatment, training), but not to the extent that animals are able to reach out of the enclosure or cage. Staff should be able to observe and hear the animals easily from the service area.

Service passages must be sufficiently wide to prevent animals from reaching out to scratch or otherwise injure the keeping staff [Lewis & Rietschel, 2004]. A brightly coloured line can be painted down the keeper aisle at the maximum reach distance from the bottom of the containment barrier. This will serve as a reminder to the keepers that the bonobos are capable of reaching out and grabbing anything within that line [McLaughlin et al., 2007]. When mesh netting is used to separate bonobos from keepers, it should be considered that these materials are flexible and can extend the reach of the bonobos.

All **locking devices** should be designed to allow for a visual determination of whether a lock or door is secured. Be aware that apes have been known to use sticks to push “out-of-reach” buttons of electrically operated slides and doors. Therefore, a safety lock is also recommended on these electrically operated mechanisms. The use of perspex boards can also help to protect certain areas and to prevent contact between humans and the animals.

Animal security areas are those areas immediately adjoining areas containing animals. Since animals occasionally escape into these areas, they should be designed to be as "ape proof" as possible. It is essential that staff have complete visibility of these areas before entering. ‘Dog legs’ and ‘blind spots’ must be avoided. Some facilities use (parabolic) mirrors or camera surveillance systems (Figure 59 b-c) to compensate for these problems, but it is better to eliminate these areas, maximise direct vision and keep cameras and mirrors to a minimum. There have been cases where camera images “froze” making it impossible to see whether there were bonobos in the inside enclosure. Where corridors change direction and blind spots are unavoidable, careful placement of an additional mesh barrier and security doors can provide an additional security zone with good visibility.

Primary animal security areas are those areas normally occupied by the animals and those areas occasionally occupied by unrestrained animals such as shift areas and transfer chutes. It is essential that staff in secondary animal security zones have excellent visibility into primary security areas so that staff can verify the rooms are empty and secure before they enter. Where **secondary security areas** provide access into large, complex indoor or outdoor exercise or display areas it may not be possible to insure complete visibility of the area before entering. Therefore, the following two precautions are essential: excellent visibility of the animal area immediately beyond the door, including overhead space, and the ability for staff to quickly account for the location of all animals to determine that no animals are present prior to opening the door. Provisions must be made to ensure that animals will not be released into any area that is already occupied by another staff member for both animal and keeper safety.

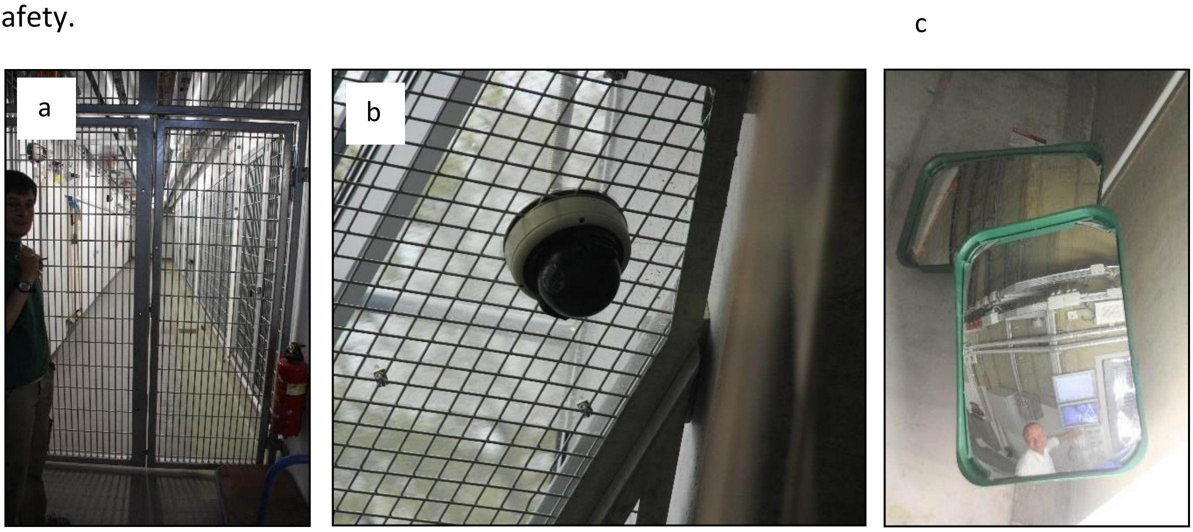

Figure 59: Safety measures to increase visibility or safety in service corridors. a: safety doors (Wilhelma Zoo Stuttgart– Jeroen Stevens); b: safety cameras (Wilhelma Zoo Stuttgart– Jeroen Stevens); c: Safety mirror to avoid blind angles (Wilhelma Zoo Stuttgart– Jeroen Stevens).

Figure 60: Veterinary procedures, preparing a bonobo for transfer (Zoo Planckendael - Jeroen Stevens)

2.7. Veterinary considerations for health and welfare

We refer to the document “Veterinary guidelines for great apes kept in zoological collections in Europe” [Liptowsky et al., 2019] for general recommendations regarding:

- 7.2. Guidelines for Apes
- 7.3. Guidelines for human personal health
- 7.4.4. Specific veterinary health concerns in bonobos
- 7.5. Contraception
- 7.6. Surgery
- 7.7. Veterinary research
- 7.8. Pathology
- 7.9. Recommended health plan
- 7.10. Protocol for great ape deaths in EAZA Collection

Below are veterinary topics that have popped up in discussions in the Bonobo EEP, usually in the context of population management, such as demography, but also regarding transfer recommendations etc.

Cardiovascular disease

Cardiac problems (myocardial fibrosis and presumptive fibrosis) are, as in all species of apes, a serious cause of death and responsible for up to 46% of deaths in bonobos older than one year, causing death in individuals as young as 11-29 years of age [Clyde, 2011; Clyde et al., 2002]. The clinical pictures can be highly variable, presenting variously as congestive heart failure with pulmonary oedema, dissecting aneurysm, haemorrhagic stroke and sudden death [Clyde, 2011]. Lethal infections of *Encephalomyocarditis* virus (EMCV) have been described [Jones et al., 2005, 2011]. Transthoracic echocardiography is a valuable tool for screening animals for cardiovascular disease [Clyde et al., 2001; 2002], and bonobos can be trained to allow these procedures without sedation [see section 2.6]. Celestino-Soper et al. [2018] found several deleterious variants in genes involved in cardiovascular disorders in a male bonobo that suffered from Arrhythmogenic right ventricular cardiomyopathy, suggesting this might be a useful screening approach in the future.

Clyde [2011] made the following recommendations:

1. Restrict caloric intake to prevent obesity in bonobos.
2. Increase exercise by increasing useable space and appropriate enrichment.
3. Evaluate stress levels of individual bonobos. Animals with higher stress levels seem more prone to the development of cardiovascular disease and warrant more frequent cardiac assessments.
4. Restrict dietary salt intake: The exact amount of dietary salt intake appropriate for apes is unknown, but high dietary salt intake may lead to hypertension in genetically prone individuals and can exacerbate existing disease. Current recommendation is to feed less

than 1200 mg of sodium per bonobo each day. This amount is based on the American Heart Association recommendation for a human to consume less than 2300 mg/day. Sodium levels in any pelleted diet product should be less than 0.25%. Many institutions are currently feeding much lower levels of sodium and restricting the amount of pelleted feed offered.

5. React promptly to signs of social withdrawal. Behaviour changes consistently noted by keepers a few weeks to months before sudden deaths in bonobos due to cardiovascular disease have included social withdrawal and avoidance of altercations/aggression. Immobilization for complete physical examination, bloodwork, blood pressure measurement, ECG, echocardiogram and radiographs should be scheduled quickly and cardiac medications initiated if signs of cardiac disease are found. Cardiovascular function can be improved if appropriate medications are started early.
6. In an ideal world, indirect blood pressure measurements could be taken in all adult bonobos. Despite years of training at several institutions, this has not been successfully accomplished. A blood pressure reading taken early during immobilizations, before inhalant gases are used, may reflect blood pressure status. If elevated pressures are seen or suspected, or if left ventricular hypertrophy is found on echocardiogram, start anti-hypertensive medications.
7. Collect baseline echocardiograms in all bonobos 15 year or older and repeat at least every five years if asymptomatic. Forward copies of echocardiograms and cardiac measurements to the SSP Veterinary Advisor Dr. Vickie Clyde through the Great Ape Heart Project as outlined above www.greatapeheartproject.org/GAHP/Forms.html.
8. Train bonobos for voluntary participation in awake echocardiograms.
9. Do not use alpha-2 adrenergic receptor agonists such as dexmedetomidine, medetomidine or xylazine in any bonobo being immobilized for an echocardiogram or in any animal suspected of having cardiovascular disease. These drugs can worsen cardiac function even in apes with normal cardiac function.

Respiratory disease

Bonobos are known to be very susceptible to upper respiratory diseases in zoos [Benirschke et al., 1980; Clyde, 2011; Janssen et al., 2006; Messinger & Bi-shamamba, 1997; Neugebauer, 1985], sanctuaries [Hance, 2009; Faust et al., 2017] and in the wild [Grützmacher et al., 2018; Haggis, 2016; Sakamaki et al., 2009]. It is one of the most common causes of death in the zoo population [Clyde, 2000]. Bonobos are highly susceptible to most respiratory viruses and bacteria carried by humans [Clyde, 2011]. Colds can quickly develop into respiratory disease. Viral and bacterial pathogens play a primary role in the respiratory diseases of bonobos, but fungal, parasitic, and other non-infectious causes of respiratory disorders should be considered on a case-by-case basis.

The following viruses have been identified as causes of upper respiratory disease, bronchiolitis, and pneumonia in humans that may also affect the health of bonobos:

respiratory syncytial virus (RSV), parainfluenza viruses (types 1-3), influenza viruses (type A, B), rhinovirus, and adenovirus. Bacterial agents that may also lead to similar respiratory disorders include: *Pneumococcus*, *Staphylococcus*, *Streptococcus*, *Hemophilus influenza*, and *Bordetella pertussis* (whooping cough) [McLaughlin et al., 2007].

Contact with contagious humans is the most like source of disease transmission in zoo-housed bonobos [McLaughlin et al., 2007]. Respiratory Syncytial Virus (RSV) is so prevalent in the human population and so contagious that exposure to bonobos is inevitable [Janssen et al., 2006]. Therefore, it is recommended to use barriers like face masks to protect the transmission of infectious agents for animal care staff members, especially during periods of high risk (e.g., cold and flu season) [McLaughlin et al., 2007]. Other recommendations include [Clyde, 2011; 2016]:

1. Restrict human access to bonobo troops over the fall/winter when respiratory infection rates are highest in surrounding human community. Bonobos remain highly susceptible to most respiratory viruses and bacteria carried by humans.
2. When respiratory disease is observed within a bonobo troop, monitor the situation carefully, and initiate therapy when appropriate. Mortality due to Acute Respiratory Distress Syndrome (ARDS) is occasionally reported in bonobos.
3. Antibiotics: choose a drug with efficacy against both *Streptococci* and *Staphylococci*, such as cephalexin or cefpodoxime. Can add azithromycin to extend spectrum. Ceftriaxone can be given by injection or via dart if necessary.
4. **Bronchodilators**: Give albuterol via nebulization if possible to relax airways and improve ventilation. If animal will not allow nebulization, albuterol can be given orally but avoid overdose which can induce lactic acidosis leading to rapid shallow breathing. Use only one route of administration for albuterol at a time; do not give oral medication and nebulize concurrently
5. **Anti-inflammatory medication**: reduce fever and alleviate pain and discomfort through use of medication such as ibuprofen 5 mg/kg every four to six hours.
6. If respiratory disease worsens, persists, or respiratory distress develops, **intervene with an anaesthetic event** to allow radiographic evaluation, diagnostic testing and therapeutic treatment with intravenous antibiotics and nebulized bronchodilators. Do not continue to “wait and see” once severe respiratory disease or distress is observed.
7. **Anesthetize animal** for ventilatory support using low tidal volume with rapid shallow breaths, if ventilation-perfusion mismatch results in decreased oxygen saturation, or if animal becomes too exhausted to continue the work of breathing. Limit fluid therapy to just enough to maintain blood pressure and urine output to avoid pulmonary oedema. Monitor blood gases if possible, and attempt to keep CO_2 (mEq/L) in 30’s to low 40’s, although can accept CO_2 up to 50 mEq/L as long as pH stays above 7.3. Avoid barotrauma to lung.

Infection of the laryngeal sac

Laryngeal sac infection in bonobos occurs in some individuals, and once it occurs, it often reoccurs [Mahamba, 2009; Rietschel, 2012; Rietschel & Kleeschulte, 1989]. Typically, the infection is caused by bacteria, usually in mixed cultures, including beta-haemolytic streptococci, *Arcanobacterium haemolyticum, A. pyogenes*; *Eschereria coli*; *Klebsiella* sp.; *Morganella sp.*; *Neisseria elongate, N. lactimica N. meningitides*; *Pasteurella multocida*; *Proteus sp.*; *Providentia stuarti*, *Pseudomonas aeruginosa*; *Pyocyaneus* sp.; *Staphylococcus aureus, S. capitis*; [Clyde, 2006; Mahamba, 2009; Rietschel, 2012; Rietschel & Kleeschulte, 1989]. Infection is visible as a lump on the throat between larynx and torso, as a distension of the laryngeal or axillary air sacs, seen as enlargement of the throat or axillary region, together with fetid breath; sometimes also coughing and/or nasal discharge [Mahamba, 2009; Rietschel, 2012; Rietschel & Kleeschulte, 1989]. It is thought that low humidity and high dust levels in the air may be important environmental factors, also respiratory infections, stress, and possibly antibiotic treatment for other conditions leading to imbalances in the normal air sac microbial flora [Rietschel, 2012]. Rietschel & Kleeschulte [1989] give a detailed description of a case and treatment of air sacculitis in a female bonobo. The most successful treatment is by opening the infected air sac at a ventral point, under anaesthesia, draining out the fluid, and attaching the epithelium of the air sac to the skin using non-absorbable sutures to create an opening of about 1 cm. The opening closes after several weeks even when non-absorbable suture material is used [Mahamba, 2009; Rietschel, 2012].

Shigellosis

Although not specific for bonobos, and not uncommon in primate collections, infection with *Shigella sp*. appears occasionally in zoo-housed collections of bonobos [e.g. Göltenboth, 1998; Rietschel, 1998]. With frequent exchanges of individuals between institutions, some strains have been distributed all over Europe [Rietschel, 1998]. Usually the time span between outbreaks within an institution is quite large, and people tend to forget the seriousness of such outbreaks, mistaking shigellosis for a simple diarrhoea. Shigellosis can have devastating consequences however, and condition of infected bonobos has been known to deteriorate fast. Care should be undertaken to use the correct, strong antibiotics, as treatment with mild antibiotics will not help, and may postpone effective treatment. When well treated, shigellosis has successfully been cured in bonobo groups without taking lives.

SIV and STLV

Simian Immunodeficiency Viruses (SIV) and Simian T-Lymphotropic viruses, also *Simian T-cell Leukemia viruses* (STLV) belong to the retroviruses, and although closely related, have different pathogenicity and different risks for people involved. Thus far, SIV has not been found in wild [Li et al., 2012] or zoo bonobos [Clyde, 2000; Van Dooren et al., 2002]. Since the 1990s, the Bonobo EEP species committee is aware that STLV is present in the zoo populations of both EEP and SSP [Digilio et al., 1997; Giri et al., 1994; Van Brussel et al., 1998; Vandamme et al., 1996]. STLV-2 and STLV-3 appear also endemic to natural populations of bonobos

[Ahuka-Mundeke et al., 2011]. Moreover, a recent study in SSP zoos showed that the virus was found in 25% of the animals tested, but this study also warns that results may be dependent on which laboratory was selected for testing [Clyde, 2000]. There is no evidence for recent direct transmission between human and nonhuman primates and the STLVs are not considered to be zoonotic [Murphy et al., 2006]. The *Human T-Lymphotropic Viruses* (HTLVs) and STLVs seem to be of low pathogenicity even in their respective hosts [Lowenstine, 2000 – cited in Clyde, 2000; see also Murphy et al., 2006]. Given the small number of bonobos in the EEP collection, further fragmentation of the population by isolating bonobos that are documented STLV positive, is not recommended, as this would decrease the genetic diversity of this small population.

Papilloma

The presence of Papilloma virus has been noted in both the EEP and SSP bonobo populations since the 1980s - 90s and seems widespread in the population [Rietschel, 1998; Sundberg et al., 1992; Van Ranst et al., 1991]. Infection of the virus can lead to lesions in the mucus membranes of oral cavity, and lower genital tract in infected bonobos [Kramer, 1997; Hoffmann et al., 2019] and the virus has been shown to remain active in animals for up to 30 years [Hoffmann, et al., 2019]. The Bonobo EEP and SSP have decided to monitor the incidence of papillomas in the North American and European population. With such a small population, neither the SSP nor the EEP can afford to manage papilloma positive bonobos separately, or to keep them in isolation indefinitely [Kramer, 1997; McLaughlin et al., 2007].

Creases and cracks/Dry skin, other skin related conditions

Dry skin and decreased hair coat condition have been observed during the winter in northerly facilities, and have been associated with over-dry environments [Neugebauer, 1980]. Offering dietary supplements containing omega 3’s, such as flaxseed oil, have been reported to reduce these symptoms [McLaughlin et al 2007]. In general, it is recommended to keep air humidity in bonobo enclosures high; the use of biofloors may help in raising humidity (see section 2.1.5 Substrate and 2.1.7. Envirornment/Humidity), and this seems to prevent dry skin. Chapman et al. [2017] describe successful treatment of lobular capillary haemangioma in a nursing female bonobo.

Parapoxvirus

Parapox was diagnosed in a bonobo in Wilhelma Stuttgart Zoo and it is suspected the virus may have been transmitted through contaminated clothes of a keeper taking care of infected sheep [Rietschel, 1992; 1998].

Tuberculosis

For a case study of *Mycobacterium tuberculosis* in a group of zoo-housed bonobos, and evidence of infection of a keeper by the bonobos see Akkerman et al. [2014].

Reproductive medical conditions

Keller et al. [2010] reviewed the reproductive medical history of 24 bonobos in Milwaukee zoo and conclude that bonobos appear relatively robust reproductively. In males, prostate-related disease was observed in two animals. Reproductive problems in females had a broader range and could be categorized as pregnancy-related conditions, issues related to contraceptive management, reproductive tract abnormalities or trauma. The most numerous reports were pregnancy-related, including abruptio placenta with subsequent death of the dam and foetus, pre-eclampsia and placental insufficiency with resultant low-weight infant, spontaneous abortion, and blighted ova identified through repetitive reproductive sonograms [Clyde,2011]. Contraceptive-associated problems included breakthrough bleeding while on lower oestrogen dose oral birth control pills. Reproductive tract abnormalities included two cases of trauma to the external genitalia and one case of suspected uterine fibroids. Placental retention has been described in bonobos, but is rare [Halbwax et al., 2009]. Persky et al. [2018]describe a successful treatment of a complete molar pregnancy in a multiparous, 47 year old female bonobo.

Lasley et al. [1977] report on a case of ovarian failure in an adult female that showed a continuous maximal ano-gential swelling, despite hypogonadism and substantial abdominal scars and adhesions. Lear et al. [2001] report trisomy of chromosome 17 in an infant female bonobo that exhibited inability to nurse and progressive weakness plus multiple congenital abnormalities including aural canal atresia and stenosis, malformed auricles, clenched hands, lordosis, agenesis of the caudal vertebra and cardiac abnormalities.

For sampling of semen post mortem, please see the protocol described in Keller et al. [2012].

The EAZA Reproductive Management Group compiled a check list for Diagnosing the Point of Reproductive Failure. If you have bonobos who should be breeding, but aren’t, please contact the EAZA Reproductive Management Group via contraception@chesterzoo.org for support in identifyingthe possible causes of reproductive failure.

2.8. Specific challenges for keeping bonobos in the EEP

- The bonobo EEP population is demographically healthy on all levels, but there is a slight underrepresentation of males in their breeding age.
- When female bonobos have multiple sons in small groups, capacity issues can arise – large facilities are needed to maintain females with multiple sons (e.g., three to four adult sons) in combination with appropriate breeding partners for all individuals involved.
- The number of wild born bonobos is going down, with most wild born bonobos now being post reproductive. All living wild-born individuals in the EEP and SSP are now founders, meaning they have contributed to the genetic diversity of the EEP population. There are no potential founders left in the EEP or SSP. This means that in the very near future all breeding will be done by captive born individuals, which may lead to further loss of genetic diversity.
- Both within EEP and SSP founder representation is skewed, and a few founders are well over represented. This skewed founder representation also influences the choice of breeding males. There are some founders in EEP that are not represented in the SSP and vice versa. A first attempt to balance this was made in 2018 by the import of two females from the SSP into the EEP, which brought new genetic founder material into the EEP population, from four new different founders.
- Another option to solve the biased founder representation, especially among the breeding males in the EEP, could be sperm collection and artificial insemination. Sperm storage from males that are not descending from one specific male that is overrepresented (Masikini) has been given priority in the EEP and has already started. In the past, sperm has also been frozen from founder males who meanwhile passed away. We, however, lack technical and theoretical knowledge on how to inseminate the females. At the last EEP/SSP meeting in 2019? also ethical problems were raised in relation to artificial insemination.
- Balancing founder representation can be challenging in combination with the multi-male-multi-female social organization and promiscuous mating system of the species. When keeping multiple breeding males in the groups, it is hard to prevent low priority males or overrepresented males from breeding, to allow breeding of high priority or underrepresented males. Managed fission-fusion has been tried as a method to group females with the recommended male(s) and can be successful, but it requires large, flexible buildings, a lot of staff time and experience. Institutions have noted, it may create stress and tension among the males when one male is separated with fertile females and the others are not given access.
- Aggression management from females to males can be challenging, even when males have staid with their mother.
- Providing challenging social and physical environments, where bonobos can achieve their goals, have choice and control is impediment for providing good a good welfare balance.
- In the future, when breeding in the EEP will have to be limited, the influence of birth control on behaviour and welfare in female bonobos might become an issue.

2.9. Recommended research

The Bonobo EEP recommends further research on bonobos in European zoo collections, as well as support to research in situ, especially, when it benefits conservation of the species in its natural environment and/or the management of the species in zoos. Good, preferably hypothesis driven research, following zoo Research Guidelines is recommended. In zoo collections research applications can be reviewed by EEP coordinators and/or by the members of the Research Group of the Great Ape TAG. Those reviewers can provide practical advise on how to do zoo research, and can evaluate if the research benefits captive populations.

The following topics have been identified as priority for research that benefits management of bonobos in zoo environments:

1. **Breeding ex situ**: Further research into genetic diversity in historic and contemporary captive and wild bonobo populations, in collaboration with the EAZA Biobank.
2. **Breeding ex situ**: Research on sperm collection, sperm storage and especially artificial Insemination is high priority, because it potentially can be used to increase genetic diversity in the populations.
3. **Social management**: Monitoring stress and aggression received, especially in males in relation to their welfare.
4. **Social management**: Monitoring effects of environmental changes and challenges, both social and non-social on bonobo welfare, including effects of all kinds of enrichment, environment such as visitor numbers.
5. **Nutrition**: Effects of dietary changes. Increase fiber, look at micronutrients from wild diets such as starch, iodine, or the influence of animal and plant protein.
6. **Nutrition**: Effects of dietary changes on regurgitation behaviour and other abnormal or undesirable behaviours.
7. **Veterinary**: Compile more physiological measures for “normal” versus “diseased” bonobos in all age/sex categories, to have better reference values.
8. **Veterinary**: Continue research into causes of mortality, especially related to cardiac disease.
9. **Veterinary**: Continue research into respiratory disease and bonobo immune systems.
10. **Veterinary**: Monitor effects of birth control methods on physiology but most importantly on social behaviour and welfare in female bonobos

Section 3: References / Bibliography

This section contains, in alphabetical order a bibliography about bonobos that is nearly complete – it contains the references used in the Bonobo Best Practice Guidelines, but also publications about bonobos that have not been used in the main text. This reference list also contains relevant publications that are not specific about bonobos, but have been referred to in the main text, such as papers on enrichment in other species of apes. A hardcopy of most publications is kept by the EEP coordinator.

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Section 4: Appendices

Appendix 1: Normal Haematological and biochemical blood values

Parameter	Mean +/- SD	Units
Haemoglobin	14.4 +/-1.6	g/dL
RBC (Erythrocyte)	15.53 +/-0.68	x106/mm3
PCV (Haematocrit)	41.2 +/-5.0	%
MCV	74.0 +/-4.9	fl (or µm3)
MCH	24.3 +/-1.8	pg/cell
MCHC	32.7 +/-1.0	g/L
(Leukocytes)	12.74 +/-5.93	x103/µl (x103/mm3)
Neutrophils	9.60 +/-6.0	x103/µl
Lymphocytes	2.65 +/-1.85	x103/µl
Monocytes	0.38 +/-0.29	x103/µl
Eosinophils	0.34 +/-0.31	x103/µl
Basophils	0.16 +/-0.7	x103/µl
Platelets	213.0 +/-116.0	x103/µl
Plasma protein	7.2 +/- 0.7	g/dl

Parameter	Mean +/- SD	Units
Total Protein	7.2 +/- 0.7	g/dl (mg%)
Albumin	3.6 +/- 0.3	g/dl (mg%)
Globulin	3.6 +/- 0.5	g/dl (mg%)
Calcium	9.1 +/- 0.5	mg/dl (mg%)
Magnesium	2.5 +/- 0.00	mg/dl (mg%)
Phosphorus	3.8 +/- 1.2	mg/dl (mg%)
Sodium	142.0 +/-3.0	mEq/L or mmol/L
Potassium	3.6 +/- 0.5	mEq/L or mmol/l
Chloride	102.0 +/- 4.0	mEq/L or mmol/l
Creatinine	0.8 +/- 0.2	mg/dl
BUN (Urea nitrogen)	10.0 +/ 3.0	mg/dl
Cholesterol	241.0 +/-50.0	mg/dl
Glucose	73.0 +/- 18.0	mg/dl
Iron	101.0 +/- 36.0	µg/dl
AST (SGOT)	21.0 +/-9.0	iu/l
LDH	368.0 +/- 236.0	iu/l
CPK (CK)	119.0 +/- 127.0	iu/L
Amylase	16.0 +/- 8.0	iu/l
Alkaline phosphatase	181.0 +/-149.0	iu/l
GGT	8.0 +/- 3.0	iu/l
Total bilirubin	0.3 +/- 0.1	mg/dl
Direct bilirubin	0.0 +/- 0.1	mg/dl
Indirect bilirubin	0.2 +/- 0.1	mg/dl
Triglycerides	69.0 +/- 29.0	mg/dl

Appendix 2: Bonobo Conservation Organisations

Bonobo Alive

- **Location:** South-western part of Salonga National Park
- **Mission:** Bonobo Alive is an organisation initiated by bonobo researchers dedicated to the protection of wild bonobos and their habitat in the south-western part of Salonga National Park, DR Congo. Bonobo Alive is funding the intensification and extension of existing anti-poaching patrols in collaboration with the Institut Congolais pour la Conservation de la Nature and with local people to stop ongoing poaching and bushmeat trade. Additionally, Bonobo Alive plans to establish a regional program for environmental education.
- **Activities:** anti-poaching patrols; education; research
- **Website:** http://www.bonobo-alive.org/

Mbou Mon Tour

- **Location**: Bolobo area, in the province Mai-Ndombe & Bandundu (300 km north of Kinshasa); Yumbi, Mushie, Inongo, Kutu.
- **Mission** Mbou-Mon-Tour acts for the conservation of the environment and local development.
- **Activities**: Habitat protection, Sustainable development; environmental education
- **Website: http://www.mboumontour.com/**

Awely Green Caps

- **Location**: Basankusu
- Mission: **To conserve bonobos through development in the Democratic Republic of Congo.** Since early 2008, we have developed a Green Cap program in the Democratic Republic of Congo, where we are working to improve the situation for the bonobos (*Pan paniscus*) and villagers sharing the same environment. Evaluate the impact of hunting and consumption of bushmeat on bonobos. Stop the hunting and sale of bonobo meat. Develop alternatives to the trading and consumption of bushmeat. Reduce pressure on forest resources.
- Activities: Sustainable development; Environmental Education
- Website: http://www.awely.org/

Lola Ya Bonobo Santuary

- **Location**: Kinshasa & Basankusu
- **Mission**: Lola ya Bonobo is the world's only organization to provide lifetime care to bonobos orphaned by the illegal trade in endangered wildlife. We are on the front line in the battle to protect bonobos in the only country they are found – The Democratic Republic of Congo
- **Activities**: Public education; Rehabilitation & release
- **Website**: http://www.awely.org/

Lukuru Foundation

- **Location**: Lomami National Park
- **Mission**: Our mission is to conserve great apes and their natural habitat within the territorial borders of the Democratic Republic of Congo. Our approach is to locate and document important populations of great apes, identify regional threats, work to secure the environment

and communities against those threats, facilitate implementation of a locally appropriate framework for protection, build local lobbies for great ape conservation, environmental security and social progress, and participate with the local people to actively protect species and habitat. We strive to change human behaviors that are contrary to conservation while we encourage behaviors that support conservation and minimize species loss. Working through and with local groups and the authority infrastructure within target regions, each project collaborates with local communities to raise public awareness for great ape conservation, as well as other targeted wildlife species, and build relationships with those people. We encourage initiatives that build sustainable relationships between human survival and wildlife conservation in order to directly impact responsible, locally-appropriate conservation management.

- **Activities**: Population Monitoring; Habitat Protection
- **Website**: www.lukuru.org

Bonobo Conservation Initiative (BCI)

- **Location:** Kinshasa; Washington DC; Bonobo Peace Forest
- **Mission**: Our mission is to protect bonobos, preserve their tropical rainforest habitat, and empower local communities in the Congo Basin. Together with Congolese communities and organizations, the DRC government, and international partners, BCI is implementing innovative solutions to address the complex problem of bonobo conservation.
- **Activities**: Public education; Population monitoring
- **Website:** www.bonobo.org

Bonobo Congo Biodiversity Initiative (BCBI)

- **Location:** Salonga National Park – Watsi Kengo sector
- **Mission**: The Bonobo & Congo Biodiversity Initiative (BCBI) studies and protects bonobos in the Salonga National Park, a World Heritage site in the DRC, to ensure the survival of this endangered great ape.
- **Activities**: Research; Population monitoring; Habitat protection; Education
- **Website:** www.bonoboconservation.com

The Bonobo Project

- The Bonobo Project is a 501(c)3 nonprofit organization that seeks to elevate the status and awareness of the endangered bonobo and coordinate activities to aid in the conservation of this uniquely matriarchal and peaceful great ape indigenous only to the Democratic Republic of Congo. 100% of all donations to the Bonobo Project are used for conservation and awareness efforts.
- Activities: Fund raising
- Website: http://bonoboproject.org/

The Great Apes Survival Partnership (GRASP)

- GRASP is United Nations Environmental Programme (UNEP) initiative first launched in 2001. The partnership works to bring together stakeholders to address issues relating to the conservation of apes.
- **Website:** http://www.un-grasp.org/

African Wildlife Foundation (AWF)

- **Location**: Lomako National Park
- **Mission**: the African Wildlife Foundation has set up a conservation plan to help stop the destruction of these gentle animals and their habitat. We created The Lomako Conservation Science Center in the heart of the bonobos habitat. This center supports wildlife surveys, training of Congolese researchers and developing wildlife conservation plans. AWF has surveyed key areas of Bonobo habitat and polled local communities on how their needs could fit within our conservation goals. By regularly monitoring the endangered bonobos numbers and keeping track of where they are, conservationists can develop strategies to find economic alternatives for communities who hunt them for protein.
- **Activities**: Habitat Protection; Population Monitoring
- **Website**: http://www.awf.org/wildlife-conservation/bonobo

World Wildlife Fund (WWF)

- WWF has provided training, equipment and field supplies for the ICCN and non-governmental organizations conducting surveys of bonobo populations. After the first survey of Salonga National Park found fewer bonobos than expected and greater amounts of human disturbance, additional efforts were made to monitor and protect these animals. A survey of large mammals in the DRC's Lac Télé-Lac Tumba Landscape revealed a previously unknown population of bonobos, a population that has the highest density and largest group size of the animals anywhere in their range. After this discovery, WWF helped to establish the Lac Tumba-Lediima Nature Reserve, which will help to protect this dwindling species.
- **Actions**: Population Monitoring; Habitat Protection; Law enforcement
- **Website**: https://www.worldwildlife.org/species/bonobo

IUCN/SSC Primate Specialist Group (PSG)

- PSG work in through Africa, Asia and Latin America to promote the conservation of primates, by supporting field research, conservation measures and education initiatives. PSG's primary responsibility is to evaluate the conservation status of primate species and sub-species for the IUCN Red List and to coordinate the production of species-specific conservation Action Plans.
- **Website:** http://www.primate-sg.org/index.htm

Appendix 3: List of browse reported for bonobos in zoos

Vernacular name	Scientific name	Protein % dry matter	NDF %	ADF %	ADL %	Notes
False banana	*Ensete sp*					
acacia	*Acacia sp.*					
Alder	*Alnus sp.* *Alnus incana, Alnus glutinosa*					
Alfalfa hay	*Medicago sativa*	88[1]	58[1]	36[1]		
Ash	*Fraxinus sp.*	27[1]				
Apple	*Malus sp.*					Wilted leaves can contain cyanides[1]
bamboo	*Phyllostachys sp.*	52[1]	66[1]	30[1]		Mostly enrichment[1]
banana	*Musa sp*	19[1]				Long fibres can create obstruction in gut[1]
beech	*Fagus sp.*	39[1]	65[1]	50[1]		
birch	*Betula sp.*	14.3-35[1]	46.7	24.3	13.4	
Bramble/raspberry	*Rubus sp.*		43.5[1]	26.8[1]		
Chinese hibiscus	*Hibiscus rosa sinensis*					
crown vetch	*Securigera varia*					
Elm	*Ulmus sp.;* *e.g. Ulmus rubra* *U. minor* *U. glabra*		45[1]	25[1]		
Fig	*Ficus sp.*					
Forsythia	*Forsythia sp.*	9.57	24.6	16.0	8.7	
Fountain grass	*Penisetum sp.*					
Georgia Cane	*Arundo donax*					
Ginger	*Zingiber officinale*					
Ginkgo	*Ginkgo biloba*					
grape vine	*Vitis sp.*		33[1]	23[1]		
Hawthorn (thorns removed)	*Crataegus sp.*	9.1	53.9	23.6	10.1	
Hazel	*Corylus sp.*	16.2	47.9	27.1	14.6	
Honeysuckle (no berries)	*Lonicera sp.*					
linden	*Tilia sp.* *T. cordata* *T. platyphyllos*	30[1]				
maple	*Acer sp.*	9.85 13.0 13.2 26[1]	38.8 38.6 26.5	15.7 18.0 14.4	6.3 18.0 6.8	Never feed when fungus on leaves[1]
mulberry	*Morus sp.*					
Natal plum	*Harpephyllum kaffra*					
Oak	*Quercus sp.*	11.2	50.4	23.6	10.1	
Plane tree; Sycamore	*Platanus sp.*					

Poplar	*Populus sp.* *e.g. Populus tremuloides; P. deltoides ; P. nigra P tremula*	25[1]				
Rhubarb	*Rheum rhabarbarum*					
sugar cane	*Saccharum sp.*					
tetrastigma	*Tetrastigma sp.*					
viburnum	*Viburnum sp.*					
willow	Salix sp. (e.g. Salix matsudana 'Tortuosa'; Salix alba 'Tristis' ; Salix caprea ; …	16.4 12.6	36.6 34.9	22.8 22.1	9.3 10.9	
European hornbeam	Carpinus betulus					
Robinia	*Robinia pseudoacacia*	25[1]				Young shoots, wilted leaves, seeds and branches contain toxines[1]
Thistle	Soncus oleraceus	13.5[1]				Especially young plants eaten by some individuals
nettle	Urtica dioica	35[1]	51.4[1]	38[1]		Stings, but eaten by some individuals

1: Nijboer & Huisman, 2010.

Appendix 4: GREAT APE BEHAVIOURAL INFORMATION SHEET

SPECIES COMMON NAME (SPECIES SCIENTIFIC NAME)

Bonobo *(Pan paniscus)*

Please send one form to the receiving institute and one to the studbook keeper

1) Identity

House name:

Studbook N°:

Local ID:

Transponder ID: Transponder location:

Owner:

Gender:

Date of Birth:

Origin:

Rearing:

Notes:

2) Reproductive history

(List any offspring born, reproductive failure, birth control…)

- Offspring – Studb# - date of birth – house name – rearing type – sire

- Reproductive failure *(provide details below)*

- Is / has been on birth control *(provide details below)*

    -

    Notes:

3) Behavioural history

• Social position and behaviour in the group:

-

• Particular behaviours worth mentioning (Coprophagy, Smearing faeces, Regurgitation, Hair plucking self, Hair plucking others)

4) Training:

• For medical reasons: - no medical training

• For husbandry

• Other: (please specify)

5) Medical history –

• Chronic illness

• Allergies

• Laryngitis

• Dental issues

• Other: *(please specify)*

6) Experience in mixed species enclosure? With which species?

- **none**

7) Kind of barriers the individual is used to? (moats, water moat, electric fences…)6)

8) Additional remarks

Appendix 5: Instructions for hair collection for paternity diagnosis.

Paternity diagnosis is vital for managing the zoo populations, as inbreeding may have deleterious effects on infant survival and for making appropriate transfer recommendations. Therefore it is recommended to take hair samples of infants as soon as possible and have paternity analysed. However there is no need to sedate youngsters especially for collecting hairs. Usually hairs can be obtained from infants when they are two years old.

When sending hair for paternity diagnosis please contact EEP coordinators first to see if material from mother and/or potential sires is also needed. When bonobos are kept in multimale groups, any male from the age of seven on should be considered a potential father of offspring, even when the group has been in managed fission fusion. The CRC now has a reference collection of most bonobos in the EEP, making it easier to assign paternities. Other commercial companies or research groups may also do paternity analysis, but may use different mitochondrial markers which makes future comparisons complicated, and they may not have the reference material of potential sires available. By concentrating the paternity analysis in one facility, we can limit the number of necessary hair samples.

Hair sampling

1. Collect hairs by direct plucking.
2. Wear gloves when taking the hairs to avoid contamination of human DNA with bonobo DNA. Change gloves if you sample different individuals to avoid contamination between individuals.
3. Collect a minimum of 10 hairs from each bonobo. The hairs must be plucked so that the root, which contains the DNA, is intact. Infant hairs are noted to be difficult to take, and may break off easily – so please make sure that the roots are attached.
4. Store the hairs in a paper envelope. Do not mix hairs from different individuals in the same envelope.
5. Mark each envelope with a studbook number and/or name or unique identifier.
6. Hairs may be stored at room temperature (in the dark) until transported to the molecular facility.

PLEASE SEND ALL MATERIAL ASAP TO:

KMDA-CRC
Molecular Lab
Koningin Astridplein 20-26
2018 ANTWERP
BELGIUM

For questions or comments please contact the Bonobo EEP coordinator

Appendix 6: Swelling score sheet

Female I.D. ________________________ Month ________________ Year ____________

1= Score area is wrinkled/detumescent

2= score area is partially tumescent, decrease in wrinkles

3= Score area is fully swollen, no wrinkles, entire area is taut and does not sway

3.1.= Score area is same as 3, but shine is visible on the labia/anus area

Day	Labia	Anus	Menses	Comments
1				
2				
3				
4				
5				
6				
7				
8				
9				
10				
11				
12				
13				
14				
15				
16				
17				
18				
19				
20				
21				
22				
23				
24				
25				
26				
27				
28				
29				
30				

31				

Appendix 7 : recorded pregnancy durations

	Name mother	Name offspring	Last max swelling	Last menses	Post ovulation	Last breeding	Not specified
Bolser & Savage-Rumbaugh (1989)	Matata	Mulika		244			
Bolser & Savage-Rumbaugh (1989)	Matata	Panbanisha		245			
Thompson-Handler (1990)	Maringa	Naomi		238			
Thompson-Handler (1990)	Maringa	Ngami		227			
Thompson-Handler (1990)	Maringa	Lomako		247			
Thompson-Handler (1990)	Margrit	Yala		237			
Thompson-Handler (1990)	Dzeeta	Nikki		(277)			
Thompson-Handler (1990)	Daniela	Okino		238			
Thompson-Handler (1990)	Daniela	Maiko		254			
Thompson-Handler (1990)	Natalie	Ukela		261			
Thompson-Handler (1990)	Salonga	Yenge		242			
Van Elsacker et al (1993)	Hermien	Riddle	235				
Van Elsacker et al (1993)	Hermien	Unga	238				
Dahl & Gould (1997)	Zalia		219				

Stevens, unpub	Hermien	Zomi	235				
Stevens, unpub	Hortense	Redy				241	
Stevens, unpub	Hortense	Vifijo	216	244			
	Hortense	Zamba	221	(234)			
J. Ruys pers comm	Kumbuka	Yahimba	241	259			
Drews et al., 2010	Ana Neema	Bila Isia			229		245
Drews et al., 2010	Ana Neema	Gilda			237		231
Drews et al., 2010	Laura				239		
Drews et al., 2010	Laura				228		
Drews et al., 2010	Maringa				208		
Drews et al., 2010	Maringa				210		
Drews et al., 2010	Kosana	Dierdre			214		
	Kimia	Zeke		(268)			
	Susie	Kimia					244
	Susie	Lola					234
	Susie	Mary-Rose	241				
	Lady	Ricky/twin					222
	Lady	Tamia					236
	Lady	Jo-T					(198)
	Lucy	ELikia	215*				
	Lucy	Andy	223				
	Lucy	Layla	231				

Appendix 8: A schedule for early infant introduction

as used in Columbus Zoo and Aquarium, Ohio

The following schedule has been adapted from Lombardi et al. (2011).

Day 1 to 15

- This is when new staff is trained, see staff training section.
- Take vitals every two hours unless medical issues require more frequently, weigh daily before the first bottle.
- Infant should be next to conspecifics from the first day with vet approval.
  Stay quiet and do not interact with the other bonobos. This is the introduction period for you and for the infant bonobo.
  Diapers should not be worn when sitting next to bonobos.
  Familiarize the infant with bedding.
  Stay away from the mesh so infant can't be grabbed.
  Bonobo behaviors are observed, record important information.
- Thrush (candida), a white coating on the tongue is a common occurrence for infant gorillas and may be seen in the bonobo. This condition is painful so treat immediately, infant may refuse bottle.
- Bottle feedings are every two hours.
  Disposable volufeeders and nipples are used for every feeding.
  Heat the volufeeder in a cup of hot water.
- Hold the Infant in an upright position ventral/ventral next to chest area for feedings, emulating mother nursing.
  If in the hand rearing space, recorded bonobo vocalizations can be played softly.
- When the infant is in the bonobo area, a small snack can be given to the group in order to elicit the appropriate vocalizations.
- The infant is held almost constantly ventral/ventral, including throughout the night. He should only be put down if necessary. Then he should be placed on his stomach in a safe, secure area.
- Infant is encouraged to hold onto the keeper not vice versa.
- Motor skills at this age consist of grasping, holding the head up, rooting and eye contact. He follows movements and looks at objects.
- The keeper should groom and inspects the infant's body.

Stool and urine output is frequent in a newborn.

When adjusting to formula, stools may be inconsistent

Day 16 to 30 Continue pertinent protocol from above

- Bottle feedings are every two hours, formula is increased based on infant's weight.
- Take vitals twice a shift or more if the infant is unstable.
- Infant and keeper should be next to conspecifics during their waking hours.
- The infant is held ventral/ventral or in the groin area.
- The infant may root and become vocal before feeding time.
- Infant sleeps and is awake for longer periods.
- Infant is exercised by limb movement, see photo.
- Infant will start pulling himself up on keeper by holding keeper's thumbs.
- Infant is exposed to food items by smell and touch and watching keeper eat.

Day 31 to 45 Continue pertinent protocol from above

- Bottle feedings are every two hours, formula is increased based on infant's weight.
- Take vitals once a shift unless medical issues require more frequently.

- Raising tummy off of the floor and may start to scoot on keeper's lap, then on floor.
- Infant should be more aware of bonobos.
- The infant should be moving their head looking around, responding to voices, and have good eye contact with keeper.
- Depending on comfort level between keeper and bonobos, infant may be held at mesh for smellming and touching conspecifics.
- The bonobo group may pass wood/wool or browse through the mesh.
- Observations are very important to determine maternal interest.
- Bonobo choice may begin to become evident.
- At night, infant sleeps on keeper. When infant is asleep, keeper can spend more time on records/chores but stays in close proximity to infant.

Day 46 to 60 Continue pertinent protocol from above

- Bottle feedings are every two hours, formula is increased based on infant's weight.
- If vitals are disruptive to sleeping at night, discontinue.
- BPA free bottles are used when the amount goes above 60 mls.
- Use bottle warmer to heat the bottle.
- Infant is scooting longer distances, pushing with legs and pulling with arms.
- Infant may use bonobo vocalizations.
- Infant is more aware of conspecifics.
- Certain group members may touch the infant.
- Keeper and infant are exploring all aspects of the cage and environment.
- At night Infant sleeps on keeper. When infant is asleep keeper can spend more time on records/chores but stays in close proximity to infant.

Day 61 to 75 Continue pertinent protocol from above

- Bottle feedings are every two hours, formula is increased based on infant's weight.
- We start training to give the bottle through the mesh, by keeper holding infant to the mesh and bonobo keeper offers bottle.
- Infant may start to sit up, will reach out and touch objects.
- He is scooting more frequently in the direction of his choice, lifting chest up with support on elbows, and pushing off with his feet.
- Infant is aware of conspecifics and may react to bonobo behavior.
- Teething may start. Infant may experience running nose, slightly elevated temperature, or lack of interest in bottle. Any change in vitals should be monitored carefully.

Day 76 to 90 Continue pertinent protocol from above

- Bottle feedings are every two or three hours, formula is increased based on infant's weight.
- We start training to give the bottle through the mesh, by keeper holding infant next to the mesh and bonobo keeper offers bottle.
- Tooth eruption, lower and upper central incisors may have erupted.
- Possibly one female is showing interest in the infant by spending more time or watching the infant from a distance.
- Keeper and infant are exploring all aspects of the exhibit, chutes, outside environment, doing whatever the troop is doing, playing, etc.

Day 91-105 Continue pertinent protocol from above

- Bottle feedings are every three hours, formula is increased based on infant's weight.
- Training to give bottle through the mesh by keeper holding infant at the mesh and bonobo keeper offers bottle.
- The infant should be weighed each morning before the bottle until introduced to a surrogate.
- See solid food protocol. Start each new food one at a time at three day intervals to assure there are no food allergies. At first offer 1 or 2 grams of cooked vegetables such as sweet potato, carrots, white potatoes and then banana. Additional vegetables are added before other fruits. Baby food is never used.
- Tooth eruptions may include upper and lower lateral incisors.
- Back riding started.
- Surrogate should be identified.
- Due to the complexity of fission/fusion management and bonobo needs, the surrogate may not be isolated prior to the introduction. Care should be taken to have the surrogate in varied groups that allow the individual to spend time mesh to mesh with the infant.

Day 106-120 Continue pertinent protocol from above

- Bottles are given every three hours, formula is increased based on infant's weight.
- Training to give bottle through the mesh by keeper holding infant next to the mesh and bonobo keeper offers bottle.
- Vitals are taken once a day unless there is a health concern.
- Crawling better daily, pulling self up to a standing position, initiating play with keeper, showing more interest in bonobo behavior, making open mouth faces.
- Practice gating through baby door.
- Tooth eruptions may include upper and lower lateral incisors.

Day 121 to 135 Continue pertinent protocol from above

- Bottle feedings are every three hours, formula is increased based on infant's weight.
- Training to take bottle through the mesh by encouraging infant to crawl short distances for his bottle at the mesh.
- He is crawling quicker, standing upright and holding onto surfaces for a longer period of time.
- Infant should be holding onto the mesh, picking up food and feeding himself, playfully mouthing keeper and toys.
- The infant should be sitting and supporting himself.
- Practice gating through baby door.
- Tooth eruptions may include molars.

Day 136 to 150 Continue pertinent protocol from above

- Bottle feedings are every three hours, formula is increased based on infant's weight.
- Continue training to give bottle through the mesh.
- Our infant was standing at mesh but not climbing. He would come to the keeper for back riding. He would have a play face and laughter.
- Infant should be very alert to the bonobos and more comfortable and confident in environment.

- Practice gating through baby door.
- Tooth eruptions may include molars.

Day 151 to 194 Continue pertinent protocol from above

- Bottle feedings are every three hours, formula is increased based on infant's weight.
- Continue training to take bottle through mesh.
- Discontinue 5 A.M. feeding.
- Continue to add new foods that are in the bonobo diet.
- Climbing is improving and may start climbing downward and rolling over.
- Infant is more comfortable playing further away from keeper, but always in the same area.
- Practice gating through baby door.
- Tooth eruptions are possible.

Day 195 to 215 Continue pertinent protocol from above

- Bottle feedings are every three hours, formulas increased based on infant's weight.
- Continue training to give bottle through the mesh.
- Discontinue 2 A.M. bottle.
- Climbing continues to improve and the infant should be hanging and swinging from ropes.
- Infant should be crawling to the mesh for bottle (fed by bonobo keeper).
- Practice gating through baby door.
- Tooth eruptions are possible.

Day 216 to 242 Continue pertinent protocol from above

- Bottle feedings are every three hours.
- Continue training to give bottle through the mesh.
- Discontinue 11 P.M. bottle.
- Bottle should be given at mesh by bonobo keeper.
- Infant should be successfully going through baby door.
- Infant should be picking up scattered food and eating it.
- Infant should be comfortable being touched by surrogate through mesh.
- Tooth eruptions are possible.
- The infant should meet criteria for introduction to surrogate.

Criteria for introduction to surrogate:

- Staff should agree on readiness of the surrogate and infant. Ideally, the infant and surrogate have established a comfortable bond. The infant feels secure beside the surrogate. The surrogate reacts if the infant shows distress.
- The surrogate has to allow the infant to receive nourishment. Cooperative feeding may exist. Either the infant is mobile and comes to the bottle or the surrogate brings the infant to the bottle.
- An introduction should not proceed with a potential surrogate that displays aggression.
- If affirmative behaviors are not observed, contact Bonobo EEP coordinator for possible relocation of the infant.
- Infant is completely familiarized with all routine and husbandry practices.
- Have a pre introduction health assessment by the vet staff on the infant.

- Prepare for a “Plan B” if possible. This involves having an alternative surrogate if the introduction does not go as expected. Contact the hand rearing surrogacy committee for assistance.
- Five days before the introduction, keeper and infant spend 24 hours a day in the bonobo area. The nighttime atmosphere of this area becomes familiar to the infant, which completes his pre-introduction criteria. We do not intend to separate infant and surrogate once they are successfully introduced, therefore, all components must be in place.

Introduction Day:

- Daily routine for feeding and cleaning is normal. Cage is prepped for introduction, heavy bedding, scatter foods and soft enrichment items.
- Surrogate is separated from the group and placed in an area next to the infant.
- Keep observers to a minimum (remote cameras can be used to facilitate observations)
- While the infant is offered a bottle through the mesh, the hand rearing keeper attending the infant leaves quietly.
- The door is opened for the surrogate to enter.
- Be patient. Surrogate and infant will determine contact time. It may take a half hour or more.
- When infant needs to rest or nap, he may be down apart from surrogate. Possible, surrogate will pick him up and relocate him as she moves around area.
- In a successful introduction, surrogate and infant are never separated. There may be variations in care from a surrogate. The surrogate is now the primary care giver.
- Due to the fact that the infant was raised in this program, there is minimal stress to the infant and surrogate. A bond that began during the introduction process can now be secured.

After the introduction:

- Allowing time for a strong bond to develop between surrogate and infant before integrating another group member is ideal, but staff should monitor surrogate for signs of stress due to isolation from other group members. Other group members may need to be introduced quickly in order to help relax the surrogate so she will focus on bonding with the infant. Appropriate choices include other adult females who the surrogate is closely bonded with or adult males who provide companionship and allow the female to elicit interaction. Juvenile males and females are not suggested as they tend to be too energetic and curious and can prevent the surrogate from resting or focusing on the infant.
- Carefully select which group member will be introduced next and allow time to adjust and solidify a level of comfort before integration of the next group member.
- Since the bonobos are managed by fission/fusion the introduction may be considered complete before the infant has been introduced to all group members or all the various sub-group combinations.
- Once the infant is introduced it is important for the infant to stay on schedule with his bottles.
- At 1 year the formula is gradually changed to whole milk as long as the infant can handle cow’s milk. This is completed in 10 days. Bottle schedule: Days 1-3, ¾ formula to ¼ milk, days 4-6, ½ formula to ½ milk, days 7-9, ¼ formula to ¾ milk, day 10, 100% milk.
- At 3 years of age the bottles are decreased to 2 times a day, at 4 years 1 bottle a day, and at 5 years the infant is weaned. Hydration is important. Juices are offered and water is always available.

Appendix 9: Sample ethogram for behavioural observations

This is an abbreviated version of the “Pictorial Ethogram for Bonobos” Stevens et al, 2019, which can be found on-line.

	Label	Code	Description	Modifier
Individual behaviours	Out of sight	OS		--
	Rest	RE	Subject lies down with eyes open, relaxed but clearly awake	--
	Sleep	SL	Subject lies down with eyes closed, sound asleep	--
	Move	MV	Subject locomotes from one point to another, quadrupedally or bipedally; includes swinging, climbing, walking, running	--
	Manipulate Object	MO	Subject manipulates an object, food or infant with hands, lips or feet	--
	Eat	ET	Subject brings, without locomotion, food to the mouth, chewing, ingesting etc.	--
	Drink	DR	Subject licks and sucks water or other fluids from various sources	--
	Autogroom	AG	“Subject manipulates own fur or body surface with lips, fingers, teeth; most often the index finger, or both thumbs or the lips are moved across the body surface, picking up skinflakes, salt, seeds etc ”	--
	Gentle Autoscratch	GA	“Subject rakes one’s own hair or skin, usually against the direction of hairgrowth, with bent fingers, excluding the thumb, mainly movements of hand or fingers”	--
	Rough Autoscratch	RA	“Subject rakes one’s own hair or skin, usually against the growth direction of hairs, with fingernails including large movements of the arm”	--
	Interact with Keeper	IK	Subject interacts with and fixates his attention on the keeper.	--
	Interact with Visitors	IV	Subject interacts with and fixates his attention on zoo visitors.	--
	Interact with Researcher	IR	Subject interacts with and fixates his attention on researcher or student.	--
	Individual play	IP	“Subject plays with objects or other items on his own, without the interaction with others”	--

Aggressive interactions	Pester	PE	“Subject repeatedly approaches Receiver, may throw things and/or swing above Receiver etc, is prepared to withdraw, and without pilo-erection or play face; at times resulting in full approaches or aimed throwing of objects without pilo-erection”	Receiver
	Aggressive intention	AI	Subject directs a sudden tense hand or body movements in the direction of the Receiver individual in a non-playful contexts or hitting, kicking etc... without locomotion	Receiver
	Short charge	SC	Subject shows tensed running towards Receiver over a few meters (or up to five steps)	Receiver
	Long charge	LC	“Subject shows tensed running towards Receiver over a longer distance (more than five steps).”	Receiver
	Direct display	DD	Subject runs tensed in the direction of, parallel to or closely passing by Receiver, often while pushing an object. This can end in a collision or other contact. There is a clear phase where the display is built up (body swaying)	Receiver
	Undirect display	UD	Subject bluffs, running with hairs erected, often pushing a canister or woodwool, or dragging branches, without directing display to another individual.	--
	Flee	FE	Subject moves away after a quick aggressive approach or charge without indication of play, and the fleeing lasts at least until the aggression stops	Receiver
Affiliative Interactions	Approach	GT	Subject approaches Receiver within arm’s reach and halts.	Receiver
	Leave	GW	Subject moves away from Receiver to a distance larger than arm’s reach.	Receiver
	Peer	PR	Subject stares into the face of R from a distance of less than 30 cm for at least 5 sec	Receiver
	Allogroom	GR	Subject manipulates Receiver’s body surface and hair with lips, fingers…	Receiver
	Social scratch	SS	Subject scratches Receiver in a gentle manner, stroking with fingernails across hair or body surface of the receiver	Receiver
	Calm play	CP	“Subject and Receiver play socially in a calm way, with play face, exaggerated movements and (occasionally) with laughing sounds”	Play partner = receiver

	Rough play	RP	“Subject and Receiver play socially in a rough way, with play face, exaggerated movements and (occasionally) with laughing sounds”	Play partner = receiver
Sexual behaviour	Masturbation	MS	“Subject stimulates or repeatedly manipulates own genitals ”	--
	Sex inspect		“Subject inspects genital area of Receiver (visual, olfactory, tactile)”	Receiver
	Sex Present	SP	“Subject clearly shows the genitals to Receiver, with the intention to have sexual contact”	Receiver
	Copulation	SX	“Heterosexual mount accompanied by pelvic thrusts and intromission between two sexually mature partners”	Receiver
	Non-copulatory mount	NC	“Subject mounts Receiver without intromission of the penis in the vagina, or without thrusting of the pelvis; or any sexual contact between 2 individuals of the same sex; or sexual contact involving immature individuals”	Receiver
undesired	Coprophagy	CO	“Subject ingests/smears of picks faeces either from other animals or from oneself”	--
	Drink Urine	DU	Subject drinks urine of self or others	--
	Regurgitation	RR	Subject deliberately regurgitates food, accomplished by various methods including lowering head to the ground, bobbing head, or sticking finger in their mouth. The vomitus may be retained within the mouth or expelled into hand or substrate before being reingested.	--
	Pluck self		Subject pulls out own hair and may or may not ingest it	--
	Pluck other		Subject pulls out hair of Receiver and may or may not ingest it	Receiver
	Finger in anus		Subject sticks finger in own anus repeatedly	

3

Appendix 10: Design of blood sleeve as used by Columbus Zoo

The blood draw sleeve was constructed in-house by Mike Tatman, and is used most frequently in the African Forest Department.

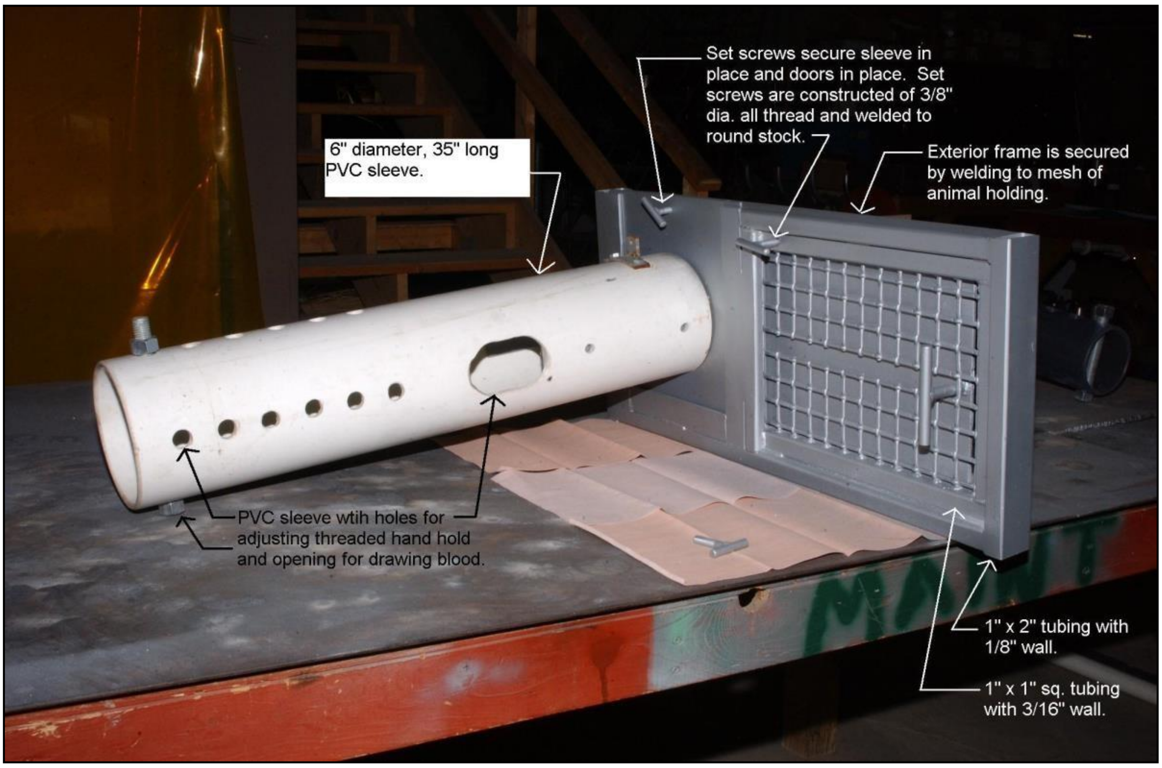
General Construction

- The blood draw sleeve (BDS) is constructed of all welded metal materials, and a PVC schedule 40 pipe.
    - 6 gauge, galvanized woven wire mesh
    - 1” x 2” tube steel
    - 1”x 1” sq. tube steel
    - Sheet stock is____gauge for slider door and structure of sleeve apparatus.
- Since the BDS is used for primates, all connections are welded for greater strength and reduction of risk with connections animals could otherwise undo.
- The PVC sleeve that is shown in these photos is being changed out to a clear acrylic tube with equal strength, but allowing for a better view of how the animal is responding to training or treatment.
- The several holes in the sleeve allow for adjustment in arm length per animal.

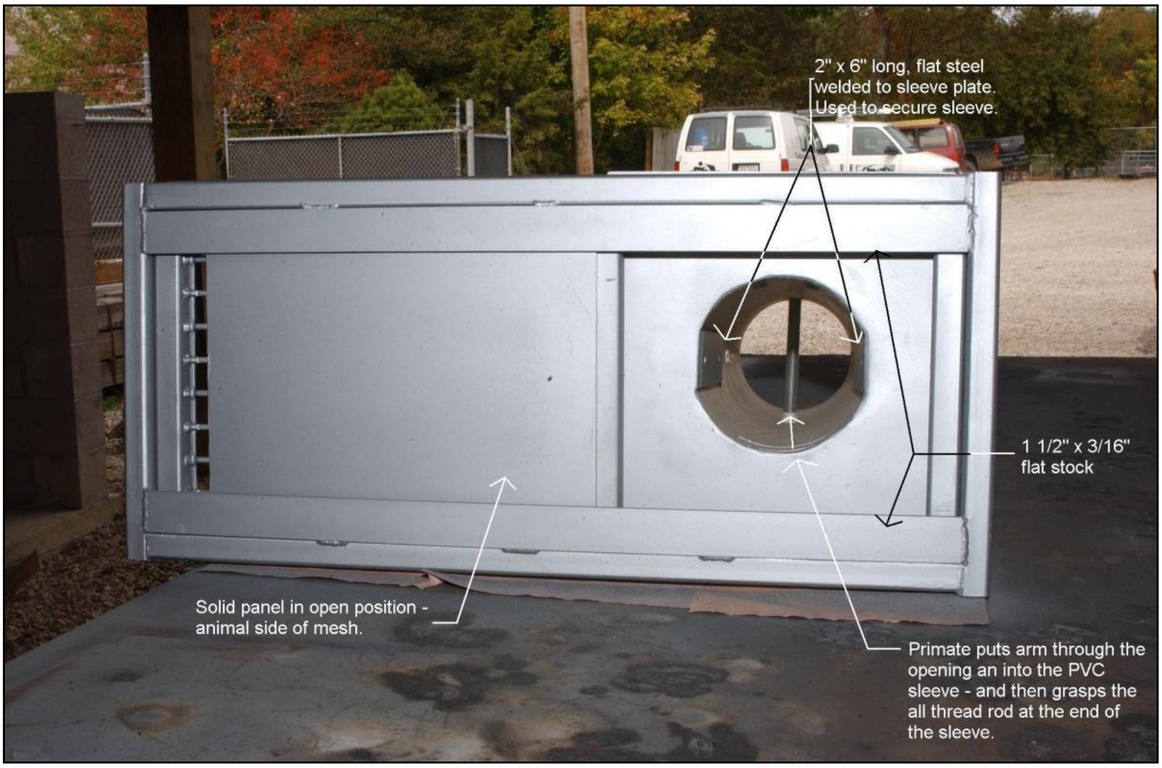
Blood Draw Sleeve Specifics

- Overall dimensions (dimensions given are outside measurements)
    - 30” long
    - 13 ½” tall
- While the BDS is not in use it can be removed to prevent injury to staff (these are usually located along a keeper aisle extending from the animal holding mesh.)
- While not in use the space for the BDS is occupied by a solid door that is secured by a set screw on the keeper side of the mesh.
- A 1” x 12” slot is cleared in the 1” x 1” mesh to provide space for the handle of the solid door to slide.
- The BDS sleeve can be assembled without providing the animal access to the sleeve until it is safely secured.
- The entire assembly is painted with zinc to prevent long-term corrosion.

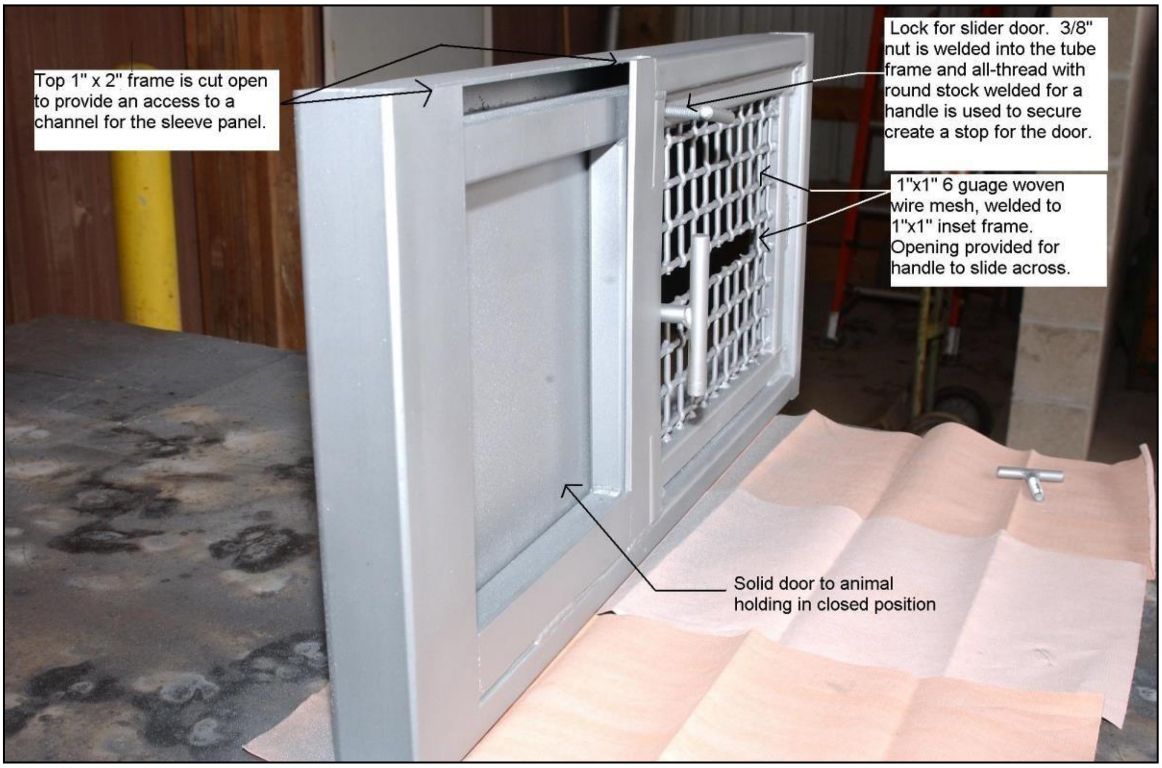
Sleeve and entire assembly – as would be viewed from Keeper aisle



View of BDS from animal holding side



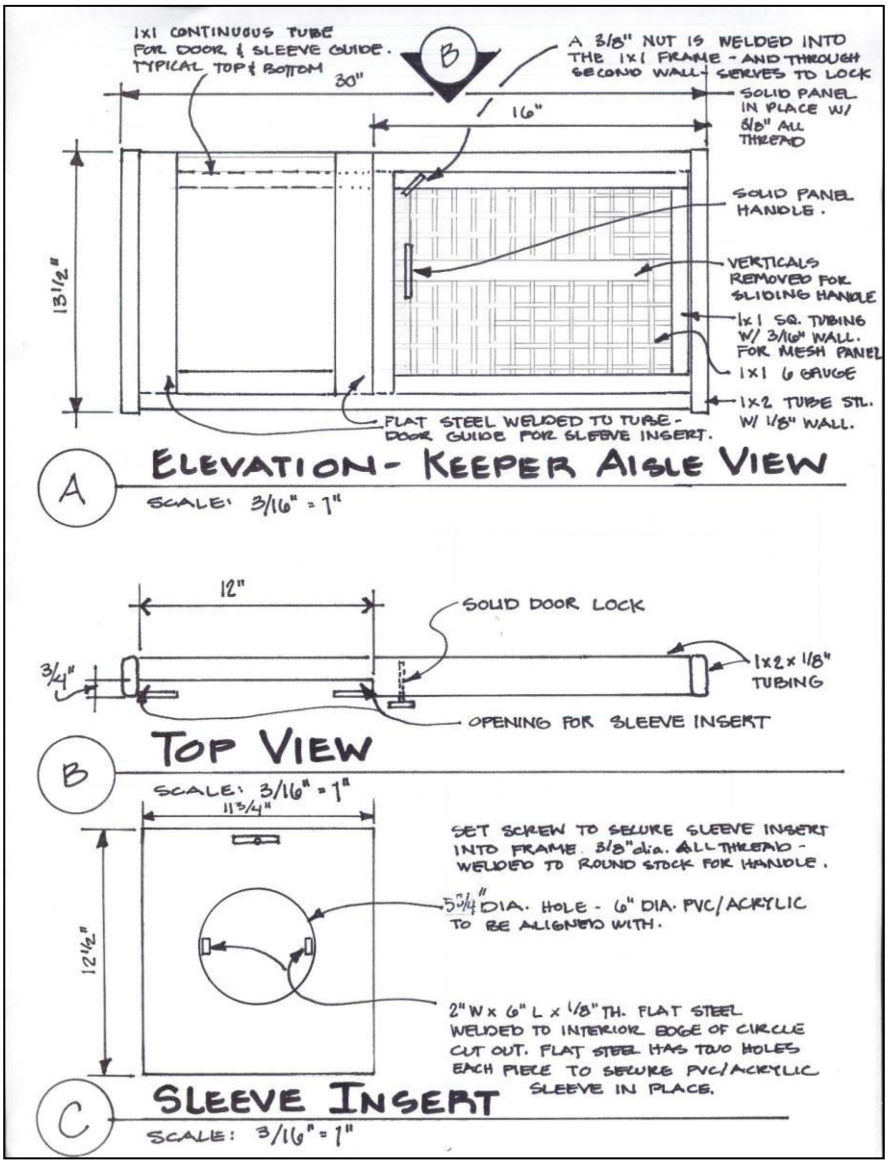
View of BDS assembly without sleeve attachment – Keeper side



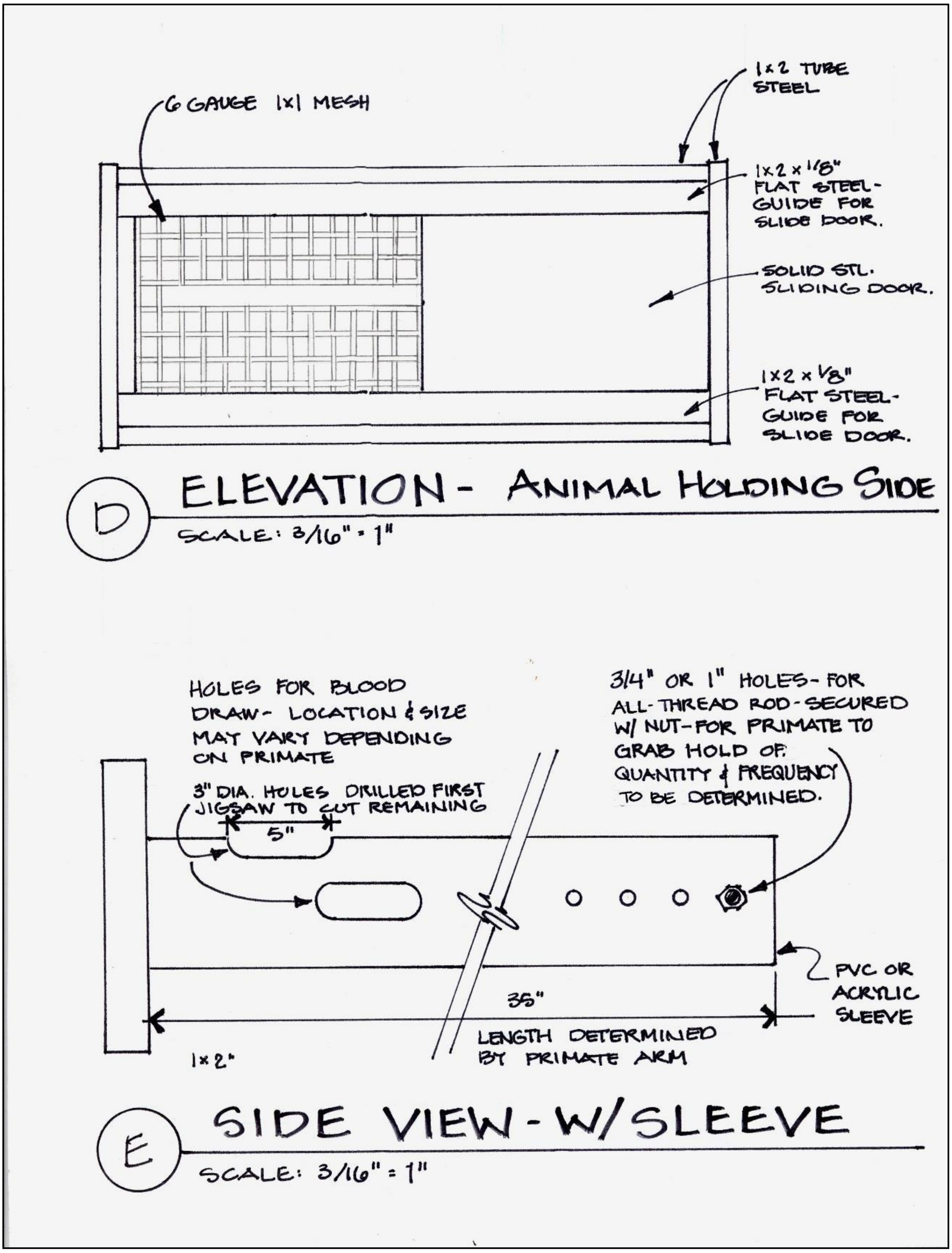
Open position – Animal side – without sleeve in position

Closed position – Animal side

Detail Drawings


1x1 CONTINUOUS TUBE FOR DOOR & SLEEVE GUIDE. TYPICAL TOP & BOTTOM
B
A 3/8" NUT IS WELDED INTO THE 1x1 FRAME - AND THROUGH SECOND WALL - SERVES TO LOCK SOLID PANEL IN PLACE W/ 3/8" ALL THREAD
30"
16"
13 1/2"
SOLID PANEL HANDLE.
VERTICALS REMOVED FOR SLIDING HANDLE
1x1 SQ. TUBING W/ 3/16" WALL. FOR MESH PANEL
1x1 6 GAUGE
1x2 TUBE STL. W/ 1/8" WALL.
FLAT STEEL WELDED TO TUBE - DOOR GUIDE FOR SLEEVE INSERT.
A
ELEVATION - KEEPER AISLE VIEW
SCALE: 3/16" = 1"
12"
SOLID DOOR LOCK
3/4"
1x2 x 1/8" TUBING
OPENING FOR SLEEVE INSERT
B
TOP VIEW
SCALE: 3/16" = 1"
11 3/4"
12 1/2"
SET SCREW TO SECURE SLEEVE INSERT INTO FRAME. 3/8" dia. ALL THREAD - WELDED TO ROUND STOCK FOR HANDLE.
5 3/4" DIA. HOLE - 6" DIA. PVC/ACRYLIC TO BE ALIGNED WITH.
2" W x 6" L x 1/8" TH. FLAT STEEL WELDED TO INTERIOR EDGE OF CIRCLE CUT OUT. FLAT STEEL HAS TWO HOLES EACH PIECE TO SECURE PVC/ACRYLIC SLEEVE IN PLACE.
C
SLEEVE INSERT
SCALE: 3/16" = 1"

Details Continued



Appendix 11: Protocol for basic post-mortem examination and sampling of the cardiovascular system of great apes (EAZA)

February 2015

GUIDELINES

A Protocol for Basic Post-Mortem Examination and Sampling of the Cardiovascular System of Great Apes

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1. Introduction

This protocol has been created as part of the EAZA Great Ape TAG endorsed Ape Heart Project. Based at Twycross Zoo (UK), the project is a Europe wide collaborative initiative striving to achieve a better understanding of great ape cardiovascular disease through a combination of epidemiological study, clinical and pathological investigation.

This protocol aims to provide a guideline for performing a systematic and comprehensive approach to the post-mortem examination and sampling of the cardiovascular system in great apes.

Cardiovascular system examination should form part of a whole body gross examination and histopathology; this protocol is therefore intended to be supplementary to the general Great Ape TAG Veterinary Guidelines for performing post-mortem examination.

The purpose of this protocol is to;

- Promote consistency and quality in post-mortem examination of the cardiovascular system in great apes
- Standardise and maximise information gathering
- Facilitate comparative study between post-mortem findings and relevant samples
- Permit consistent sampling of the heart for subsequent examination by a designated pathologist

It is our ambition that all veterinarians and pathologists will follow these guidelines when performing post-mortem examination of great apes within EAZA collections.

If you still wish to use your own pathologist for examination of the heart, please refer them to us for a copy of our full cardiac post-mortem examination protocol.

When post-mortem examination of the cardiovascular system is performed, it is requested that photographs are taken at all stages of the process, and in particular of any abnormalities.

If the abnormal accumulation of fluid is noted at any stage, it should be quantified (in ml, or weighed if clotted), characterised (colour, consistency, specific gravity) and where possible a sample stored.

2. Identifying Information

All information requested in the sample submission form should be provided. All photos, paperwork and samples must be clearly labelled with patient identifying information, including the following:

- Studbook number
- Species (and subspecies if known)
- Individual institution ID (name/number)
- Zoological collection
- Date of birth
- Date of death

3. Supporting Documents/Files

A copy of the full post-mortem report or summary of the findings elsewhere in the body should also be sent, where possible. Other documents of use are;

- Copy of the animal's clinical history
- A copy of the animal's records (e.g. ARKS/ZIMS report)
- Photographs taken during the post-mortem examination;
    - Ideally photographs should be taken at all stages of the examination
    - Photographs of any abnormalities found are of particular use

4. Sending Samples

Once the heart is in formalin, please contact the project co-ordinator at the email address below. Once the heart is fixed, remove it from the formalin (this can be re-used) and wrap it in saline soaked gauze swabs or similar to prevent desiccation. Double bag the sample and package suitably for postage/courier to the address below. Send all samples with a completed sample submission form.

If sending the sample from a zoological collection ***within the EU*** no CITES permit is required, but the sample should be accompanied by a letter detailing the nature of the contents (e.g. chimp post-mortem sample), and the reason for the transfer (i.e. research). If sending the sample from a zoo ***outside the EU*** additional advice from CITES should be sought.

5. Report of Findings

A preliminary report of macroscopic findings will be sent to the submitting zoo/vet within a week of receipt of the sample (by email or phone), and a full written report within 6 working weeks.

Protocol for Post-Mortem Examination and Sampling of the Cardiovascular System of Great Apes

STEP	ACTION	EXPLANATORY NOTE
1	Weigh the animal	Record the weight (in kg)
	Body condition score	BCS scale 1-5
	Measure crown-rump length	From top of the head (crown) to the bottom of the buttocks
2	Open the chest and examine the thorax	Note appearance of lungs, pleural cavity etc. Assess for presence of lesions or fluid Take photos of the heart 'in situ' (use scale marker as shown overleaf)
3	Examine the pericardium	Assess for lesions, thickening or fluid (if present quantify, characterise and sample). Formalin fix the pericardium.
4	Remove the pluck	Check the anatomy of the great vessels before sectioning (especially in young animals) Use a needle and syringe to draw blood from the right atrium before opening and freeze the sample as whole blood (-80°C if possible, -20°C otherwise) Cut the pulmonary trunk transversely 3cm above the pulmonary valve – assess the lumen for thrombi
	Remove heart from pluck	Transect all vessels as far from the heart as possible
5	Examine the epicardium	Note any thickening, lesions, changes in appearance, colour etc. Wash/rinse the heart before taking photos of the heart from all sides
6	Open the ventricles	Make a single transverse incision through the lower third of the apex perpendicular to the long axis of the heart to expose the chamber of both ventricles– see explanatory image overleaf Remove any clots and rinse the heart before weighing
7	Weigh the heart	Record the weight (in grams)
8	Sample the apical myocardium	Take one 1x1x0.5cm portion of the sectioned piece of apex and place in a universal tube for freezing (at -80°C if possible, or -20°C otherwise) If RNA later is available, also preserve an additional portion of myocardium approx. 3x3x3mm in size and immerse in fluid
9	Fix the heart	Fully submerge the heart in 10% neutrally buffered formalin ensuring all surfaces are covered and there is sufficient formalin around the heart Leave to fix for at least 48 hours.
10	Perform gross post-mortem examination of rest of carcass	Open the entire aorta along itself length to the level of the iliac bifurcation; sample and formalin fix any lesions Examine the remaining major body organs as per the GATAG post-mortem protocol and take relevant samples for histopathology. Take special note of the lungs, liver and kidneys and where possible also provide a formalin fixed sample (1x1x1cm) of these
11	Complete paperwork	Complete the sample submission form
12	Contact us	Email heartproject@twycrosszoo.org
13	Send the heart	Refer to point 4 entitled "Sending Samples" above

Don't forget to take photos at all stages of the cardiac post-mortem examination (include a scale marker)

Figure 1: Shows the approximate location of the transverse cut to be made across the lower third of the apex. The cut should be made perpendicular to the long axis of the heart approximately 4cm from the apex in gorillas and 3cm in the other three great ape species. A single cut at this location should expose the chambers of both ventricles, allowing clots to be removed prior to weighing and fixing.

Don’t forget to take photos at all stages of the cardiac post-mortem examination (include a scale marker)