The Importance of Family Bonds and Their Impact on Social Behavior of African Elephants

An Analysis of *Loxodonta africana's* Olfaction, Greeting Behavior, Holding Systems, and *in situ* vs. *ex situ* Living Calves

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Abstract

To shed light on the family bonds and social behavior of *Loxodonta africana* in human care, their olfactory abilities, greeting behavior, holding systems in zoos, and *in situ* and *ex situ* living calves were investigated.

(I) Olfactory long-term memory and elephants' means to express family bonds by olfaction were examined with an olfactory test. Two zoo-housed mother-daughter pairs were presented with fecal samples of their separated relatives and control samples of an unknown elephant and a known elephant that was present. Behavioral reaction, excitement, and shifts in behavior were registered by applying an ethogram and Focal-Animal Sampling.

(II) Greeting behavior and species-specific social behavior of *Loxodonta africana* housed in zoos were investigated during the reunifications of the two mother-daughter pairs and compared to two unifications of unrelated and unfamiliar elephants. Greeting behavior, excitement, fear, elephants' distance to the separating fence/animal, and time until the first tactile contact between elephants were measured utilizing an ethogram, Focal-Animal Sampling, and the Social Distance Method.

(III) African elephant calves' (social) behavior and mother-child bond were investigated in four European zoos for the three holding systems *free contact*, *protected contact*, and *no contact*. For three calves of each holding system, the general and social behavior, the distance to the mother, and the distance to the next-neighbor were examined using an ethogram, Scan Sampling, the Next-Neighbor Method, and the Social Distance Method.

(IV) For further investigations of zoo-born African elephant calves' species-specific social behavior and bonds, the (social) behavior and the mother-child bond were investigated for calves of the F1 and F2 generation *ex situ* and calves *in situ*. For each sample group, 120 observation hours were conducted, utilizing an ethogram, Scan Samling, and the Social Distance Method.

Statistical analysis for all studies was calculated with SPSS Version 27/29. Statistical tests were chosen according to the distribution of the data set and number of sample groups. (I) To investigate the data on the olfactory abilities of the elephants, the Friedman Test with a Post-Hoc Test, an ANOVA calculation, and the Mann-Whitney-U-Test were used. (II) Statistical analysis for the greeting behavior of elephants was conducted with the Chi-Square Test and Fisher's Exact Test, a t-test with Levene's Test, and the Mann-Whitney-U-Test. (III) Data sets for differences in social bonds of calves in the three holding systems were analyzed with the Kruskal-Wallis calculation and the Monte Carlo Simulation. (IV) For the analysis of data on differences in social behavior and mother-child bond of *ex situ* and *in situ* living calves, the Kruskal-Wallis calculation with a Post-Hoc Test was calculated.

(I) In the olfactory test, elephants reacted significantly stronger to the scents of their absent relatives than to the control samples. Additionally, mothers showed stronger reactions than daughters did. Results testified to an olfactory long-term memory in *Loxodonta africana* of up to twelve years, the first finding of a memory of such length. (II) Related elephants showed significantly more affiliative and less agonistic behavior during reunifications and performed full Greeting Ceremonies. Unrelated elephants reacted hesitantly during unifications and held significantly bigger distances to the separating fence. (III) No significant differences in social behavior and mother-child bond between calves of the three holding systems were detected. However, data indicated differences between *ex situ* and *in situ* living calves. (IV) The immediate comparison between social behavior and the mother-child bond of *ex situ* and *in situ* living calves revealed significant differences between the two sample groups regarding social behavior and spatial distance between calves and their mothers. However, there was no increase in those differences with the F2 *ex situ* generation.

The investigations give ambiguous results regarding zoo elephants' social bonds and behavior. (I) and (II) indicate close family bonds and species-specific behavior in the zoo-housed females of the study. (III) and (IV) found significant differences in the zoo-housed calves' family bonds and social behavior compared to their wild-living conspecifics. The detected differences seem reasonable considering zoos' different environments and lack of threats. The results of the adult females in (I) and (II) indicate that the differences in social bonds and behavior of the calves in (III) and (IV) will not manifest when those animals grow up and will not have a significant impact long-term. Nevertheless, to prevent increases in behavioral differences in *ex situ* elephants and to enhance their species-specific social behavior, elephants should be handled as close to natural conditions as possible, and carers should reduce contact with the elephants to the necessary minimum.

1 Introduction

„If elephants are to survive, human being will have to be convinced that these magnificent, intelligent creatures are entitled to retain some share of the living space left on earth.“

(Attenborough in Moss & Colbeck, 2002, 12)

The conservation of the African elephant (*Loxodonta africana*) is a paradox. Since 2021, the IUCN has labeled this species *endangered,* with the status *decreasing* as numbers constantly shrink [Gobush et al. for IUCN, 2022]. This is made clear by the fact that the African continent lost 30 % of its elephant stock [Chase et al., 2016]. However, at the same time, it can be argued that there are more African elephants than the African continent can host due to fast-increasing habitat loss [Chase et al., 2016; Thouless et al., 2016]. South-eastern Africa is an evolving environment; the south-eastern African countries are developing rapidly, and the continent's population has quintupled since the 1950s [BBF, 2020; Klingholz, 2018]. Africa has the biggest population growth of all continents [BBF, 2020]. The African economies strive to achieve the same living standards as the global West [WBG, 2023].

The expanse this economic growth requires puts the people in Africa into conflict with their wild animals [Nicole, 2019]. The growing populations need room, and formerly wild habitats are frequently replaced by cities and new infrastructures [Gobush et al., 2022; Nicole, 2019]. This reduces the habitat of flora and fauna, and human-wildlife conflict develops into a topic of more urgency [Gobush et al., 2022]. Especially concerning the African elephants, the biggest mammal on land [Douglas-Hamilton & Douglas-Hamilton, 1989], which can raid an entire crop field within a night, can destroy railways, cars, houses, and even wire systems, thereby cutting off entire cities from energy [Nicole, 2019]. The human-elephant conflict is difficult to avoid—elephants are killed by farmers who are under threat, and vice versa, humans are killed by elephants [Nicole, 2019]. While animal welfarists and environmentalists seek to find a solution to protect flora and fauna in Africa [Gobush et al., 2022; Nicole, 2019; Shaffer et al., 2019], some researchers ultimately concluded that the future of African wildlife is limited in space and quantity [Shaffer et al., 2019]. There is not enough space for the current amount of nature to co-exist with societies the size African economies strive to achieve [Nicole, 2019; Thouless et al., 2016; WBG, 2023].

Therefore, research needs to take a different angle. While in the past, most research focused on investigating the biology and behavior of elephants in the wild for conservational purposes [Mcdonald et al., 2009; Nicole, 2019; Thouless et al., 2016], it is now crucial to investigate how African elephants behave in limited space. This opportunity is given in zoo or reservation environments [Kleiman, 1992; Powell et al., 2023]. Zoos have held African elephants for decades [Kurt, 2006]. Thus, the knowledge of the (social) behavior of elephants in zoos can be immensely beneficial for African reserves, as they will soon face the obstacles of holding those large mammals in limited areas [Nicole, 2019; Thouless et al., 2016].

This study investigates African elephants' behavior and abilities in zoos and the wild and compares those two target groups. The focus lies on the family bonds of elephants, which is the critical feature for their breeding and survival success [Douglas-Hamilton & Douglas-Hamilton, 1989; Moss, 2001].

Four studies were conducted in zoos. The first study investigated the olfactory long-term memory and long-lasting family bonds of African elephant cows living in zoos. The second study examined their greeting behavior. In a third study, the three holding systems, *free contact*, *protected contact*, and *no contact*, found in European zoos were evaluated regarding calves' (social) behavior. Finally, in the fourth study, a basic comparison between the (social) behavior and especially the mother-child bond was drawn between calves living *ex situ* (under human care) and *in situ* (wild).

1.1 *Loxodonta africana*

To fully understand this unique mammal, its systematics, environment, and habits must be explained. All elephants belong to the order of the Proboscidea. The order originated approximately 55 million years ago during the Eocene. Back then, the Mastodons and Mammuts, which are extinct now, also belonged to this order. Today, the only remaining, recent family of the order of the Proboscidea is the Elephantidae – the elephants, which emerged roughly seven million years ago. The family consists of three species: the African savanna elephant (*Loxodonta africana*), the African forest elephant (*Loxodonta cyclotis*), and the Asian elephant (*Elephas maximus*) (Fig. 1.1) [Bruce & McGhee, 2007; Estes, 1991; Mcdonald et al., 2009, Rohland et al., 2010].

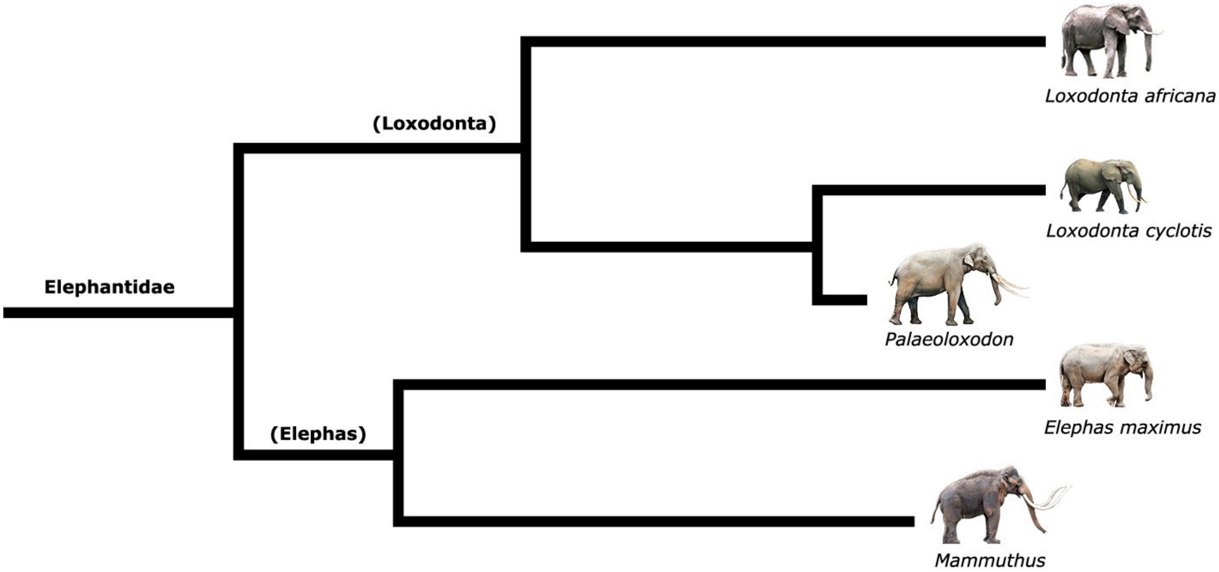


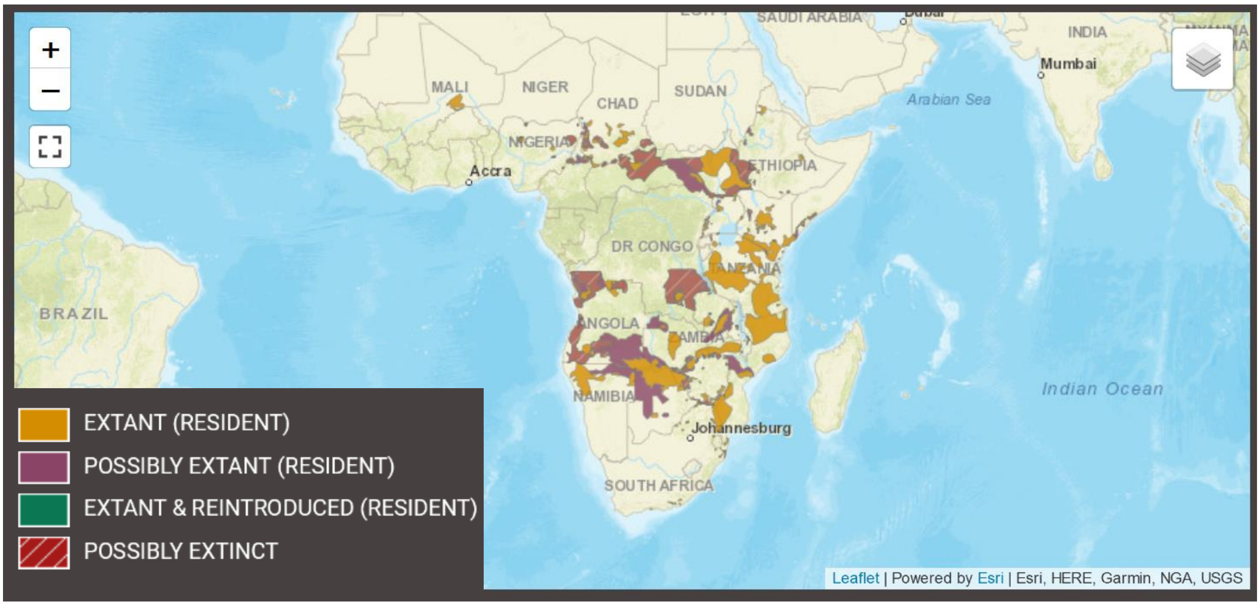
Fig. 1.1: Systematic of elephants [Rohland et al., 2010].

As the research at hand only comprises African elephants, the following theoretical background focuses on this species. Johann Blumenbach first described *Loxodonta africana* in 1797 [Kurt, 2006]. Its taxonomy is as follows:

- Kingdom: Animalia
- Phylum: Chordata
- Class: Mammalia
- Order: Proboscidea
- Family: Elephantidae
- Subfamily: Elephantidae
- Species: *Loxodonta africana*

The approximate population of *Loxodonta africana* comprises 415,000 individuals. While once living on the entire African continent, climatic changes made the African elephant withdraw from the northern, arid territories during the early Holocene. Nowadays, it can only be found in regions south of the Sahara, covering approximately 3,1 million km^2 (10.0 %) of Africa.

Although its habitat was once coherent, the expansion of the various environments constantly decreased the territories roamed by elephants and resulted in a fragmentation of its parts (see Fig. 1.2) [Gobush et al., 2022; Thouless et al., 2016].



Fig, 1.2: Distribution areas of *Loxodonta africana* [Gobush et al., 2022].

Nowadays, the most considerable territory (42.0 %) of African elephants is in southern Africa. Eastern Africa hosts 28.0 % of the population of African elephants, Central Africa 25.0 %, and Western Africa only 5.0 %. An enormous population can be found in Botswana, Zimbabwe, and Tanzania. Only 30.0% of its territories are protected areas [Gobush et al., 2022; Thouless et al., 2016].

The various territories the African elephant lives in are very diverse. It lives close to the sea in Namibia, in river areas and deltas in Botswana, and in areas with enormous rainfalls and severe droughts in Kenia, Tanzania, and Zimbabwe. Some areas are deserts, some are savannas, and others are dense bush- and forest-landscapes. In search of resources, elephants can wander considerable distances. Therefore, as long as human co-existence is possible, elephants can be found anywhere in the named areas [Whyte, 2005].

Being the biggest of the three species, the African elephant is the most prominent recent land mammal. A male can reach a shoulder height of 3.3 m, and a female 2.7 m. Their weight ranges between 3-6 t. Hence, their food intake is immense [Douglas-Hamilton & Douglas-Hamilton, 1989; Estes, 1991; Hanks, 1972]. Besides its size, the African elephant is known for its social structure and abilities, as described in the following chapters.

1.2 Social structure

„Elephants are extremely social animals. Led by the matriarch, the herd undertakes all activities together. Whether on their rambles, grazing, bathing, drinking and resting – the herd always stays together and the social order is preserved.“

(Hall-Martin, 1994, 50)

Among the animal kingdoms, the social structure of the African elephant is considered one of the most complex [Mcdonald et al., 2009]. They live in herds of varying size, between three to 25 individuals, following a fission-fusion structure influenced by successive levels of sub-groups within the herd [Shoshani et al., 1997]. The cow builds the first and smallest social group with its youngest calf. They display the closest social bond. On the second level are the cow's elder calves, which still depend on her. Several mother-calf groups counted together form the third sub-group, the herd, also called a family. The cows of the herds are usually mothers and their adult daughters or sisters [Estes, 1991; McComb et al., 2001; Shoshani et al., 1997; Wittemyer & Getz, 2007].

In times of droughts, or if a herd becomes too big, it will split up into several herds of closely related elephants and remain close to each other. Those related families form a new level of the social structure of elephants, the bond group (see Fig. 1.3). Bond groups will still socially encounter frequently and spend about 35-70 % of their time together [Estes, 1991; McComb et al., 2001; Shoshani et al., 1997; Wittemyer & Getz, 2007]. A genetic analysis of the relationship status of bond groups by Archie et al. [2006] showed that most families in bond groups are related and only have few animals that are not genetically related. Herds seek to form alliances for better survival. The social relation between those unrelated bond groups does not differ in its peculiarity [Archie et al., 2006; Payne, 2001].

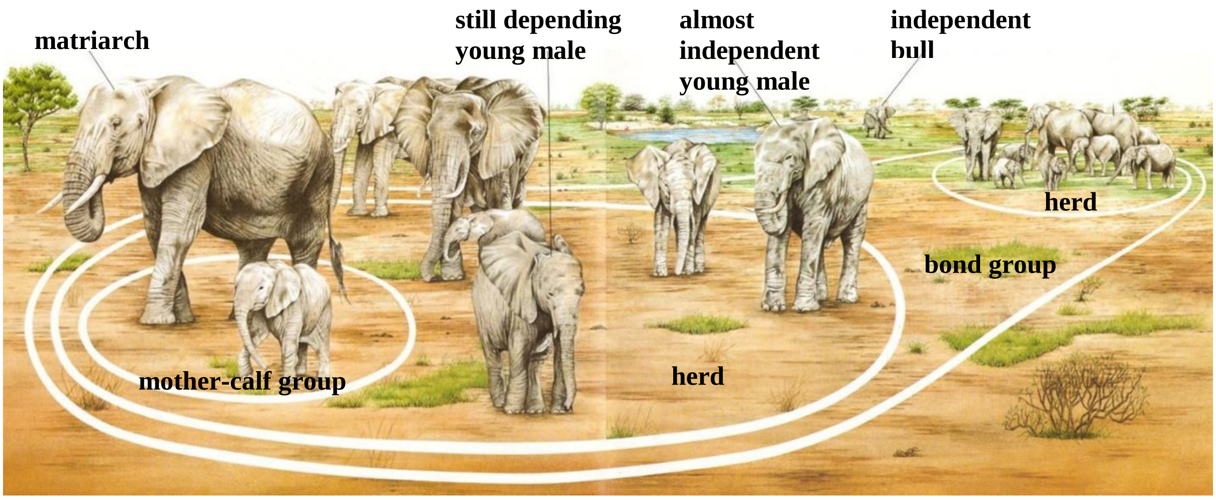


Fig. 1.3: Herd structure of *Loxodonta africana* [Shoshani et al., 1997].

More independent from the above-described levels of social structures are clans. A clan consists of several herds, including bond groups and others, comprising up to 50 animals. Clans are territorially defined as clan herds who live and stroll in the same territories and follow the same routes. Therefore, they are familiar, and their social contact is primarily shaped positively [Mcdonald et al., 2009; Shoshani et al., 1997].

As elephants live in a matriarchy, the oldest and most experienced cow, the matriarch, leads the herd. The hierarchy then goes linear downwards by the age and size of the cows. The matriarch decides on the walking routes of the herd and is consequently responsible for the herd’s safety and food- and water supply. When the matriarch dies, the next oldest female will take over. The early death of a matriarch, however, can be fatal for an entire herd, as herds rely on the matriarch to guide them to water and food supplies, and she is the main protector of the herd [Archie et al., 2006; Estes, 1991; McComb et al., 2001; Shoshani et al., 1997; Wittemyer & Getz, 2007].

The status and social structure of the males strongly differ from that of the females in their herds. While females tend to stay with their herd forever, grown males are independent. The older cows will bully young males when they reach puberty until they finally leave the herd at twelve to fifteen years when they reach maturity. They then join bachelor groups with other young males. Those groups form loose bonds of two to twelve animals that mainly interact in play fights with one another. With ongoing age, bulls will even dispatch from those groups and roam independently. Grown, independent and mature bulls will subsequently only join herds when they seek to mate [Archie et al., 2006; Charif et al., 2005; Douglas-Hamilton & Douglas-Hamilton, 1989; Estes; 1991; Gould & McKay, 2002; Hanks, 1972; Lee, 1987; McComb et al., 2001; Mcdonald et al., 2009; Moss, 2001; Ortolani et al., 2005; Schulte, 2000; Shoshani et al., 1997].

1.3 Social behavior

„Some of their social behaviour suggests that they possess the mind tool to imagine what other elephants are feeling."

(Mcdonald et al., 2009, 91)

Like their social structure, the social behavior of African elephants is equally distinct and versatile. The social behavior between the elephants of the different social system levels differs just as much as it does between every two individuals. This behavior is influenced by age, gender, hierarchy, relationship status, and individual character of the elephants and can change with time [Moss, 2001; Moss & Colbeck, 2002]. In terms of ethological research, a profound understanding of the social behavior of the studied animal is essential [Kappeler, 2020; Naguib & Krause, 2020]. As this study mainly focuses on the social behavior of African elephants concerning their family bonds and how they maintain them, the required scientific background is detailed in the following chapter.

1.3.1 Communication

"With their highly mobile trunks, keen sense of smell, glandular secretions, great ears, and varied vocalizations, elephants are notably well equipped to express themselves."

(Estes, 1991, 262)

Social behavior can always be interpreted as a way of communication [Naguib & Krause, 2020]. Hence, looking into their means of communication is crucial when investigating elephants' social behavior. Elephants can communicate by body position and movement and by tactile, acoustic, and chemical means [Archie et al., 2006; 2011; Douglas-Hamilton & Douglas-Hamilton, 1989; Estes, 1991; Hall-Martin, 1994; Mcdonald et al., 2009; Moss & Colbeck, 2002; Payne, 2001].

Body position is the one way of communication that is always present and is closely attached to body movement. An elephant's body posture can express its mood. The ears, tail, and trunk position and movement enhance this. With only minor shifts in their body parts, they can express neutral, affiliative, and agonistic behavior. Closely connected to the communication by body position and movement is communication by tactile contact. They can emphasize their communication by touching other elephants with either their body or, more peculiarly, their trunk [Archie et al., 2006; 2011; Douglas-Hamilton & Douglas-Hamilton, 1989; Estes, 1991; Hall-Martin, 1994; Poole & Granli, 2011; 2021; Mcdonald et al., 2009; Moss & Colbeck, 2002; Payne, 2001].

Elephants can communicate acoustically with a wide range of sounds. The most frequently used acoustic signal is infrasound, which can reach up to 104 decibels with a frequency of 14 hertz. These sounds are so low that the human ear cannot perceive them. Elephants, however, can hear those sounds over a distance of up to 20 km, covering an area of 400 km^2. They feel the vibration of the sounds with their feed [Estes, 1991; Douglas-Hamilton & Douglas-Hamilton, 1989; Moss & Colbeck, 2002; Payne, 2001]. Elephants express those sounds almost consistently [Payne, 2001]. Communicating within a wide radius enables them to locate mating partners and herds and stay in touch with their bond group [Moss & Colbeck, 2002]. Besides infrasound, elephants also express sounds audible to humans, albeit less frequently. The trumpeting noise is only made when elephants – especially calves – sense danger or when bulls fight. They will make a low rumbling noise when they greet others or when they want to calm each other down. When elephants are nervous, they rumble loudly, with a higher frequency. In cases of anger or to threaten others, the rumbling might reach the volume of a lion's roar. Calves express a scream when they want to suckle their mother’s milk, a squeak while playing, and a screech when they believe themselves in danger. Expressing this sound will attract the entire herd’s attention [Douglas-Hamilton & Douglas-Hamilton, 1989; Estes, 1991; Moss & Colbeck, 2002; Payne, 2001].

Extraordinary is the elephants’ ability of chemical communication. Elephants exude hormones with intense scents through their body liquids – urine, dung, saliva, and gland secretions [Hall-Martin, 1994]. Chemical communication can be used for all kinds of communication; however, it will be found most frequently regarding mating behavior [Archie et al., 2006; Estes, 1991; Hall-Martin, 1994; Moss & Colbeck, 2002].

To perceive those scents, elephants have the susceptible vomeronasal organ placed at their palate. Elephants will touch the subject of interest with their trunk and then put the tip in their mouth to examine it with their vomeronasal organ [Archie et al., 2006; Estes, 1991; Hall-Martin, 1994].

They mostly use a combination of all their communicational skills to manage their complex social structure and to maintain their close social bonds [Moss & Colbeck, 2002; Poole & Granli, 2011; 2021].

1.3.2 Greeting Ceremony

"Combinations of postures and movements, together with sounds and odors, usually make an elephant's feelings, if not its intentions, perfectly plain."

(Estes, 1991, 623)

When meeting, elephants greet each other [Moss & Colbeck, 2002; Moss, 2001; Poole & Granli, 2011]. How they do this depends on their relationship and the time they have not seen each other. Usually, they will flap their ears and lift their heads. Sometimes, this is accompanied by touching the head of the other elephant with the trunk. This behavior sequence is called Little Greeting [Poole & Granli, 2011]. If separated for a longer time, elephants of the same herd or bond group greet one another more profoundly. They are then known to perform the unique Greeting Ceremony [Moss & Colbeck, 2002; Poole & Granli, 2011]. During the Greeting Ceremony, they use all four general types of communication described above (see chapter 1.2).

The procedure of the Ceremony follows a set sequence of behaviors: The elephant runs toward the elephant they intend to greet. They click their tusks and entwine their trunks by winding them around each other. They touch one another's trunk tips. During this, their ears are in motion, folding back, lifting, enfolding, and flapping rapidly. Their tail sticks out. They raise their heads as high above their shoulder as possible. Their mouth is wide open. They touch the other elephant's eyes, mouth, and temporal glands with the trunk. They turn around rapidly, also changing direction. All this is accompanied by loud vocalizations such as oral rumbles, roars, and trumpets, dropping feces and micturating, and exuding fluid from the temporal glands [Moss & Colbeck, 2002; Poole & Granli, 2011]. A complete list of the behavioral items characteristic of the Greeting Ceremony can be seen in Table 1.1.

Table 1.1 Behavior of the Greeting Ceremony.

Item	Behavior
Running towards elephant	Elephants run towards the elephant they intend to greet.

Clicking tusks and entwining trunks together	Elephants click tusks and entwine their trunks by winding them around each other.
Touching trunk	Elephants touch the trunk of the other elephant with their trunk.
Folding, lifting, spreading, and flapping ears	Elephants' ears are in motion by folding them back, lifting, enfolding, and flapping them rapidly.
Raising head	Elephants raise their heads as high as possible above their shoulders.
Opening mouth	Elephants open their mouth widely.
Touching head	Elephants touch the head of the other elephant at the eyes, mouth, and temporal glands with their trunk.
Spinning round	Elephants rapidly turn around repeatedly, also changing direction.
Lifting tail	Elephants lift their tail and stick it out.
Acoustic signals	Elephants emit loud vocalization as oral rumbles, roars, and trumpets.
Defecating and urinating	Elephants drop feces and micturate.
Glandular secretion	Elephants exude fluid from the temporal glands.

The procedure is notable and impressive; an image of two adult elephants and a calf performing the Greeting Ceremony is presented in Figure 1.4.

Fig. 1.4: ***Loxodonta africana*** **performing the Greeting Ceremony [Whyte, 2005].**

1.3.3 Calves within the herd

„Care of offspring is a centralizing component of elephant society, and broader acts of cooperation may stem from these interactions."

(Schulte, 2000, 448)

African elephants' gestation time is about 22 months, and females almost solely deliver one calf at a time [McComb et al., 2001; Mcdonald et al., 2009], making them the mammal with the slowest reproduction rate on earth [Seet, 2013]. Hence, a calf's survival is essential for preserving the herds, and calves have a unique position in the herds and the elephant society [Moss, 2001; Kurt, 1994b]. This starts early on when the cows go into labor. On those occasions, the whole herd will be involved in the procedure: They stand around the cow giving birth and form a wall of protection around her. The other females calm her down by touching her temporal glands, putting their trunks into her mouth, and making rumbling noises. Once the calf is born, the entire herd makes loud rumbling and trumpeting noises, excrete fluids, and huddles around the newborn [Andrews et al., 2005; Dröscher, 1990; Estes, 1991; Grzimek, 2000; Kowalski et al., 2010; Kurt, 1994b; Moss & Colbeck, 2002; Puschmann, 2004].

The newly-born calf tries to stand up within the first few minutes, encouraged by its mother and other females, who support it with their trunks and feed [Douglas-Hamilton & Douglas-Hamilton, 1989; Estes, 1991; Moss & Colbeck, 2002]. Most calves manage to stand within the first five to fifteen minutes and start suckling on their mother's breast shortly afterward [Andrews et al., 2005; Estes, 1991; Moss & Colbeck, 2002]. Calves will be breastfed for approximately two years, adding solid food to their diet after six months. The mother stops breastfeeding her calf when she delivers the next. Hence, a calf can survive without its mother at the age of approximately two years [Moss & Colbeck, 2002; Moss & Lee, 2011]. Until then, the connection– socially and spatially– between mother and calf is very close [Garaï & Kurt, 2006; Künkel, 1999; Lee & Moss, 1986; Lee, 1987; Mcdonald et al., 2009; Moss & Colbeck, 2002].

The rest of the herd is also closely attached to the calves and participates in their upbringing, which is crucial for a successful upbringing [Hall-Martin, 1994]. They look after, protect, socialize, and play with the young. Especially young females that do not have calves yet, function as kindergarteners, and are strongly attracted to the calves. This is referred to as allomothering [Lee, 1987]. It helps young females learn parenthood early on, gives the mothers the freedom to feed appropriately to produce enough milk, and increases the calves' survival rate [Lee, 1987]. The calves, on the other hand, are given a high amount of tolerance within the herd, allowing them to develop freely and learn from the elder [Garaï & Kurt, 2006; Grzimek, 2000; Kurt, 1994a; 1994b; Lee, 1987; Moss, 2001; Puschmann, 2004; Schulte, 2000]. The closest non-parental behavior observed in females towards calves is allosuckling– letting a calf that is not theirs suckle from their breast [Lee, 1987; Moss & Colbeck, 2002].

Agonistic behavior toward calves, such as pushing or slapping with the trunk, can only be observed rarely [Lee, 1987]. In her study, Lee [1987] states that it is mainly the mothers who might show agonistic behavior toward their calves. Those acts of agonistic behavior are intended primarily to rear them. However, even this can barely be observed within the first two years of a calf's life [Lee, 1987]. When calves are older than two years, agonistic behavior towards them is mainly shown by bulls and females with their own calves [Lee, 1987; Moss, 2001]. The allomothers show the least agonistic behavior toward calves [Lee, 1987; Moss, 2001].

1.3.4 Contact behavior and distance keeping in calves

Tactile contact is vital for African elephants' well-being and (social) development – in the wild as well as in zoos [Freeman et al., 2021; Lee & Moss, 2011]. As pointed out above, mothers are essential for the calves' survival [Archie et al., 2006; 2011; Lee & Moss, 2011; Moss & Colbeck, 2002], even in captivity [Lahdenperä et al., 2016]. Calves living *in situ* frequently have tactile, visual, olfactory, and acoustic contact with their mothers [Lee & Moss, 2011]. During the first weeks, they are almost constantly in tactile touch, and during the first six months, they spend about 56 % of the time at a contact distance [Charif et al., 2005; Lee & Moss, 2011]. Later, this tight bond loosens slightly; however, only at the age of well over two years, calves start striving at distances further than five meters from their mothers [Charif et al., 2005; Lee & Moss, 2011]. Females of up to ten years spend about 50 % of their time at a distance of fewer than five meters from their mother [Estes, 1991; Lee & Moss, 1986; Moss & Colbeck, 2002]. Both mother and calf maintain this close (spatial) contact during the first years of the calf's life. This shifts after two years, when the calf no longer suckles from its mother, and the bond becomes weaker. From then on, the bond is maintained more by the mother [Charif et al., 2005; Lee & Moss, 2011; 1986].

It is not only the contact between calves and mothers that is close. During the first two years, calves spend approximately 20 % of their time in contact distance to their next neighbor. Only 10 % of the time, they can be seen at a distance of more than five meters from the next elephant [Lee & Moss, 2011]. Calves under the age of five years can seldom be seen without a herd member close by. In rare cases, a calf was found separated from its herd; it expresses severe signs of stress, such as loud screaming, trumpeting, and running around, searching for its family [Douglas-Hamilton & Douglas-Hamilton, 1989; Lee, 1987; Moss & Colbeck, 2002].

1.4 Olfaction

Elephants are known for their extraordinary olfactory senses. Investigations on elephants' ability to differentiate scents showed that they can distinguish between more than 100 scents [Hart et al., 2008; McComb et al., 2000]. Asian elephants can discriminate between odors to one changed molecule [Rizvanovic et al., 2013], and experiments demonstrate an enormous learning ability to memorize scents within a short time [Arvidsson et al., 2012; Rizvanovic et al., 2013]. They can also smell food and water from a distance of more than 100 km [Blake et al., 2003; Plotnik et al., 2014; Rasmussen & Krishnamurthy, 2000; Viljoen, 1989]. Bulls can smell when cows are in oestrus, and cows can sense when a bull is in musth – a state of highly increased blood testosterone and fertility in males [Rasmussen & Munger, 1996; Sukumar, 2003].

These findings agree with neuronal discoveries. The area for the olfactory sense is the largest part of the elephants' brain [Shoshani et al., 1997]. Investigation of the olfactory receptor genes of thirteen placental mammal species found that African elephants have ~2000 olfactory receptor genes, the biggest repertoire reported so far [Niimura et al., 2014].

Considering their immense olfactory abilities, smelling is of significant importance to elephants. They require their olfactory senses to find resources and mating partners [Blake et al., 2003; Plotnik et al., 2014; Rasmussen & Krishnamurthy, 2000; Rasmussen & Munger, 1996; Sukumar, 2003; Viljoen, 1989]. However, as their olfactory senses do not have to be that complex to ensure their survival, researchers hypothesize that elephants also use it as a form of social intelligence and family bond [Bates et al., 2008]. Interestingly, the well-established olfactory sense coincides with one of the best memories in the animal kingdom [Douglas-Hamilton, 1972; Moss, 2001], combined with a remarkable olfactory memory [Bates et al., 2008; Rasmussen, 1995a; 1995b]. It is anticipated that elephants need those abilities to recognize family members even after long periods of absence, which happens with male members due to the highly migratory nature of elephants [Bates et al., 2008; Rasmussen, 1995a; 1995b]. Rasmussen [1995a] and Bates et al. [2008] hypothesize that elephants have an olfactory memory that lasts at least 19 years. Rasmussen [1995a] speculates that male elephants that left their herds need to be able to discriminate the urine sample of their mothers from potential mating partners to prevent incest after a renewed encounter. He observed that bulls do not show as much interest in urine samples of females in oestrus when it is their mother's urine sample. He hypothesizes that elephants can remember scents for up to 19 years – the longest time a bull lived separate from his family and did not react with mating attempts to the mother's estrous urine sample [Rasmussen, 1995a]. However, Rasmussen gives no empirical data or evidence for this olfactory long-term memory of elephants. Bates et al. [2008] observed that elephants show more interest in urine samples of absent family members, some of whom lived separately for 27 years. Again, empirical data is missing, as Bates et al. only hypothesize that elephants recognize the scent and could not give empirical findings. Studies give empirical proof of elephants' olfactory long-term memory state of sixteen weeks [Arvidsson et al., 2012] and one year of memory [Rizvanovic et al., 2013]. However, no empirical data proves a long-lasting olfactory memory longer than this.

Elephants' reaction to scents of interest is widely investigated. Studies by Polla et al. [2018], von Dürckheim [2021], and von Dürckheim et al. [2018] found that elephants show more interest in familiar scents than in unfamiliar ones. This interest is expressed by a long time of lingering around the sample (in this case, urine), reaching for it more often with the trunk, and touching it more often with it [Polla et al., 2018; von Dürckheim, 2021; von Dürckheim et al., 2018]. Bates et al. [2008] made similar observations in a study where elephants were presented with urine samples of herd members on their path, some of which were of elephants walking ahead of the tested animal and others of elephants walking behind the tested animal. The elephants in this study showed more interest in the samples of the animals that were walking behind them, indicating that they knew the whereabouts of their herd members. Their interest was also expressed here by lingering around the sample, reaching for it, and touching it [Bates et al., 2008].

1.5 Zoo environment

„Elefantenhaltungen mit Zucht bieten […] den Tieren verhaltensgerechte Lebensbedingungen und tragen dazu bei, die Menschen für diese Tiere und damit auch für deren Interessen im Freiland zu begeistern.“

(Kurt, 1992, 136)

As all studies of this project also investigate the social bonds of *Loxodonta africana* living in zoos, the following chapter will give a theoretical background for African elephants living in this environment. Due to their impressive appearance and complex social structure and behavior, African elephants *in situ* have been a popular subject for research for a long time, reaching their peak in the 1970s [Douglas-Hamilton, 1972; Kurt, 2006]. However, research on African elephants in a zoo environment only started to pick up around 2000, when breeding African elephants in zoos became more successful [EEG, 2002; Kurt, 2006]. Research on those individuals becomes more important with the increasing number of African elephants born and socialized in zoos.

1.5.1 Management systems

As with most animals in zoos, management systems for elephants have changed over the last decades [Bechert et al., 2019; Clubb & Mason, 2002; Dale, 2010; Garaï & Kurt, 2006; Kowalski et al., 2010; Kurt, 1994a; 1994b; 2006; Meehan et al., 2016; Olson, 1994; Veasey, 2006; Williams et al., 2019]. Recently, three different management systems have been present in zoos: *free contact*, *protected contact*, and *no contact* [Bossy, 2019; EAZA, 2019; Meehan et al., 2016]. These three concepts are different in terms of enclosure construction and in the way carers take care of and interact with the elephants.

In the management system of *free contact* (also called *hands-on*), carers directly interact with the elephants without a separating barrier between them. To facilitate that, the carers function as a dominant member of the social system of the elephants. The absence of a fence between carers and animals holds the advantage of better access to the animals, which is beneficial during medical treatment, ultrasound examination, or transport training [Bossy, 2019; Lundberg et al., 2001; Samson, 2000; Tanner, 2000]. However, elephants are still wild and massive animals, and direct contact with them holds undeniable risks for carers. Therefore, when they enter the elephant enclosure, carers must carry an ankus for safety. The ankus is for the carers' safety and helps them lead the elephants and correct them during training, as seen in Figure 1.5 (Zoo Wuppertal) [Bossy, 2019; EAZA, 2019]. A picture of the washing routine in *free contact* in Zoo Wuppertal can be seen in Figure 1.6.

Fig. 1.5: Training in *free contact* [Hörner, 2023].

Fig. 1.6: Washing routine in *free contact* [von Gilsa, 2023].

Free contact is the most criticized and least applied of the three holding systems. It is considered dangerous for the carers and not species-appropriate for the animals by critics, as the elephants must accept the carers as dominant members of the herd [Bossy, 2019]. This is why, in 2019, the EAZA enacted a change from *free* to *protected* or *no contact* for all elephant facilities by 2030 [Bossy, 2019; EAZA, 2019].

In the handling system *protected contact*, all interaction and care of the elephants are facilitated through bars, separating fences, or particular training walls and cages. Here, the main principle is the voluntary work of the animals with the carers at all times. The carers never enter the enclosures when the elephants are in them [Desmond & Laule, 1991; 1993; Harris et al., 2008; Laule & Whittaker, 2001]. Hence, risks during interactions with the elephants are reduced enormously. *Protected contact* is the management system most frequently applied in European zoos [EAZA, 2019]. Pictures of the enclosure, training, and medical care in *protected contact* in Tierpark Schönbrun can be seen in Figures 1.7 and 1.8.

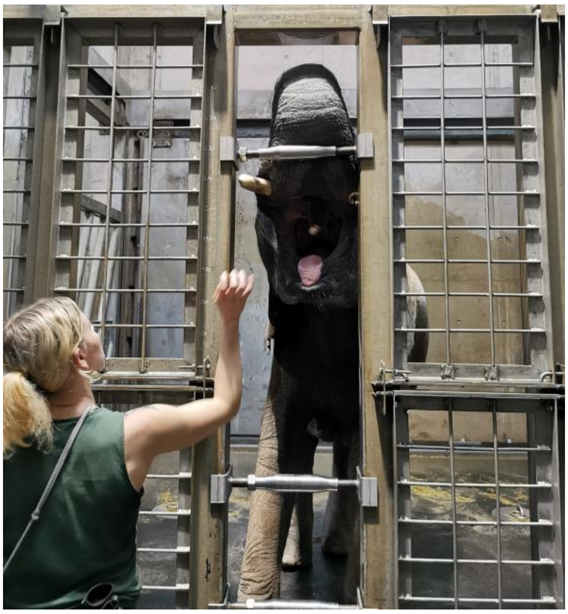


Fig. 1.7: Training in *protected contact* [Hörner, 2022].

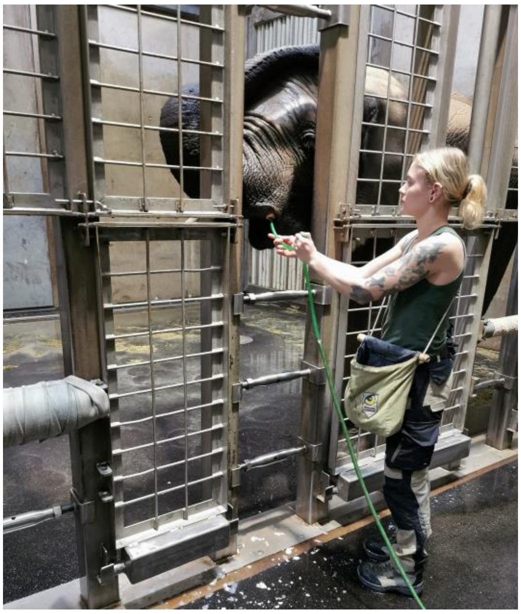


Fig. 1.8: Medical care in *protected contact* [Hörner, 2022].

The management system of *no contact* functions without any contact between carers and elephants other than providing food and water and cleaning the enclosures. Hence, elephants are not being trained. Zoos facilitating this management system allow the elephants to roam freely in the outside enclosures. The holding system refers most closely to the conditions in the wild. However, it strongly limits the medical care for the elephants, and the logistics when animals have to be moved are challenging. It is the rarest holding system in Europe [Laule & Whittaker, 2001]. Pictures of the stables and the outside enclosure in the Parque Cabarceno can be seen in Figures 1.9 and 1.10.

Fig. 1.9: Stables in *no contact* [Hörner, 2021].

Fig. 1.10: Outside enclosure in *no contact* [Hörner, 2021].

All zoo elephants are generally familiar with humans at a close space, regardless of the holding system. In all holding systems, calves observe their mothers and other herd members interacting with the carers and adapt this behavior from them. In *protected contact*, the training for the calves starts when they voluntarily approach the fence and are willing to interact with the carers. In the holding system of *free contact*, interaction, and training start from an early age, as the calves must respect humans as sensitive and vulnerable beings [Bossy, 2019; EAZA, 2019].

1.5.2 Breeding in zoos

Zoos holding African elephants are the minority compared to those having Asian elephants [Kurt, 1994a; 2006]. This and the fact that African elephants breed less successfully under human care [Kurt, 2006] is why the number of *Loxodonta africana* in zoos is limited. In the early history of African elephants in zoos, breeding had little success. In the early 2000s, when research on African elephants in zoos finally increased, and holding conditions were improved, the breeding of African elephants eventually became more successful [Eigener, 2004; Garaï & Kurt, 2006; Grzimek, 2000; Kowalski et al., 2010; Kurt, 2006; Launer, 1994; Schulte, 2000; Sauer & Frank, 1993]. This is necessary to generate an independent stock of zoo elephants, as importing wild elephants is now frowned upon [CITES, 2019]. Many zoos holding African elephants now reach the F2 generation, and very few are already reaching the F3 generation [Rees, 2021]. Those new generations of zoo-born elephants are not solely socialized by African elephants that initially came from the wild, but also by animals that were born and socialized in a zoo environment themselves.

1.6 African elephants *in situ* and *ex situ*

This study investigates the social bonds and social behavior of African elephants socialized and living in a zoo environment and compares it to their wild conspecifics. Therefore, the following chapter will give insights into these two sides of elephant environments. Besides being familiar to close contact with humans, there are differences in the breeding, social constellation, and behavior between elephants living *in situ* and *ex situ*.

The most striking difference is the age at which cows and bulls reach fertility. While *in situ* cows give birth for the first time at an average age of sixteen years, the average age for first delivery *ex situ* is twelve years, which is a significant difference [Kowalski et al., 2010; Oerke, 2004].

Musth in zoos also differs from musth in the wild. While bulls *in situ* are reported to reach musth for the first time around the age of 20-25 and are considered an appropriate mating partner at the age of ~30 years, *ex situ* bulls can reach musth for the first time at the age of fifteen years and also mate successfully at this age [Kurt, 1994a; Moss & Colbeck, 2002; Poole, 1989; Schulte, 2000]. Furthermore, the musth is distinct in zoos. While in the wild, musth has a reappearing rhythm in the bulls' cycle, in zoos, bulls can be observed to be almost constantly in musth, making the bulls willing and ready to mate at any given time [Kurt, 1994a; Schulte, 2000]. The advantages that musth provides for wild bulls cease in zoos, as bulls there are almost solely kept alone–without another bull–and, therefore, without a rival. The optimal food supply supports the consistency of musth in zoos [Schulte, 2000].

The constellation of herds living in zoos also differs from wild ones. While zoos strive to hold elephants as species-appropriate as possible, adapting their complex herd structures (see chapter 1.2) is difficult to maintain. Herds in zoos are often smaller, sometimes consisting of only two individuals [EAZA, 2019]. They might have different age distributions, as the birth rate does not match that in the wild [EAZA, 2019; Kurt, 2006]. Moreover, zoo herds can differ in the relationships of the elephants, as zoos must hold unrelated females and their offspring together frequently due to limited space [EAZA, 2019; Kurt, 2006; Rees, 2021].

Furthermore, significant differences in the behavior of elephants living *ex situ* and *in situ* can occur, as elephants living under human care are more likely to experience trauma during transports or when held and handled under inadequate conditions [Schulte, 2000]. Such cases can cause hospitalism in the *ex situ* animals. The most frequent form of hospitalism displayed by elephants in zoos is waving, a rhythmic swinging of the head, which puts them into a condition of trance [Schulte, 2000]. In *in situ* living elephants, hospitalism was never reported.

Besides the differences between *ex situ* and *in situ* mentioned above, further differences were detected in previous studies: Webber [2017], Freeman et al. [2021], and Hörner [2017; 2019] found differences in the distance keeping of calves living in zoos. Calves were observed to hold more considerable distances from their mothers and next neighbor than reported for their conspecifics *in situ*. Hörner [2019] observed calves spending up to 31 % of their time at a distance of more than five meters from their mothers, standing apart from the habit of *in situ* calves (see 1.2.4). This phenomenon was already observed at the age of three days. A spatial detachment that extends with the age of the calves, reaching its peak with elephant calves of only five months that spend more than fifteen minutes inside the stable while the rest of the herd is outside and therefore out of sight [Freeman et al., 2021; Hörner, 2017; 2019; Webber, 2017]. However, Webber [2017] solely made this observation in Asian elephant calves and not in African elephant calves.

Predators, humans, or a lack of food and water do not endanger elephants in zoos; thus, the close bond necessary for their survival in the wild seems to become less crucial in zoos [Kurt, 1994a; 1994b; Schulte, 2000]. It can be hypothesized that the differences in distance keeping will increase with the ongoing breeding in zoos, as elephants are educated and socialized by their relatives already born in zoos, adapting their behavioral patterns [Moss, 2001; Moss & Colbeck, 2002; Ortolani et al., 2005].

1.7 Cortisol level as welfare parameter

Animals living under human care often experience more stress, leading to a rise in the primary metabolite of cortisol, 11-oxo-eti-118 ocholanolone (11-oxo-CM) [Heimbürge et al., 2019]. When not treated, this can lead to trauma, hospitalism, and health issues, as the increased cortisol level damages the hippocampus [Pawluski et al., 2017]. Hence, the cortisol level of animals can be used as an indicator of their well-being, and the measurement of glucocorticoids can be used as a tool to determine animal welfare [Heimbürge et al., 2019; Meyer & Novak, 2012; Novak et al., 2013].

While cortisol can be measured in any body liquid of an animal (most frequently used are saliva, blood, urine, and feces), the data on the glucocorticoid level depicted in the different body fluids all represent the cortisol level for a different moment and period [Heimbürge et al., 2019; Meyer & Novak, 2012]. Glucocorticoid in saliva depicts the stress the animal experienced in the last fifteen minutes. Glucocorticoid in blood shows the stress of the last two to twelve hours. Feces display stress experienced during the last 24 hours. Cortisol comprises a diurnal variation, with higher levels in the morning and decreasing values over the day [Ganswindt et al., 2005; Heimbürge et al., 2019; Meyer & Novak, 2012; Novak et al., 2013].

1.8 Scope of this thesis

Regarding the close social bonds between herd members and especially related elephants and the possible differences in breeding and behavior of African elephants in zoos, the question arises if the conspecifics bred in zoos will develop and adapt an altered behavior with the ongoing zoo generations. Suppose zoos keep breeding elephants, which is necessary to generate an independent stock of zoo elephants, as the import of wild individuals is frowned upon nowadays [CITES, 2019]. In that case, they must ensure that the elephants bred and socialized in the zoos show species-specific behavior, as species-specific behavior is associated with animal welfare, as it measures animal well-being [Andrews et al., 2005]. Four approaches were designed to evaluate the social bonds of zoo-kept African elephants compared to wild individuals, investigating the species-specific behavior of the zoo population of *Loxodonta africana*; thereby taking a first step to close this research desideratum.

I. The first project investigated if African elephants in zoos can recognize their relatives after two and twelve years of separation just by the scent of their feces and can differentiate the feces scent of related and unrelated elephants. Thereby, not only the olfactory abilities and long-term memory of African elephants were investigated, but also the long-lasting family bonds of zoo elephants displayed in their reactions to the scent of relatives. Recognizing relatives after a long absence by olfaction should testify to intense family bonds [Bates et al., 2008; Moss & Colbeck, 2002; von Dürckheim et al., 2018; von Dürckheim, 2021]

II. After the fecal smelling test, the related elephants of this study were reunited, and a second project was conducted to investigate their reactions on first encounters after long-term absence. Here, it was examined whether zoo-socialized elephants also perform the Greeting Ceremony [see chapter 1.3.2]. Also, unrelated elephants were observed during unifications to detect possible differences in greeting habits between familiar and unfamiliar individuals.

III. While African elephants have been kept in zoos for decades [Kurt, 1994a; 2006] and holding systems are frequently adjusted to guarantee the best welfare conditions [Bossy, 2019; EAZA, 2019], the different management systems for *Loxodonta africana* were never assessed regarding social behavior and family bonds. The third project investigated this aspect for calves with their mothers and other herd members for all three management systems represented in European zoos. The three systems were compared regarding their possible impact on the calves' social contacts and behavior and possible differences to individuals living *in situ*.

IV. Finally, the general question of a possible difference in social behavior and social bonds between zoo-born and socialized African elephant calves of the F1 and F2 generation and wild-living calves was tackled in project IV. Additionally, this project investigated if possible differences between *in situ* and *ex situ* living calves increase with the ongoing zoo-generations. Social behavior data for all three test groups was collected and tested for possible differences. This project was designed to investigate whether elephants *ex situ* and *in situ* display differences in social behavior and bonds in a broader context.

All these projects follow the shared goal of collecting data on the social behavior, bonds, and welfare of zoo-kept elephants and examining the sustainability of zoos in terms of those parameters. It is a first step towards joined research on *in situ* and *ex situ* elephants–a research collaboration that is widely missing.

2 Material and Methods

2.1 Elephants and fields of studies

This study includes approximately 116 elephants, 26 living *ex situ*, and ~90 living *in situ*. Data for zoo-elephants was collected in eight European zoos: Zoo Wuppertal, Bergzoo Halle, Tierpark Berlin, Serengeti Park Hodenhagen, Opel-Zoo Kronberg, in Germany, Borås Djurpark, in Sweden, Safari Park Dvůr Králové, in the Czech Republic, and Parque de la Naturaleza Cabárceno, in Spain. Data for wild elephants was collected in the Jafuta Reserve, Victoria Falls, Zambezi Nationalpark, and Hwange Nationalpark in Zimbabwe. Detailed information on the elephants of the four studies is presented in Table 2.1. Information is valid for the time of data collection.

Table 2.1 Elephants participating in this dissertation.

Name	Sex	Date of birth	Origin	Placed*	Holding system	Participating studies
Bibi	F	1985	*in situ*	Serengeti-Park Hodenhagen	*Protected contact*	I & II
Panya	F	22-08-2007	*ex situ*	Bergzoo Halle/ Serengeti-Park Hodenhagen	*Protected contact*	I & II
Pori	F	1981	*in situ*	Tierpark Berlin/Bergzoo Halle	*Protected contact*	I & II
Tana	F	04-05-2001	*ex situ*	Bergzoo Halle	*Protected contact*	I & II
Lilak	F	1971	*in situ*	Tierpark Berlin/Opel-Zoo Kronberg	*Protected contact*	II
Kariba	F	17-03-2006	*ex situ*	Tierpark Berlin/Opel-Zoo Kronberg	*Protected contact*	II
Zimba	F	1982	*in situ*	Opel-Zoo Kronberg	*Protected contact*	II
Drumbo	F	1990	*in situ*	Zoo Vienna Schönbrunn/Safaripark Dvůr Králové	*Protected contact*	II
Saly	F	1982	*in situ*	Safaripark Dvůr Králové	*Protected contact*	II
Umbu	F	1981	*in situ*	Safaripark Dvůr Králové	*Protected contact*	II
Tuffi	F	16-03-2016	*ex situ*	Zoo Wuppertal	*Free contact*	III & IV
Gus	M	20-04-2019	*ex situ*	Zoo Wuppertal	*Free contact*	III & IV
Tsavo	M	06-03-2020	*ex situ*	Zoo Wuppertal	*Free contact*	III & IV

Chindi	F	14-04-2017	*ex situ*	Borås Djurpark	*Protected contact*	III & IV
Elani	F	20-09-2019	*ex situ*	Bergzoo Halle	*Protected contact*	III & IV
Kudio	M	05-04-2021	*ex situ*	Borås Djurpark	*Protected contact*	III & IV
Toribio	M	29-08-2018	*ex situ*	Parque de la Naturaleza Cabárceno	*No contact*	III & IV
Maruca	F	22-02-2020	*ex situ*	Parque de la Naturaleza Cabárceno	*No contact*	III & IV
Neco	M	08-01-2021	*ex situ*	Parque de la Naturaleza Cabárceno	*No contact*	III & IV
Jogi	M	14-08-2014	*ex situ*	Zoo Wuppertal	*Free contact*	IV
Saja	F	06-08-2017	*ex situ*	Parque de la Naturaleza Cabárceno	*No contact*	IV
Majira	F	23-06-2017	*ex situ*	Borås Djurpark	*No contact*	IV
Tamika	F	26-06-2016	*ex situ*	Bergzoo Halle	*Protected contact*	IV
Ayo	M	03-08-2016	*ex situ*	Bergzoo Halle	*Protected contact*	IV
Toranzo	M	26-07-2018	*ex situ*	Parque de la Naturaleza Cabárceno	*No contact*	IV
Kimana	F	20-04-2020	*ex situ*	Zoo Wuppertal	*Free contact*	IV
None**	F & M	unknown	*in situ*	Zimbabwe	-	IV

*Both facilities are listed for elephants transferred during projects (study II).
**Sample group comprising approximately ~90 calves; information on those is limited due to wild heritage.

2.2 Ethological methods

Five ethological methods were applied to collect behavioral data on the elephants within the four projects. A list of the ethological methods and in which study they were used is presented in Table 2.2.

Table 2.2: Ethological methods applied in this dissertation.

Method	**Study**
Ethogram	I, II, III, IV
Scan Sampling	I, II
Focal Animal Sampling	III, IV
Next-Neighbor Method	III
(Social) Distance Method	II, III, IV

Ethogram

An ethogram is a register of all discrete species-specific behaviors a species shows. It represents the fundamental behavioral repertoire of that species and describes those behaviors. All behaviors listed in an ethogram are explained and assigned with an abbreviation, which makes it easier for future use. The ethogram is the basis for most ethological methods and research, as usually an ethogram of a species is utilized when collecting behavioral data [Kappeler, 2020; Naguib & Krause, 2020; Poole & Granli, 2021; Randler, 2018].

Scan Sampling

Scan-sampling is the opposite of Focal-Animal Sampling. Not a single individual is observed continuously, but a whole group of animals is observed, and within a previously determined interval– depending on the number of animals and activity budget– the behavior of the individuals at moment of measurement is documented. Again, the basis for this method is an ethogram [Kappeler, 2020; Krull, 2000; Naguib & Krause, 2020; Randler, 2018].

Data collected with this method can be used for a particular behavioral group profile. Even though this method is more prone to errors by observers, as attention has to be split between several animals, it is very efficient to collect data for big groups of individuals [Kappeler, 2020; Naguib & Krause, 2020].

Focal-Animal Sampling

When applying Focal-Animal Sampling, the observer chooses one specific animal, which is then observed continuously during the observation time. The observation period is determined beforehand, and all behavior relevant to the study is documented–usually applying an ethogram. Doing this, not the duration of a specific behavior shown by the focus animal is registered, but the frequency [Kappeler, 2020; Krull, 2000; Naguib & Krause, 2020; Randler, 2018].

This method allows to collect behavioral data of a single individual within a bigger group of animals. The observer does not have to divide their attention between several animals. The data collected with this method is less inflicted for errors due to the inattentiveness of the observer and, therefore, more reliable [Kappeler, 2020; Krull, 2000; Naguib & Krause, 2020; Randler, 2018].

Next-Neighbor Method

The Next-Neighbor Method is facilitated in combination with Focal-Animal Sampling. In a previously determined interval– depending on the activity budget of the observed species– the next neighbor of the focus animal is registered. The next neighbor is identified as the closest to the focus animal [Kappeler, 2020; Naguib & Krause, 2020; Randler, 2018].

The data collected with this method allow for an analysis of the spatial attachment of an animal to other individuals. It indicates the focus animal's social relationship with specific individuals. However, the Next-Neighbor Method alone does not allow for a comprehensive analysis of an animal’s social relationship, as it does not document social contacts [Kappeler, 2020; Naguib & Krause, 2020; Randler, 2018].

(Social) Distance Method

The (Social) Distance Method was explicitly designed for the projects of this dissertation and is not based on a guide for behavioral studies. Therefore, there are no references listed for this method.

The Social Distance Method is an extension of the Next-Neighbor Method. Here, it is not only documented who the closest neighbor of the animal is but also at which distance they stand to one another. This distance is registered in previously determined distance parameters, e.g. *tactile contact*, *<1 m*, *1-3 m*, *3-5 m*, and *>5 m*. This method can be facilitated for one animal (Focal-Animal Sampling) or several group animals (Scan Sampling). Data is registered in an interval, not on occurrence. The Distance Method is applied like the Social Distance Method, with the difference that the animal’s distance to an object, not an animal, is measured here.

This method allows for an extended analysis of individual’s spatial attachment or willingness to encounter other individuals or objects. It gives information on the independence level of animals within groups and the general group structure in terms of spatial relationships.

2.2.1 Setting and procedure study I

Study I was conducted in 2020. The study design followed a similar experiment with smelling samples conducted by Bates et al. [2008]. However, with a fundamental difference in time, as Bates et al. only tested the olfactory short-term memory. Study I investigated African elephants' olfactory long-term memory and social bonds. Test animals were two mother-daughter pairs (*n*

= 4, two mother elephants, two daughter elephants) living separated for two and twelve years, respectively. They were located in three different German zoos.

All females were presented with three different fecal samples: (a) a sample of an unrelated female they were currently living with, (b) a sample of an unrelated female they had never seen or smelled before, (c) a sample of the relative they were living separated from. Samples were collected within 24 hours before the test and stored in a cooling box to preserve the scent.

All three tests were conducted for each individual within a day. The time between tests was at least two hours. The samples were placed within the animals' enclosure at a prominent spot before the test elephant was granted access. Then, the gates were opened, and the test elephant entered the enclosure. Elephants were always tested alone. Test areas were cleaned after each test to eliminate the remains of the previous fecal sample.

All tests were video recorded with a Panasonic HDC-TM60 camera. The first twenty minutes of each test were analyzed, as reactions after that time cannot reliably be traced back to the fecal sample [Dürckheim, 2021].

The elephants' reaction to the three test samples was documented by Focal-Animal Sampling, applying an ethogram extracted from Poole & Granli [2011], listing 27 behavior items. Those behaviors where further divided into four categories: *excitement*, *mental processing*, *sample examination,* and *neutral* (see Table 2.3).

Table 2.3 Ethogram of study I, based on Poole & Granli [2011].

Category	**Behavioral item**
Neutral	Walking around the enclosure
	Locomotion trunk
	Eating
	Body care
	Comfort behavior
	Weaving
Excitement	Folding, lifting, spreading, flapping ears
	Raising trunk
	Shaking trunk
	Raising head
	Shaking head
	Raising tail
	Shaking tail
	Pacing
	Pacing backwards

	Acoustic signals
	Defecating and urinating
	Glandular secretion
	Throwing feces
	Intense weaving
Mental processing	Freezing
	Listening
	Smelling air
Sample examination	Sniffing on sample
	Examining samples with trunk and feed
	Squashing sample
	Throwing sample

Additionally, the number of behavioral items of the category *excitement* elephants showed during the sample presentation was counted to evaluate the extent of their excitement. Also, the number of shifts in elephant behavior was measured as a marker for the pace with which they reacted to the samples. The females' reactions to the different test samples and possible differences in the reactions between mothers and daughters were investigated. The observation sheets used for this study can be seen in Appendix I. Raw data of study I can be found on the attached hard drive.

As the smelling test might cause physiological stress in the animals, for each elephant, five fecal samples were collected and controlled for a rise in 11-oxo-etiocholanolone. The control sample, representing the average cortisol level of the animals, was collected in the morning before the tests. Another sample was collected 24 hours later, in the morning after the tests. Additionally, three more samples were collected at intervals of twelve hours, the last being collected the evening of the second day after the test.

2.2.2 Setting and procedure study II

The zoo elephants participating in study I in 2020 were reunited shortly afterward. The reunifications of the two mother-daughter pairs were ethologically documented (n = 4) to investigate long-lasting social bonds between African elephants and the performance of the Greeting Ceremony in a zoo-environment. In comparison, two unifications of unrelated females were observed, who did not know each other before. Here, one female was transferred to an existing group of two females and united with them, and an existing group of two females was transferred to a single female and united (n = 6).

During all four (re)unifications, the first encounters of the elephants were through a separating fence for safety reasons. However, elephants had visual, tactile, olfactory, and acoustic access to the other individual/s.

All (re)unifications were video recorded with a Panasonic HDC-TM60 camera. The first 30 minutes of (re)unifications were analyzed, as the carers ended three of the four (re)unifications after that time to give the elephants time to calm down and get used to the new situation.

The elephants' reactions during (re)unifications were also documented by Focal-Animal Sampling, which was possible as the (re)unifications were video recorded. Therefore, a detailed analysis of the reaction of every single elephant was possible. The ethogram applied during this study focused on behavioral items characteristic of the Greeting Ceremony (see chapter 1.3.2, Table 1.1) and on sings of agitation that are related to excitement or fear, hence having an affiliative or agonistic connotation, as well as neutral behavior [Poole & Granli, 2011] (see Table 2.4).

Table 2.4 Ethogram of study II, based on Poole & Granli [2011].

Affiliative	
Running towards the fence/animal	Elephants run towards the elephant they intend to greet or the fence separating them from the elephant.
Pushing against the fence	Elephants press their head or body against the fence to touch the other elephants.
Touching trunks	Elephants touch the trunk of the other elephant with their trunk.
Affiliative agitation	Elephants raise their head, shake their tail, click their tusks, and flap their ears.
Acoustic signals	Elephants emit rumbles (low-frequent calls).
Defecating/urinating	Elephants drop feces and micturate.
Agonistic	
Agonistic agitation	Elephants shake their head, stick out their tail, role in their trunk, and fold their ears close to their head.
Acoustic signal	Elephants emit roars (high-frequent calls).
Pacing backwards	Elephants quickly diverge from fence/other elephants.
Showing servility	Elephants bow their head, lower their shoulders, furl their trunk, and jam their tail between their hind legs.
Showing dominance	Elephants stand tall, with raised heads and spread ears; they lift their trunk,

	place the trunk on the other elephants' heads, and run swiftly towards other elephants.
Neutral	
Eating/drinking	Elephants eat and drink.

Additionally, the distance elephants kept to the separating fence was measured using the Distance Method. Here, the following distance parameters were used: *direct contact* (to animal or fence), *<1 m*, *1–2 m*, *3–4 m*, and *>4 m*. Parameters were chosen according to the size of the enclosures. The distance elephants kept to the fence was noted every 10 seconds. This data was used to analyze the elephants' urge for contact with the elephants they were (re)united with.

Also, the time it took for the elephants to have the first tactile contact was measured. This data indicates the elephants' willingness to approach the other animals as a sign of existing social bonds [Moss & Colbeck, 2002; Poole & Granli, 2011]. The observation sheets for this data collection can be seen in Appendix II. Raw data of study II can be found on the attached hard drive.

2.2.3 Setting and procedure study III

Study III compared the social behavior and development of *Loxodonta africana* calves living in the three management systems: *free contact, protected contact*, and *no contact*. The study also analyzed the behavioral parameters in correlation to different enclosure sizes. Three calves living in four zoos were observed for each system (n = 9). They were observed for fifteen hours each, resulting in an observation time of 45 hours for each holding system. Calves were chosen to represent homogenous sample groups in terms of gender, age, and number of playmates. As gender-related differences in behavior become significant at the age of four [Lee & Moss, 2011], the age limit was drawn there.

Behavioral data was only collected when carers were outside the enclosures and did not interact with the animals. Observations for each calve were spread over two weeks, in late summer and early fall. Data was collected between 2019 and 2021.

Applying the Social Distance Method, the calves' distance to their mothers was measured in the distance parameters *tactile contact*, *<1 m*, *1-3 m*, *3-5 m*, and *>5 m*, following the distance parameters of a similar study by Lee & Moss [2011]. Social Distance data was recorded in a 60-second interval. Data was used to investigate the social and spatial relationship between calves of the different holding systems to their mothers [Kappeler, 2020; Krull, 2000; Martin & Bateson, 2007; Naguib & Krause, 2020; Randler, 2018].

With a combination of the Next-Neighbor Method and the Social Distance Method, the calves' distance to their next neighbors, other than their mothers, was investigated. Here, the distance parameters *tactile contact, <2 m*, 2-4 *m,* and *>4 m* [Lee & Moss, 2011], were applied, and data were recorded at an interval of 60 seconds.

The frequency of affiliative and agonistic behavior initiated and received by the calves was documented during observations. Thereby, the social behavior and relationships of the calves of the three management systems were analyzed [Kappeler, 2020; Krull, 2000; Martin & Bateson, 2007; Naguib & Krause, 2020; Poole & Granli, 2021; Randler, 2018].

Additionally, the general behavior displayed by the calves was documented in an ethogram, retrieved from Poole & Granli [2021; 2011], listing the following eight behavioral items: *eating, drinking, suckling, locomotion, locomotion trunk, comfort behavior, sleeping,* and *playing*. Data was collected in a 60-second interval. This data was used to generate a behavioral profile of the calves on the different management systems and environments [Kappeler, 2020; Krull, 2000; Martin & Bateson, 2007; Naguib & Krause, 2020; Randler, 2018]. The observation sheets for the data collection of this study can be seen in Appendix III. Raw data of study III can be found on the attached hard drive.

2.2.4 Setting and procedure study IV

Study IV compared zoo-born African elephant calves of the F1 and the F2 generation (*ex situ*) and *in situ* living African elephant calves regarding family bonds and distance keeping. For the calves of the F1 and F2 generations, data were collected in four European zoos for eight calves of each generation. Data for calves living *in situ* was collected on ~106 calves in Zimbabwe. Altogether, observations were made for $n \approx 122$ calves. Calves of all sample groups were only observed when there was no human interaction and calves could behave freely. The data was collected between 2016 and 2023. The observation time for each sample group was approximately 120 hours. Calves were chosen to form homogenous sample groups regarding age and sex. The age limit was four years [Lee & Moss, 2011].

With the Social Distance Method, the spatial distance of the calves to their mothers was measured, applying five distance parameters: *tactile contact*, *<1 m, 1-3 m, 3-5 m,* and *>5 m* [Kappeler, 2020; Krull, 2000; Naguib & Krause, 2020]. Data was collected in a 60-second interval. This data was used to analyze the spatial attachment between calves and mothers of the different sample groups.

Applying an ethogram extracted from Poole & Granli [2011; 2021] and Scan-Sampling, a behavioral profile of the calves was generated. Those methods were used to detect possible differences in the general behavior of calves of the three sample groups. Behavioral data was collected in an interval of 60 seconds. The ethogram can be seen in Table 2.5.

Table 2.5 Ethogram of study IV, based on Poole & Granli [2011; 2021].

Label	Behavior
Eat	Eating food with trunk
Drink	Drinking water with trunk
Suckle	Suckling milk from the mother's breast
Walk	Walking at a slow pace
Run	Running in an enhanced space
Locomotion trunk	Moving trunk
Washing	Washing the body with mud/water, sand bathing, rubbing body on sth.
Sleep	Sleeping or resting in a lying or standing position
Social play	Playing with other individuals
Neutral play	Playing individually
Affiliative behavior	Behaving positively to other individuals (e.g., touching with the trunk, helping behavior)
Agonistic behavior	Behaving negatively to other individuals (e.g., pushing with trunk, tusk, or body)
Escaping	Running from sth. while showing signs of fear (scream, low tail, head high)
Seeking rescue	Hiding under/behind other individuals for protection
Rescuing	Standing over/in front of other individuals for protection
Threatening	Pacing towards sth., head, trunk, and ears high

Like in study III, the frequency of affiliative and agonistic behavior initiated and received by the calves during the observation time was documented. Thereby, the social behavior and relationships of the calves within the herd were analyzed [Kappeler, 2020; Krull, 2000; Martin & Bateson, 2007; Naguib & Krause, 2020; Randler, 2018]. The observation sheets for this project can be seen in Appendix III. Raw data of study IV can be found on the attached hard drive.

2.3 Hormone analysis

The measurement of 11-oxo-eti-118 ocholanolone in the elephants’ feces was applied in projects I and II (results only displayed in project I) to evaluate whether the procedures of those projects impacted the elephants' physiological stress levels.

During project, I, the fecal smelling test, 11-oxo-CM, in the elephants’ feces was measured to control whether the test caused any rise of stress in the animals. Therefore, five fecal samples from each elephant were collected and analyzed. One sample was collected in the morning before the test as a control sample, where no rise in cortisol was expected. Another sample was collected 24 hours later, the morning after the experiment. After that, three more samples were collected in 12-hour intervals, the last being collected on the evening of the second day after the experiment.

Controlling whether the experiment caused stress in the elephants was essential to evaluate the welfare during the experiment [Ganswindt et al., 2005; Heimbürge et al., 2019; Meyer & Novak, 2012; Novak et al., 2013]. Only if the animals' well-being during the experiment can be guaranteed this experiment is appropriate to be conducted again and be used as a tool for future tests on olfactory abilities.

During project II, the (re)unification of the elephants, 11-oxo-CM in the animals’ feces was measured once again to control the stress caused by the transfer of the animals and the stress caused by the (re)introduction into a new herd. Samples were collected daily in the early morning hours one week before the transfers until one week after. The German Primate Centre, Göttingen, Germany, facilitated the endocrinological analysis of the samples. Cortisol in the samples was measured by an enzyme immunoassay following the procedure described by Hambrecht et al. [2020].

The results of the hormonal analysis for project II were not presented in the publication, as the results did not indicate any impediment of welfare or depict any irregularities.

2.4 Statistical analysis

Statistical analysis for all four studies was conducted with SPSS Version 27/29. Data sets were first controlled for distribution to determine whether parametric or non-parametric tests should be used for statistical analysis [Bortz & Döring, 2006]. Afterward, statistical tests were chosen according to the number of sample groups [Bortz & Döring, 2006]. Statistical tests were then run to detect possible significant differences between the various sample groups in the studies. The significance level was set at $p \leq 0.05$ (normal significance) and $p \leq 0.001$ (strong significance) [Fritz et al., 2012; Ryan, 2013]. A list of the data sets for all studies, their distributions, and the statistical tests run for them can be seen in Table 2.6.

Table 2.6 Statistical procedures for data sets of studies I-IV.

	Data set	Distribution	Statistical test
Study I	Behavioral reaction to sample	Uneven	Friedman Test + Post-Hoc Test
	Frequency of behavioral items of excitement	Even	ANOVA
	Number of shifts in behavior	Even	ANOVA
	Changes in 11-oxoetiocholanolone level	Uneven	Mann-Whitney-U-Test
Study II	Behavioral reaction during (re)unification	Uneven	Mann-Whitney-U-Test
	Behavior of Greeting Ceremony	Uneven	Chi-Square Test + Fisher’s Exact Test
	Excitement and fear	Even	t-test + Levene’s Test
	Distance to fence/animal	Uneven	Mann-Whitney-U-Test
	Time until first tactile contact	Even	t-test + Levene’s Test
Study III	General Behavior	Uneven	Kruskal-Wallis calculation + Monte Carlo Simulation
	Social behavior	Uneven	Kruskal-Wallis calculation + Monte Carlo Simulation
	Distance to mother	Uneven	Kruskal-Wallis calculation + Monte Carlo Simulation
	Distance to next neighbor	Uneven	Kruskal-Wallis calculation + Monte Carlo Simulation
Study IV	General behavior	Uneven	Kruskal-Wallis calculation + Post-Hoc Test
	Social behavior	Uneven	Kruskal-Wallis calculation + Post-Hoc Test
	Distance to mother	Uneven	Kruskal-Wallis calculation + Post-Hoc Test

3 Results

The results are presented in the following format:

Chapter I:	Article I: Long-term olfactory memory in African elephants The results are published in ‘Animals’, 2023, vol. 4:13. doi: doi.org/10.3390/ani13040679
Chapter II:	Article II: Monitoring Behaviour in African Elephants During Introduction into a New Group: Differences between Related and Unrelated Animals The results are published in ‘Animals’, 2021, vol. 11:2990. doi: doi.org/10.3390/ani11102990
Chapter III:	Manuscript I: Behavior and social bonds of African elephant calves under different holding systems in European zoos The results have been submitted to ‘Journal of Zoo and Aquarium Research’ on 21. Novemver. 2023
Chapter IV:	Manuscript II: Differences in social behavior and mother-child bond of *in situ* and *ex situ* living African elephant calves The results have been published to ‘Animals’, 2023, 13:3051. doi: 10.3390/ani13193051

3.1 Chapter I:

Running Head: The scent memory of *Loxodonta africana*

Title: Long-term olfactory memory in African elephants

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Article

Olfactory long-term memory in African elephants

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Simple Summary: African elephants are known for their impressive memory, this is also valid for their olfactory memory and their ability to discriminate scents. This feature is highly important for these impressive mammals to maintain their family bonds and to differentiate familiar and unfamiliar individuals. So far, scientific data only testifies an olfactory memory of up to one year for African elephants. The study at hand investigated the olfactory long-term memory of two mother-daughter pairs that were living separated for two and 12 years, respectively. Results showed that all four elephants of the study were able to recognize their separate living relatives just by scent of faeces and thereby gives the first empirical proof of an olfactory memory in African elephants of up to 12 years.

Abstract: African elephants are capable of discriminating scents on a molecular scale and show the largest reported repertoire of olfactory receptor genes. Olfaction plays an important role in family bonding. However, to the best of our knowledge, no empirical data exist on their ability to remember familiar scents long-term. In an ethological experiment, two mother-daughter pairs were presented faeces of absent kin, absent non-kin and present non-kin. Video recordings showed reactions of elephants recognizing kin after long-term separation (up to 12 years), but only minor reactions to non-kin. Results give first empirical proof that elephants have an olfactory memory longer than 1 year and can distinguish between kin and non-kin by scent. These findings confirm the significance of scent for family bonds in African elephants.

Keywords: *Loxodonta africana*; scent memory; long-term memory; human care

1. Introduction

African elephants use a complex olfactory system to discriminate between scents to one changed molecule [1-3], allowing them to precisely detect resources and find mating partners in the wild [4-9]. It is assumed that the olfactory sense of elephants is also essential for maintaining their family bonds [10], which is an important trait for herds, considering the strenuous environment of the African drylands with its limited resources [11-12]. Elephant bonds are among the strongest in mammals and especially the relationship between mothers and daughters is the longest, closest and most intense of all known family bonds [2; 11]. The capacity of recognizing long-time absent and even mortal remains of relatives is hypothesized to be the result of their complex olfactory abilities [2; 13-14]. However, there are no empirical data giving evidence for an olfactory memory in African elephants longer than 1 year, neither under *ex situ* nor *in situ* conditions [3]. It is the *ex situ* environment that holds the opportunity to investigate elephant olfactory abilities under controlled and reliable conditions as it allows for an artificial setting, barely possible in wildlife environments [15-16].

Species-specific behaviour, as an association with animal welfare, is a crucial aspect when it comes to zoo-kept elephants and is frequently applied as evidence for the animals' well-being [17-18]. At the same time, species-specific reactions by zoo elephants to a certain scent, e.g. when smelling familiar scents or finding scents in a new setting, are an indicator of the animals' natural development and behaviour, similar to their conspecifics in the wild, and are therefore valued as a welfare-indicator [13; 17-18]. An additional tool to determine animal welfare is the determination of concentrations of glucocorticoids often used for assessing physiological stress in elephants [19].

In this study, a faeces smelling test was developed as a new tool for the investigation of the olfactory abilities of elephants. Our examination group consisted of four female African zoo-kept elephants, two mothers and their two daughters. The study aimed to answer the following research questions: (i) Do elephants differentiate between family members and non-kin just by the scent of their faeces? (ii) Does the scent recognition exceed a separation period longer than the 1 year reported by Rizvanovic et al. [3]? (iii) Does the familiar social behaviour of elephants under human care, regarding the expression of excitement or indifference, agree or correspond with that of elephants living *in situ*? (iv) Do the tests cause any physiological stress measurable as faecal glucocorticoid metabolites before and after presentation of the faecal samples? (v) Is there a difference between mothers and daughters in reaction to scent recognition?

The test settings described here were performed to predict the reactions of the elephants in two planned re-unifications of the mother-daughter pairs of this project, that were separated for 2 and 12 years, respectively. Since experiences of such transports are missing, the tests are also of practical use for future elephant transfers.

2. Materials and Methods

2.1. Animals and Designs of the Study

In 2020, the European studbook for African elephants recommended the re-unification of two mother-daughter groups living separately in three German zoos:

Table 1. Record of elephants of the study

	Sex	Place of birth	Date of birth	Transferred from to	Relation	Years living separated
BIBI	F	Zimbabwe	1985	-	Mother	2
PANYA	F	Tierpark Berlin	2007-08-22	Bergzoo Halle to Serengeti-Park Hodenhagen	Daughter	
PORI	F	Zimbabwe	1981	Tierpark Berlin to Bergzoo Halle	Mother	12
TANA	F	Tierpark Berlin	2001-05-04	-	Daughter	

This study was performed as a pre-test for the reunifications of the two mother-daughter pairs, which was also monitored scientifically [27]. To evaluate elephant reactions before reunifications and to test their olfactory memory, they were all presented with three different faecal samples beforehand: (a) the absent kin sample from a separated mother or daughter. (b) the present non-kin sample from an unrelated female. (c) the absent non-kin sample from a female elephant that all the observed elephants had never met before and were therefore entirely unfamiliar with.

All tests were performed under the same testing conditions. All samples were presented separately. As all three experiments were conducted with the four elephants, there was a total number of 12 experiments ($n = 12$). Samples were presented in random order, all on the same day in the same enclosure. Elephants were alone during the tests. The testing area was cleaned after each iteration so that there were no leftovers of the scent of the previous sample. The whole experiment was conducted once for each animal. The test time for each sample presentation was limited to twenty minutes since after this time elephants showed no new reaction. All samples were collected in the morning hours between 7 to 8 a.m. and used within 24 hours. The diet of all cows was the same.

2.2 Data-Collection

The study was designed according to Bates et al. [13]. Elephant reactions to sample presentation were analysed by scan-sampling with an ethogram by Poole & Granli [20-21], which consists of 27 behavioural items (Table 2). Those items were further divided into four behavioural categories: excitement, mental processing, sample examination and neutral. Time elephants showed a certain behavioural category during the sample presentation was measured. It was also observed which behavioural items of excitement were shown during the different tests. The signs of excitement that the elephants showed and the shifts in behaviour that they performed were measured.

Videos were analysed with a focus on the items of measurement. The ethological data were collected by human observation [15-16; 30-32].

Table 2. Behaviours during sample presentations and their categories

Category	Behaviour
Neutral	Walking around the enclosure
	Locomotion trunk
	Eating
	Body care
	Comfort behaviour
	Weaving
Excitement	Folding, lifting, spreading, flapping ears
	Raising trunk
	Shaking trunk
	Raising head
	Shaking head
	Raising tail
	Shaking tail
	Pacing
	Pacing backwards
	Acoustic signals
	Defecating and urinating
	Glandular secretion
	Throwing faeces
	Intense weaving
Mental processing	Freezing
	Listening
	Smelling air
Sample examination	Sniffing on sample
	Examining sample with trunk and/or feed
	Squashing sample
	Throwing sample

To evaluate if the smelling test possibly caused physiological stress in the four study animals and to avoid stress by sample collection, 5 faecal samples were taken from each elephant. A control sample was collected in the morning before the experiment, another sample 24 hours later, on the morning after the experiment, and then 3 more samples were obtained in 12 hours intervals with the last on the evening of the second day after the experiment. This protocol was used since the main metabolite of cortisol, 11-oxo-etiocholanolone (11-oxo-CM), in African elephant faeces is only excreted 24 hours after a stress event [22] and compensates the diurnal variation of cortisol, with higher levels in the morning and decreasing values over the day. Since no increase of 11-oxo-CM was detected in all four elephants, neither mothers nor daughters experienced measurable stress during the smelling test despite all observed reactions. This also proves that experiments like this can be performed without affecting the welfare of elephants and are a safe method to be applied in future elephant transfers.

2.3 Data Analysis

Sets of data were classified numerically [33-34]. Statistical analysis for all data was carried out with SPSS 27. An analysis of the graphical distribution for all data sets determined that, except for the data on the different behavioural reactions by mothers and daughters, none of them had normal distribution [35-37]. Therefore, the Friedman Test for not normally distributed data sets with more than two connected samples was calculated for the data set of the behavioural categories, to detect significant differences in reactions to faecal samples (a)-(c). The significance level was set at $p \leq 0.05$ [38-40]. If significant differences were detected, a post-hoc test with the Bonferroni correction was calculated to determine the significance [41-42]. For differences in simultaneously shown behavioural items and shifts in behaviour, an ANOVA for normally distributed data was conducted [36]. The changes in 11-oxoetiocholanolone level in the elephants' faeces before and after the tests were analysed utilizing the Mann-Whitney-U-Test [35].

3. Results

With the aim to explore how related female elephants react to the faecal scent of the absent kin after long-time separation, the two zoo-kept mother-daughter pairs living apart for 2 and 12 years were confronted with faecal samples of absent kin, absent non-kin, and present non-kin. Data of elephant behavioural reactions during sample presentations were video-recorded and collected by scan-sampling, utilizing an ethogram focused on agitation [20-21], including 27 behavioural items.

All 27 sampled behavioural items expressed during the tests were initially divided into four behavioural categories: excitement, mental processing, sample examination and neutral (Table 1). As shown in Fig. 1, time spent on the presented faecal samples of absent kin was significantly higher in the active response categories of excitement, mental processing, and sample examination. Time spent on the neutral reaction was significantly lower towards samples of absent kin. Present and absent non-kin caused fewer reactions and here less time was spent on the active response categories, while neutral behaviour was distinctive.

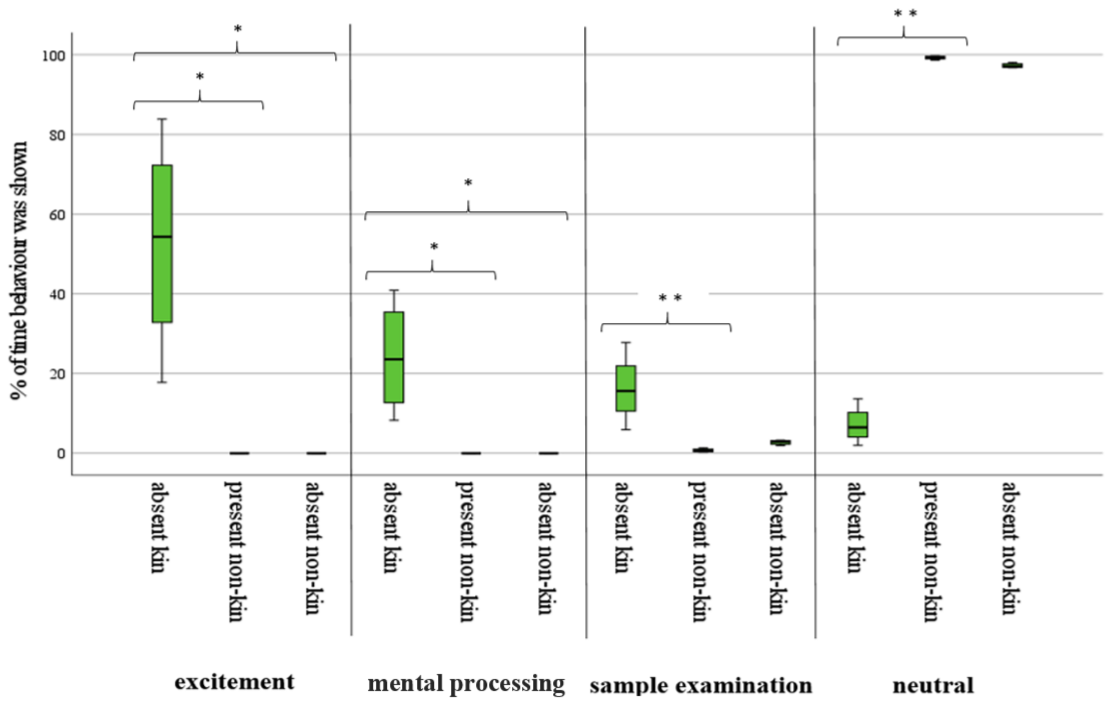

Figure 1. Reaction (in percentage of time) shown after confrontation with faecal samples (*p < 0.05; **p < 0.01).

Table 3. Corresponding statistics after Friedman Test and Post-Hoc Test.

		Excitement	Mental Processing	Sample examination	Neutral
N	4				
df	2				
Asymp. Sig.	.018				
Sig.	a: abs. kin/pres. n-kin	.034	.034	0.005	0.005
	b: abs. kin/abs. n-kin	.034	.034	.157	.157
	c: pres. n-kin/abs. n-kin	1.0	1.0	.157	.157

During tests, elephants expressed all behavioural items of excitement and mental processing when presented with samples from absent-kin. However, they did not show any particular interest to the scent of absent or present non-kin.

Examination of the difference in reaction toward the sample of the absent kin between mothers and daughters revealed that mother elephants reacted more vigorously and expressed up to 11 excitement items simultaneously, while daughters only expressed 2-3 items at the same time (ANOVA: $F(1,2) = 289.0$, $p = .003$). Mothers performed 55-64 shifts in behaviour, while daughters showed a less intense reaction with just 15-16 shifts (ANOVA: $F(1,2) = 94.44$, $p = .01$).

11-oxoetiocholanolone (11-oxo-CM) was measured as the main metabolite of cortisol in African elephant faeces [22]. Whilst all elephants had individual cortisol levels, none did react with a measurable increase of physical stress after the sample presentations within the following two days. 11-oxo-CM varied before and after the olfactory test for the four elephants from 966.91 to 728.09 ng/g faeces (mother elephant BIBI, age 35), 659.89 to 644.9 ng/g faeces (daughter elephant PANYA, age 13), 1216.00 to 914.29 ng/g faeces (mother elephant PORI, age 39) and 759.71 to 593.26 ng/g faeces (daughter elephant TANA, age 19), respectively. The statistical analysis of the glucocorticoid metabolite revealed no significant changes in metabolite level in correlation to the olfactory tests for any of the elephants (Mann-Whitney-U-Test: $U = 0.0$, $Z = -1.0$, $p = .317$).

4. Discussion

Even though this study was performed only on four elephants, data testify that elephants can recognize the scent of their relatives after up to 12 years of separation. It is the first empirical proof of an olfactory memory for such a long time in African elephants. It thereby also demonstrates the intense social bond of elephants [11-12; 20]. Even after 12 years of absence, the scent of a relative causes reactions of excitement.

The data also indicate the capacity of zoo-kept elephants to clearly discriminate between kin and non-kin faeces. This is affirmed by the time and quantity of reactions and interest expressed towards the sample of their absent kin. The elephants studied here exhibited all behavioural categories associated with agitation and interlinked the scent to their respective relative, whereas only minor interest and agitation, but major neutral behavioural items were shown during non-kin sample presentation. Evidently, the sample presentation of the absent kin led to a positive connotation of the prompted emotions, which means that behavioural and bonding concepts by the elephants with their family members are still present *ex situ*, and do not get lost in the zoo environment [17-18]. Missing significances in the differences between absent-kin and absent non-kin samples in the categories of sample examination and neutral behaviour, despite high differences in expressed behaviour, can be traced to the limited sample size of segregated related females [23].

These findings agree with the situation of elephants in the wild, where the encounter with and differentiation of the scents of herd members or unfamiliar elephants of other herds occur constantly [12-13]. Usually, *in situ* non-kin scents, as well as common, neutral and entirely unfamiliar scents do not cause any major positive reaction or emotional connotation [12-13; 24-26]. Related elephants rely on olfactory recognition for bonding and herd maintenance [11-12]. In this study, the recognition of and reaction to the scent of absent kin exceeded the interest in new or unfamiliar scents, as also described by Bates et al. [13].

In a joint study, Hörner et al. [27] confirmed the positive reaction to the presentation of a relative during the re-unification of mothers and their daughters. However, unrelated elephants living in zoos reacted with tension and agonistic behaviour during first encounters as part of unification. This occurs more so than in the wild [12; 20], where total spatial avoidance is possible. The means to avoid tension and agonistic behaviour and to enhance animal welfare under human care are delimited due to restrictions on the site and research gaps. A prerequisite to further exploring these means is the knowledge of elephant stress levels during (re-)unification. Our results indicate that a faecal sample presentation did not induce an increase in physiological stress, expressed in the level of glucocorticoids, and can be a great monitoring test in advance of future (re-)unifications [27].

Interestingly, the data suggest that the mother-offspring bond in elephants is stronger than the offspring-mother bond, as shown in the higher reaction of the mothers to the faeces of the absent daughter when compared to the reaction of the daughters to their mothers' faeces. So far, no other studies on African elephants tackled this question, however, other mammals living in a fission-fusion society with strong family bonds, such as chimpanzees, uncovered similar results [28-29]. In elephants, a possible cause for this reaction is the different relationships mothers and daughters have within elephant herds. Whilst the mothers within a matriarchial group structure seek to protect and keep their family (and thus their daughters) together throughout their entire life, it is common for the daughter elephants to survive their mothers. Thus, losing the mother is a normal (although once-in-a-lifetime) experience. The finding of remains (even scents) of mothers should, therefore, not motivate further reactions. The rediscovery of a lost female offspring, however, may trigger searching behaviour, resulting in stronger behavioural reactions when smelling their scent.

5. Conclusions

This report gives clear empirical evidence for an olfactory long-term memory of up to 12 years in African elephants. The study testifies that the reaction to scents of relatives is positive, and therefore attests species-specific behaviour in zoo-socialized elephants [20-21]. The olfactory long-term memory and the positive reaction to the relatives' scent are further confirmation of the close family bonds, especially from mother to daughter, in African elephants. The study also models a new testing tool for future transfers, as it can be used as a method to familiarize elephants with scents before unification, to predict their reaction on re-unification as described in Hörner et al. [27], and to secure elephant safety and welfare, which was one of the main aims of test setting described the here.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1, Figure S1: title; Table S1: title; Video S1: title.

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3.1.1 Conclusive summary study I

This study gave a new insight into the complex olfactory abilities of African elephants. While it is clear that olfaction is crucial for African elephants to build and maintain their close family bonds [Rasmussen, 1995a; 1995b], proof of those bonds by olfaction is unique. Previous studies testified to elephants' abilities to discriminate different scents [Rizvanovic et al., 2013], to locate scents [von Dürckheim, 2021; Dürckheim et al., 2018], and to have knowledge of the whereabouts of certain scents [Bates et al., 2008]. However, no study has proven a sound, olfactory long-term memory in African elephants.

In study I, a test was designed to investigate elephants' olfactory long-term memory. The unique situation of two mother-daughter pairs (n = 4) living separately gave the basis for the project. One mother-daughter pair lived separately for two years and the other for twelve years. The olfactory test was designed to test whether they could recognize their absent relative's scent. Each female was presented with three fecal samples of elephants successively. Sample (a) was the fecal sample of an unrelated female they were currently living with. Sample (b) was the fecal sample of an unrelated female they had never encountered before. Sample (c) was the fecal sample of the separated related female. The samples were presented separately; the elephants were alone in their enclosures during the tests, and reactions were video-recorded.

The elephants' reactions to the different samples were measured by three parameters: Their general behavioral reaction to the three test samples was documented by applying an ethogram [Poole & Granli, 2022; 2021]. The number of behavioral excitement items [Poole & Granli, 2011; 2021] shown during the sample presentations was counted. The number of shifts in elephants' behavior was registered. Data were statistically analyzed with SPSS Version 29, applying the Friedman Test in combination with a Post Hoc Test for the data set on the general behavior [Agresti, 2007; APA, 2013] and an ANOVA calculation for the other two sets of data [Blanca et al., 2017]. Significant differences were detected between the reactions to the three test samples for all four elephants in all data sets. Elephants reacted with significantly more agitation and excitement to the fecal sample of their absent relative (p = .034). Another finding was that mothers reacted stronger than daughters (p = .003).

These results do not only give the first empirical proof for an olfactory long-term memory in African elephants of at least twelve years. They also testify to their intense family bonds. While elephants are known to maintain those deep family bonds [Moss, 2001], it is the first time they were observed to express them in the context of olfaction. The smell of a relative arising such extreme emotional reactions in elephants opens a new perspective on these mammals' social abilities and facets.

The finding of mothers reacting stronger than daughters is also a new insight into the composition of elephants' family bonds. While it is known that in the early stages (birth – two years) of mother-child bonds, the connection is maintained mutually by both sides, this shifts to a more considerable responsibility on the mother's side later on [Charif et al., 2005; Lee & Moss, 2011; 1986)]. However, this bond being persistently stronger on the mother's side was never observed before. A possible explanation for this phenomenon is that children are expected to survive their mothers, while mothers do not expect to lose their children [Moss & Colbeck, 2002].

Besides the findings on olfaction and new facets of family bonds in this study, the results also testify that *ex situ* elephants maintain close family bonds, even though they live in an environment without the threat of predators, limitations of recourses, or losing their herds. This is a positive finding for the species-specific social behavior and development of African elephants in zoo environments.

3.2 Chapter II:

Running Head: Greeting Ceremony in *Loxodonta africana*

Title: Monitoring Behaviour in African Elephants during Introduction into a New Group: Differences between Related and Unrelated Animals

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animals

MDPI

Article

Monitoring Behaviour in African Elephants during Introduction into a New Group: Differences between Related and Unrelated Animals

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Simple Summary: African elephants are highly social animals that perform a so-called *Greeting Ceremony* in the wild when meeting elephants they are familiar with but have not seen for a certain timespan. Until now, it has not been known whether zoo elephants also show this unique behaviour. Therefore, this study was designed around the reunifications of two mother–daughter pairs that had been separated for 2 and 12 years, and two unifications of unrelated elephants, as a comparison. First contact was conducted in a protected setting, i.e., there was a fence between the animals to prevent possible fighting. Signs of the *Greeting Ceremony* shown by the elephants, the distance they kept to the separating fence, and the time until the elephants' trunks touched for the first time were observed. The results demonstrate that the related elephants showed all behavioural characteristic of the *Greeting Ceremony*, kept close to the fence, and touched trunks after only a few seconds, while elephants that were not familiar with each other did not show a full *Greeting Ceremony*, stayed further from the fence, and touched trunks for the first time only after several minutes upon meeting. This study testifies that zoo elephants show the same typical social behaviour known from wild elephants (namely the *Greeting Ceremony*) and, therefore, behave species-specific. It also confirms the strong family bonds of elephants and the cognitive abilities of elephants, specifically their long-term social memory.

Abstract: The introduction of elephants into new groups is necessary for breeding programmes. However, behavioural studies on the reactions of these animals at first encounters are missing. In the present study, female African elephants *(Loxodonta africana)* living in zoos were observed during unifications with unfamiliar elephants (introduction of two to one females and one to two females; n = 6) and reunifications with related elephants (two mother–daughter-pairs; n =

4) that were separated for 2 and 12 years, respectively. First encounters of the elephants were observed and recorded by scan sampling. The parameters measured were (a) signs of the characteristic *Greeting Ceremony*, (b) distance to the fence separating the elephants during first contact, and (c) time until trunks touched for the first time. The data were statistically analysed with SPSS. The results showed that related elephants performed a full *Greeting Ceremony* on reunifications. Unrelated elephants only expressed a minor greeting. During first encounters, related elephants predominantly showed affiliative behaviour (p = 0.001), whilst unrelated elephants expressed more agonistic behaviour (p = 0.001). The distance to the fence was significantly smaller for related elephants than for unrelated elephants (p = 0.038). first contact of trunks occurred on average after 3.00 s. in related elephants and 1026.25 s. in unrelated elephants. These findings indicate that related elephants recognise their kin after up to 12 years of separation, meet them with a full *Greeting Ceremony* during reunification, and seek contact to the related elephant, while unrelated elephants are hesitant during unifications with unfamiliar elephants and express more agonistic behaviour. The results testify that zoo elephants show the same species-specific social behaviour as their conspecifics in the wild. It also confirms the cognitive abilities of elephants and the significance of matrilines for breeding programmes.

Keywords: African elephant; zoo elephants; unification; reunification; communication; behaviour; greeting ceremony

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1. Introduction

1.1. Elephant Communication

1.1.1. Greeting Ceremony

Known to be highly sensitive mammals with a complex social structure and extraordinarily developed ways of communication, elephants and their behaviour have been a frequent topic of research [1–7]. However, it is mainly olfactory [8–12] and auditory [4,13–19] communication that has been investigated [7]. While sexual and breeding behaviour and communication are well-represented [20–26], the so-called *Greeting Ceremony* [7] with its enormous olfactory, visual, tactile, and acoustic aspects is investigated poorly for *ex situ* living African elephants, so far.

While elephants usually greet other elephants by flapping their ears, lifting the head, and sometimes touching the head of the other individual with their trunk (referred to as *Little Greeting*) [27], the *Greeting Ceremony* is much more complex and usually restricted to interactions between closely related elephants [7]. The ethogram in Table 1 shows the behavioural items that form the *Greeting Ceremony* [7,18,28–31].

Table 1. Behaviour expressed during a *Greeting Ceremony*.

Item	Behaviour
Running towards elephant	Elephants run towards the elephant they intend to greet.
Clicking tusks and entwining trunks together	Elephants click tusks and entwine their trunks by winding them around each other.
Touching trunk	Elephants touch the trunk of the other elephant with their trunk.
Folding, lifting, spreading, and flapping ears	Elephant's ears are in motion by folding them back, lifting them, enfolding them, and flapping them rapidly.
Raising head	Elephants raise their heads as high as possible above their shoulders.
Opening mouth	Elephants open their mouth widely.
Touching head	Elephants touch the head of the other elephant at eyes, mouth, and temporal glands with their trunk.
Spinning round	Elephants rapidly turn around repeatedly, also changing direction.
Lifting tail	Elephants lift their tail to stick it out.
Acoustic signals	Elephants emit loud vocalisation as oral rumbles, roars, and trumpets.
Defecating and urinating	Elephants drop faeces and micturate.
Glandular secretion	Elephants exude fluid from the temporal glands.

1.1.2. Affiliative and Agonistic Communication

Communication expressed by behaviours during greetings can be further classified as affiliative, agonistic, and neutral [7,18,28–31]. The neutral behavioural *eating/drinking* is listed under (re)unification, as it is used as an indicator for stress in the animals. Since stress induces a rise in cortisol, it operates anorexiant [32–37]. Thus, only animals that are more relaxed during (re)unification are expected to show this behaviour. Table 2 lists all behaviours included in this study.

Table 2. Affiliative, agonistic, and neutral behaviours of greetings.

Affiliative	
Running towards fence/animal	Elephants run towards the elephant they intend to greet or the fence separating them from the elephant.
Pushing against the fence	Elephants press their head or body against the fence to touch the other elephant/
Touching trunks	Elephants touch the trunk of the other elephant with their trunk.
Affiliative agitation	Elephants raise their head, shake the tail, click their tusks, and flap with their ears.
Acoustic signals	Elephants emit rumbles (low-frequent calls).
Defecating/urinating	Elephants drop faeces and micturate.
Agonistic	
Agonistic agitation	Elephants shake the head, stick out the tail, role in their trunk, and fold their ears close to their head.
Acoustic signal	Elephants emit roars (high-frequent calls).
Pacing backwards	Elephants quickly diverge from fence/other elephants.
Showing servility	Elephants bow their head, lower their shoulders, furl the trunk, and jam their tail between their hind legs.

Showing dominance	Elephants stand tall, with raised heads and spread ears; they lift their trunk over their heads; they place the trunk on the other elephants' head; and they run towards other elephants with sudden speed.
Neutral	
Eating/ drinking	Elephants eat and/or drink.

1.2. Elephant Transfers

1.2.1. Unifications

The management of the African elephant population in European zoos has to maintain a defined birth rate to ensure the viability of the population and its biodiversity [38–45]. Thus, elephant transfers to bring animals in potential breeding situations are common. This applies mostly for males, but when space becomes limited, sometimes females need to be transferred as well [44,45]. Hence, elephants have to be acquainted with new housing conditions; new surroundings; and most importantly, new herd members. Those unifications of unrelated elephants are very difficult situations when handling elephants [38,44]. Maintaining such a situation with the right caution is essential for the successful joining of different elephant groups. Knowing how elephants behave on such occasions is highly beneficial to prevent possible aggressive behaviour or a failure in merging the two groups.

1.2.2. Reunifications

Nowadays, European zoos seek to keep elephants in herd structures similar to the way elephants live in the wild [38,40,45], with cows living with their female offspring in multigenerational herds [37,38]. In the past, however, occasional separation of mothers and daughters took place in European zoos [42]. Given the information from the wild, a reunification of related individuals might provide different results in comparison with unification of unrelated animals, with possibly different behaviour in the elephants involved. Scientific understanding of the underlying factors during (re)unification are important for the preservation of the species-specific social structure and the well-being of African elephants in modern zoos.

1.3. Aims of the Study

The so-called *Greeting Ceremony* is an indicator for elephants' recognition of and a friendly attitude towards each other [7,31]. Whilst frequently described for wild-ranging elephants [28,29], to the best of our knowledge, there is no empirical data on the *Greeting Ceremony* for zoo-living elephants. This study aims to investigate the behaviour of related and unrelated African elephants at first encounters during (re)unification and the possible expressing of the characteristic *Greeting Ceremony* in a zoo environment. Confirming that zoo-socialised elephants express the same social behaviour and make use of the same ways of communication as *in situ* living individuals is of particular importance, as the zoos and studbooks aim to ensure a species-specific development of the zoo-bred African elephants [38–45].

It can be expected that elephants that were separated for a certain timespan will make use of the *Greeting Ceremony* on reunification, while unfamiliar elephants will not show signs of a *Greeting Ceremony* when unified [7]. Hypothesising that related elephants will easily be adjoined and show intense emotional behaviour on reunification, it would give evidence of the long-term memory of this species. Recognition of a related animal after a longer period of separation, using the *Greeting Ceremony*, would attest to this particular ability in African elephants.

2. Material and Methods

2.1. Animals

In the framework of the European Endangered Breeding Programme (EEP) for the African elephant, recommendations were made to transfer a daughter (Panya) to her mother (Bibi) and a mother (Pori) back to her daughter (Tana). It was also recommended to transport two unrelated cows (Lilak and Kariba) to another place with another single elephant (Zimba) and one unrelated elephant (Drumbo) to two unrelated cows (Saly and Umbu).

Even though most of the elephants were born in the wild, they were transferred to European zoos at a young age and socialised under zoo conditions.

For more detail on the elephants, see Table 3.

Table 3. List of elephants.

Elephant	Sex	Origin	Date of Birth	Date of Transfer from Wild to the Zoo	Transferred from to	Related to (Only Elephants Included in the Study Are Listed)	(Re)united with
Panya	F	Zoo-born	2007-08-22	-	Bergzoo Halle to Serengeti Park Hodenhagen	Daughter of Bibi	Bibi
Bibi	F	Wild-born	1985	1987	-	Mother of Panya	Panya
Pori	F	Wild-born	1981	1983	Tierpark Berlin to Bergzoo Halle	Mother of Tana	Tana
Tana	F	Zoo-born	2001-05-04	-	-	Daughter of Pori	Pori
Lilak	F	Wild-born	1971	1973	Tierpark Berlin to Opel-Zoo Kronberg	-	Zimba
Kariba	F	Zoo-born	2006-03-17	-	Tierpark Berlin to Opel-Zoo Kronberg	-	Zimba
Zimba	F	Wild-born	1982	1984	-	-	Kariba and Lilak
Drumbo	F	Wild-born	1990	1992	Zoo Vienna Schönbrunn to Safaripark Dvur	-	Saly, Umbu
Saly	F	Wild-born	1982	1984	-	-	Drumbo
Umbu	F	Wild-born	1981	1983	-	-	Drumbo

All unifications and reunifications took place under the same (testing) conditions. The sample size for related elephants was $n = 4$, and the sample size for unrelated elephants was $n = 6$. The sample size for reunifications of the related and unrelated elephant groups waws $n = 2$.

During the unification of Zimba with Lilak and Kariba, Zimba was in her stable when Lilak and Kariba were released separately into the enclosure next to hers; therefore, two data sets are presented (Zimba&Lilak and Zimba&Kariba). During the unification of Drumbo with Umbu and Saly, Drumbo was in the stable and Umbu and Saly entered the enclosure next to hers together, resulting in one data set. During the reunifications, the daughters (Tana and Panya) were in their enclosures and their mothers (Pori and Bibi) entered the adjacent enclosure.

2.2. Ethological Data Collection

All behaviours of the elephants on first protected meeting through a fence were documented utilising the ethogram (Table 1) according to scan sampling by the same human observer [46–51], focusing on signs of behaviour characteristic for the *Greeting Ceremony* [7,18,28–31,52,53]. Acoustic signals (trumpets, rumbles, and roars) were noted and specified when heard. Additionally, the ethogram differentiated between signs of agitation related to excitement (affiliative connotation) and signs of agitation related to fear (agonistic connotation) [7,27,45,46]. Procedures were observed while elephants were still separated through a fence, though in tactile, visual, auditory, and olfactory contact, as first meetings during the introduction of new herd members were performed with a barrier for safety reasons. Even though observation times ranged between 35 to 78 min, most behaviours occurred in the first 30 min. Therefore, only the first 30 min were used for analyses.

The distance that the elephants kept to the fence throughout the (re)unification was measured in meters to assess their willingness to touch the other individual [47]. The distance was based on direct contact (meaning tactile contact to the fence or animal) or distance of <1 m, 1–2 m, 3–4 m, and >4 m. The elephants' distance to the fence was recorded every 10 s during the (re)unification.

For all elephants, the first moment of tactile contact during (re)unification was determined and is referred to as *first contact of trunks* throughout this paper. This indicator was used to describe the willingness of the elephants to reach for and touch the other elephant and for their curiosity [47].

The sets of data for behaviour and distance to the fence were classified numerically [54,55]. Statistical analysis for all data was performed using SPSS 27, and whether there were significances in the differences in the data sets between elephants on reunifications and unifications was calculated. Utilising the Kolmogorov–Smirnov test, it was determined whether the data distribution was normal, followed by intercorrelation calculations (Spearman's ρ) of the subscales [56,57]. As the data of both the behaviour analysis and the distance analysis showed no even distribution of significance ($p \leq 0.05$) [58,59], the data sets were not normal in distribution and the Mann–Whitney *U* Test was used to determine the significant differences ($p \leq 0.05$) [55–58] between (re)unifications.

For the analysis of the signs shown in the *Greeting Ceremony*, a Chi-Square Test was performed and the Fisher's Exact Test was used to detect the significance, as the data sets partially had less than size items and the effect size was calculated utilising the Monte Carlo Simulation (x^2) [60,61].

The distribution for the data set of affiliative and agonistic behaviours was normal, and a t-test and the Levene's Test for Equality of Variances was calculated to determine the significance in the differences between related and unrelated elephants during (re)unifications [51,62–64].

As the data for the measurement of first trunk contact during (re)unifications were distributed evenly according to the Kolmogorov–

Smirnov test, an unpaired t-test and the Levene's Test for Equality of Variances were calculated to show the significant differences between the two sample groups [51,62–65].

The distribution differed between both groups for the shown distinct behaviours during the (re)unifications, (Kolmogorov–Smirnov $p < 0.05$); therefore, the Mann–Whitney U Test was used to determine if there were significant differences in greeting behaviour [61–64].

The distribution between both groups for the data set *distance to fence* differed (Kolmogorov–Smirnov $p < 0.05$); thus, the Mann–Whitney U Test was calculated again, to determine if there were differences in the distance that the elephants kept from the fence between related and unrelated elephants [55–58].

The effect size was calculated with Pearson's correlation coefficient: $r = \frac{z}{\sqrt{n}}$ [57,59]. For all tests, the significance level was set at $p \leq 0.05$ [65].

3. Results

3.1. Signs of Greeting Ceremony and General Behaviour during (Re)Unifications

Based on the behavioural components of the *Greeting Ceremony*, listed in Table 1, a first analysis was performed to determine if elephants expressed the typical signs of the *Greeting Ceremony* during (re)unifications. Table 4 summarises the results and shows that all elephants that were reunited showed every behavioural item of the *Greeting Ceremony.* The behavioural items of the *Greeting Ceremony* that were also shown by all of the elephants on unifications were *raising head* and that with minor exceptions of one to two elephants were *touching trunk*, *lifting tail*, and *glandular secretion*. Only one elephant on unification emitted acoustic signals and the behavioural items *running towards elephant*, *clicking tusks, entwine trunks together*, *opening mouth*, *touching head*, *spinning around*, and *defecating/urinating* were not shown by elephants on unifications.

The statistical analysis of the data shows a significant difference for the behavioural items running towards each other, clicking of tusks, entwining trunks together, opening mouth, touching head, spinning round, acoustic signals, and defecating and urinating. There was no significant difference for the items touching trunk, folding, lifting, spreading, flapping ears, raising head (is a constant), lifting tail, and glandular secretion.

Table 4. Differences in expressed behaviour during (re)unifications.

	Unrelated						**Related**				**Exact Sig. (2-sided) (Fisher's Exact Test)**	**Effect Size (Monte Carlo Simulation)**
Behaviour	Saly	Umbu	Drumbo	Zimba	Kariba	Lilak	Bibi	Panya	Tana	Pori	p	X^2
Running towards elephant	-	-	-	-	-	-	+	+	+	+	0.003	11.00
Clicking tusks, entwine trunks together	-	-	-	-	-	-	+	+	+	+	0.003	11.00
Touching trunk	-	+	+	+	+	+	+	+	+	+	1.0	0.629
Folding, lifting, spreading, flapping ears	+	-	+	+	+	+	+	+	+	+	1.0	0.629

Raising head	+	+	+	+	+	+	+	+	+	+	-	-
Opening mouth	-	-	-	-	-	-	+	+	+	+	0.003	11.00
Touching head	-	-	-	-	-	-	+	+	+	+	0.003	11.00
Spinning round	-	-	-	-	-	-	+	+	+	+	0.003	11.00
Lifting tail	+	-	+	+	+	+	+	+	+	+	1.0	0.629
Acoustic signals	-	-	-	-	+	-	+	+	+	+	0.015	7.543
Defecating and urinating	-	-	-	-	-	-	+	+	+	+	0.003	11.00
Glandular secretion	-	-	+	+	+	+	+	+	+	+	0.491	1.397

The results for affiliative and agonistic behaviours based on the ethogram in Table 2 show that elephants on reunification showed ~79.52% of the affiliative and ~19.65% of the agonistic behaviours while ~0.82% was neutral behaviour, and that unrelated elephants showed ~12.5% of the affiliative, ~85.08% of the agonistic, and ~2.41% of the neutral behaviours during unification (Figure 1).

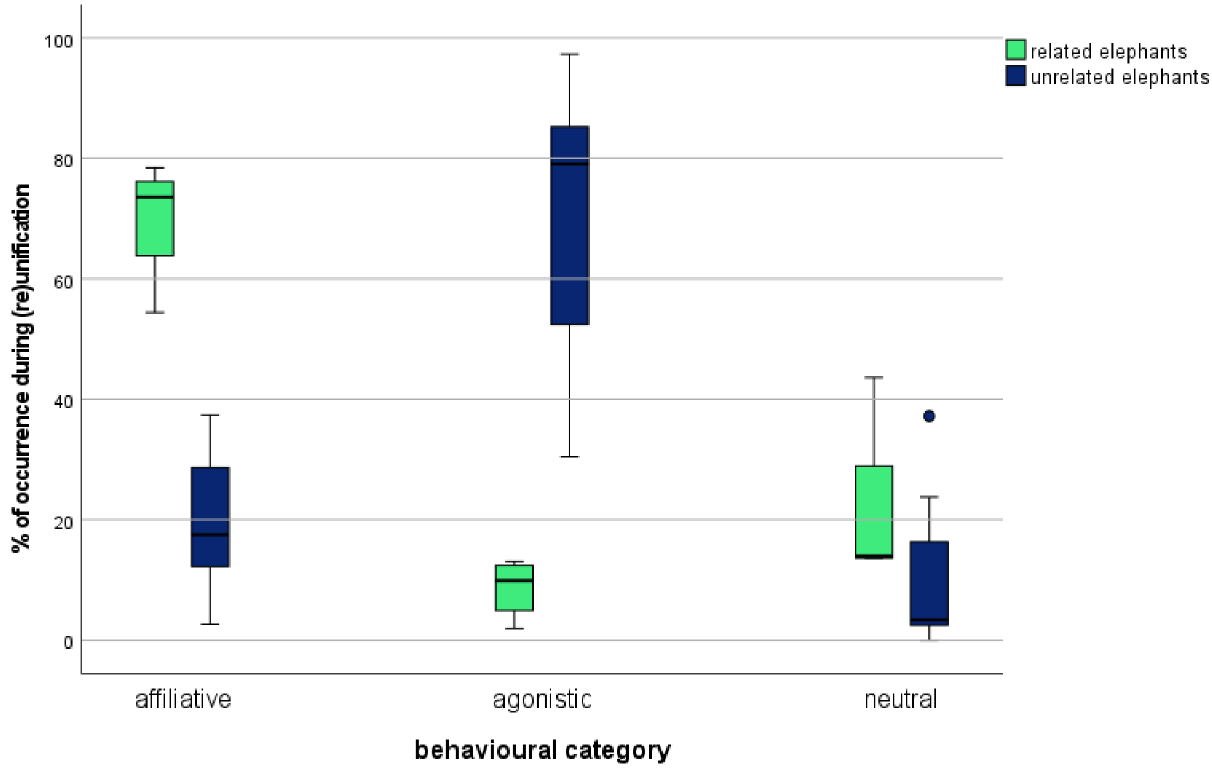

Figure 1. Percentage of affiliative and agonistic behaviours of the total behaviour shown by related and unrelated elephants during (re)unifications.

Levene's Test shows no statistical significance for the category *affiliative behaviour* (0.568); therefore, equal variance is given. The t-test shows that the mean time of affiliative behaviour was more than 50% higher for related elephants (95%-CI[33.30641, 66.87859]) than for unrelated elephants. There was a statistically significant difference between the time that the two groups expressed *affiliative behaviour*: $t(9) = 6.751$, $p = 0.001$, $d = 4.231$. For the category *agonistic behaviour,* the variance is unequal. The *t*-test shows that the mean time of *agonistic behaviour* was more than 60% lower for related elephants (95%-CI[−82.62850, −37.75650]). There was a statistically significant difference of $t(9) = -6.370$, $p = 0.001$, $d = -3.026$ (Table 5).

Table 5. Significances for affiliative and agonistic behaviours for related and unrelated elephants on behaviour during (re)unifications.

		Levene's Test for Equality of Variances	t-Test for Equality of Means							Effect Size
		Sig.	t	df	Sig. (2-tailed) *p*	Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference		*d*
								Lower	Upper	
affiliative	Equal variances assumed	0.568	6.751	9	0.000	50.09250	7.42039	33.30641	66.87859	4.231
	Equal variances not assumed		7.066	7.271	0.000	50.09250	7.08876	33.45589	66.72911	
agonistic	Equal variances assumed	0.010	−4.827	9	0.001	-60.19250	12.46980	−88.40116	−31.98384	−3.026
	Equal variances not assumed		−6.370	6.862	0.000	-60.19250	9.44953	−82.62850	−37.75650	

3.2. Distance to Fence during (Re)Unification

The percentage of time that the elephants spent at a certain distance to the fence at first encounter with the (un)related elephant/s is presented in Figure 2. Elephants reuniting spend ~28.31% of time in direct contact, while elephants uniting for the first time spend ~10.23% of time in direct contact. For the category *<1* m, the percentages were ~23.19% (related elephants) and ~7.93% (unrelated elephants); for *1–2* m, they were ~30.12% (related) and ~15.17% (unrelated); for *3–4* m, they were ~13.05% (related) and ~33.18% (unrelated); and for *>4* m, they were ~5.32% (related) and ~33.49% (unrelated).

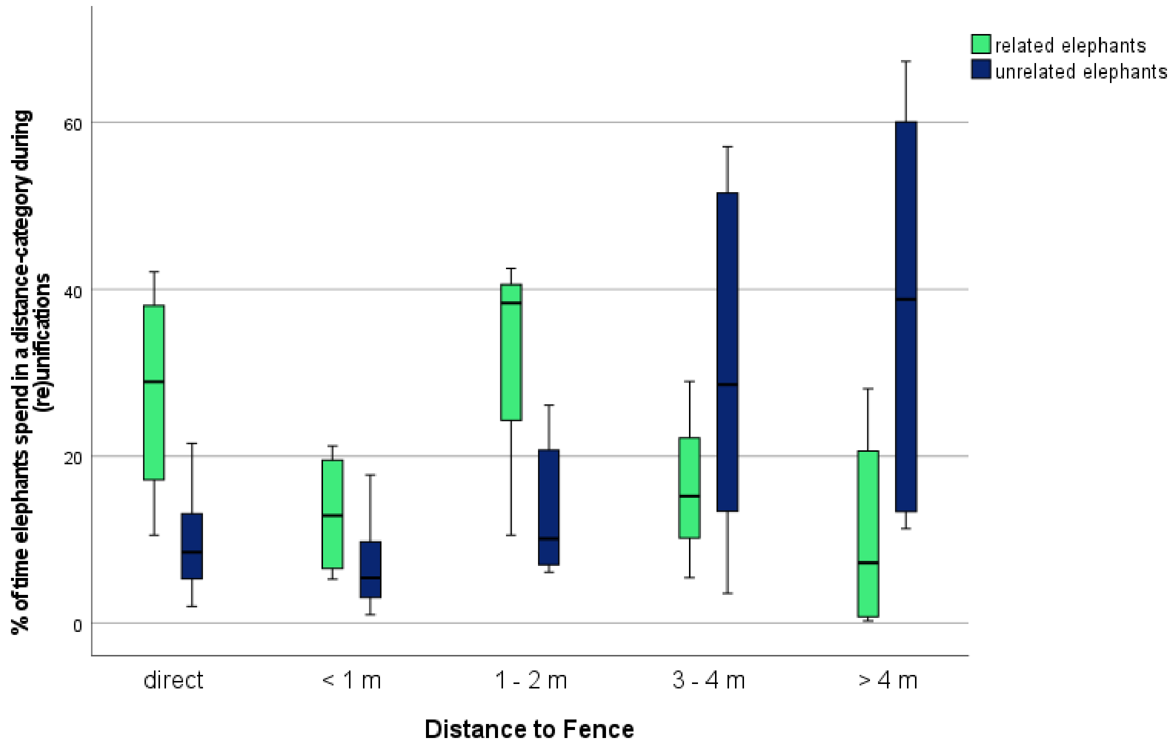

Figure 2. Percentage of time that related and unrelated elephants stood at a certain distance to the fence during (re)unification.

There was a statistically significant difference in the distance to the fence in the categories *direct* and *1–2 m* but not in the categories *<1 m*, *3–4 m*, and *>4 m* (Table 6).

Table 6. Significances for distance to the fence between related and unrelated elephants during (re)unification.

	a				
	direct	**<1 m**	**1–2 m**	**3–4 m**	**>4 m**
Mann–Whitney U	3.000	6.000	3.000	10.000	5.000
Z	−2.079	−1.512	−2.079	−0.756	−1.701
Asymp. Sig. (2-tailed) *p*	0.038	0.131	0.038	0.450	0.089
Pearson's correlation coefficient *r*	−0.627	−0.456	−0.627	−0.228	−0.513
a. Group variable: related, 1; unrelated, 2					

3.3. First Contact of Trunks

The time until first contact of trunks is shown in Table 7. Related elephants demonstrated instant contact of trunks, whilst the time until trunk contact in unrelated elephants ranged from ~100 s to more than 900 s. The elephants Umbu and Drumbo did not touch trunks during unification. Therefore, a value is not shown for this pair.

Table 7. Seconds until first contact of trunks during (re)unifications for the different pairs that were (re)united.

Setting	**Elephant Pair**	**Time Until Contact (s)**	**Average**
Unification	Saly and Drumbo	107	450
	Umbu and Drumbo	not displayed	
	Zimba and Lilak	936	
	Zimba and Kariba	362	
Reunification	Bibi and Panya	2	3
	Pori and Tana	4	

Table 8 shows the statistical differences between the two test groups for first contact of trunks. The Levene's Test yields no statistical significance (0.165); therefore, equal variances are given. The t-test shows that the mean time until first contact of trunks was −1023.25 s (95%-CI[−3456.35, 1409.85]) lower for the related elephants than for the unrelated elephants. The difference between time until first contact of trunks for related and unrelated elephants during (re)unifications was statistically significant, $t(10) = -2.453$, $p = 0.034$.

Table 8. Significances for related and unrelated elephants on first contact of trunks during unification.

		Levene's Test for Equality of Variances	***t*-Test for Equality of Means**						
		Sig.	**t**	**df**	**Sig. (2-tailed) *p***	**Mean Difference**	**Std. Error Difference**	**95% Confidence Interval of the Difference**	
								Lower	**Upper**
First Contact of Trunks	Equal variances assumed	0.002	−2.453	10	0.034	−723.250	294.809	−1380.126	−66.374

4. Discussion

4.1. Signs of Greeting Ceremony and General Behaviour during (Re)Unifications

Free-ranging elephants live in a complex fission–fusion society, and separations and unifications are common events [28,47]. Zoo elephants, in contrast, live in stable groups, and re-unifications of related animals are very rare. We used the opportunity to monitor the exceptional situations of the reunification of two mother–daughter pairs and compared them to the unifications of six unrelated females. The results presented here are the first to describe and analyse the occurrence of behaviours displayed in both situations at first encounters in zoo elephants. We found differences in the *Greeting Ceremony* expressed for elephants united and reunited. While all elephants on reunification expressed all behavioural items described for the *Greeting Ceremony* [7,18,28–31], elephants on unifications only showed some of those behavioural items and, therefore, not a full *Greeting Ceremony* [27]. This testifies that, even in a zoo environment, the whole ceremony is only displayed if elephants know each other. This study also attests that related elephants living *ex situ* express the same characteristic *Greeting Ceremony*, as African elephants living *in situ*. This provides signs for their species-specific evolvement and preservation of species-specific behaviour. As shown in Table 3, elephants of the study were either zoo-born or transferred to zoos at an early age of just two years. This implies that they were still too young to learn all of the behaviour of the *Greeting Ceremony* in the wild and that the shown behaviour must be genetically determined in the species. The study also confirms that African elephants living in zoos recognise family members after up to 12 years of separation [7]. This provides further evidence for the long-term memory reported also for free-ranging animals [66]. The study reveals that *ex situ* living elephants generally showed certain greeting behaviours, even when they were unrelated, and therefore certifies the highly social behaviour in African elephants living in zoos, which is also known for the species *in situ* [7,67–71]. The study also investigated the affiliative and agonistic behaviours shown by the elephants during (re)unifications. The results clearly prove that there is a statistically significant difference for the categories *affiliative behaviour* and *agonistic behaviour*, with related elephants expressing ~50.00% more affiliative and ~60% less agonistic behaviour during reunifications than unrelated elephants. Elephants encountered familiar animals friendly and forward going (~79.52% affiliative behaviour), while elephants on unifications were hesitant and showed predominantly agonistic behaviour (~85.08%) (see Figure 1). This confirms the significance of family bonds and the general understanding of the intense social relationships of elephants [7,45,67–71] and their hesitation when confronted with unfamiliar individuals, which is also known from the wild [7,47]. Elephants living *in situ* rely on family members when raising calves, protecting the herd, and searching for food and water [1–3,5,47]. The results of the study indicate that behaviour that is connected to a close family bond, such as the *Greeting Ceremony*, is generically anchored in elephants and preserved in zoo-socialised elephants. It was also observed that elephants on reunifications spend more time on the *neutral* behaviour *eating/drinking* than elephants on unifications. It can be assumed that elephants on reunifications were relaxed enough to spend time eating and drinking, as the situation did not cause them an exceedingly high amount of stress [32–37], whereas elephants being united with unfamiliar elephants did not calm down enough to eat and drink, a behaviour they display typically most of the time [32–37].

4.2. Distance to Fence during (Re)Unification

The analysis of the distance that the elephants kept from the fence (and therefore to the closest point of contact they could reach during (re)unification) shows that elephants being reunited lingered closer to the fence than elephants that were united. Related elephants spent most of the time during reunification at a distance under two meters from the fence, while unrelated elephants stood most of the time at a distance of three meters or more, maintaining a wider distance (see Figure 2). This shows that elephants on unifications were reluctant to approach during the unifications and did not want to get close to the unfamiliar elephant. Unknown individuals can always be a threat and elephants avoid living with individuals they are not related to [47]. Their reluctance to meet unknown elephants must therefore be considered species-specific. Equally, approaching familiar and related elephants on an encounter and especially during the *Greeting Ceremony* is species-specific for African elephants [7,18,27–31]. These data give further evidence for species-specific behaviour present in *ex situ* living African elephants and the preservation of strong family bonds. Even after several years of separation, they seek close contact with their relatives.

4.3. First Contact of Trunks

The results of the time until first contact of trunks during (re)unifications also show a major difference between related and unrelated elephants (see Table 7). The time until first contact of trunks for related elephants is only 3 s on average; for unrelated elephants, in contrast, it is 1026,25 s, being on average 342 times higher. Of the four pairs that were observed during unification, one group did not touch trunks at all during the entire first encounter. However, the range for the time until first contact of trunks during unifications is wide in unrelated elephants. Some elephants seemed to be less hesitant to touch the unfamiliar elephants than others (Saly and Drumbo, 107 s; Zimba and Lilak, 336 s). An individual distinctive disposition can be assumed, which might originate from some elephants being more curious than others, having a different social status, being of different age (and therefore less or more experienced), or having made certain previous experiences. Generally, unrelated elephants are described to be reluctant to touch the unfamiliar elephant on first encounter, while related elephants immediately seek contact with the familiar individual [1,7,47]. This observation additionally attests to the strong bonds between mother–daughter groups, which this study also found in African elephants in zoos even after a long period of separation from each other. It also confirms that related elephants on reunifications immediately approach, reach out for, and seek tactile contact with the other animal. As the olfactory and auditory senses in elephants are highly developed [9,18], these results indicate that the individuals recognised the other animal before the moment of first direct contact and wanted to engage in tactile contact with the other individual as soon as possible. Unrelated elephants, on the other hand, are aware that they are not familiar with the other individual and therefore hesitate to engage in tactile contact.

5. Conclusions

Even though the number of animals in the present study is small, the data presented here give further evidence of the strong bonds between mother–daughter groups. They also testify that elephants recognise each other after long-term separation by showing a full *Greeting Ceremony*, even after living apart for up to 12 years and therefore feature a species-specific behaviour even under zoo conditions, comparable with that shown in the wild. This provides evidence of recognition of their kin for the exceptional memory of this species. Keeping mothers and daughters together to build up matrilines can be considered as an important goal in the care of elephants living in European zoos [43–50,74–75].

The strong reactions expressed by mother and daughter elephants during reunifications and the empirical data of this study, demonstrating their urge to seek contact with the related animal, testify that zoo elephants, whether wild-caught or zoo-born, still belong to those species-specific mother–daughter groups. This verifies the hypothesis that elephant cows and their female offspring are better held together and that separations should be avoided in the future, where possible, to facilitate better living conditions for the animals.

Even though unifications of unrelated female elephants are a part of the European breeding programme for African elephants, elephant transfers are not frequent events and behavioural data were missing so far. Additionally, chances to observe reunifications of family members are extremely rare. Therefore, caution must be taken when interpreting ethological data, as sample size and statistical power are limited in this study [72,73]. Our preliminary findings support the need for further research.

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Institutional Review Board Statement: Animal welfare was not affected by the collection of data at any point of the study, as the elephants were not affected by the study's behavioural observations and transports were conducted according to the recommendations within the network of the European population management programme. The observations did not involve any direct contact with the animals or any changes in the zoo-given conditions during transport and (re)uniting. All handling of the animals during the observed process was conducted by the zoos with the greatest care and with a high focus on the animals' welfare.

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3.2.1 Conclusive summary study II

Study II investigated the species-specific behavior of the Greeting Ceremony and the social bonds of *Loxodonta africana* in zoos. African elephants in the wild are known to perform the so-called Greeting Ceremony when meeting an elephant with a close social bond [Moss & Colbeck, 2002; Poole & Granli, 2011]. This ceremony involves a specific row of behaviors, where elephants encounter each other, entwine their trunks, click their tusks, touch the other elephant's eyes, ears, mouth, and temporal glands, excrete fluids, and roar [Poole & Granli, 2011]. Unknown elephants, on the other hand, are met with caution in the wild [Poole & Granli, 2011].

The two related mother-daughter pairs of study I (n = 4) were reunited, succeeding the olfactory testing. The reunifications were ethologically monitored to investigate the elephants’ reactions. In comparison, the unifications of two groups of three elephants each (n = 6) that were unrelated and unfamiliar were observed. The (re)unifications were conducted with a separating fence between the elephants to ensure animal safety. However, visual, tactile, olfactory, and acoustic contact was possible. All (re)unifications were video-recorded.

Elephants’ behavior during (re)unification was measured in five parameters: The general behavioral reaction following an ethogram [Poole & Granli, 2011; 2021]; behavioral items that are part of the Greeting Ceremony [Poole & Granli, 2011]; excitement and fear shown by the elephants were recorded; the elephants’ distance to the separating fence/animal was measured; and the time until elephants had first tactile contact was documented. Statistical analysis was calculated with SPSS Version 27, using the Mann-Whitney-U-Test, the Chi-Square Test with the Fisher’s Exact Test, and a t-test with the Levene’s Test [Adery & Hope, 1968; Bortz & Döring, 2006; Dinneen & Blakesley, 1973; Fritz et al., 2012; Kubinger et al., 2009; Lakens, 2013; Mehta & Patel, 1983; Rasch et al., 2011; Ruxton, 2006; Siegel & Castellan, 1988].

Results show that related elephants expressed all behavioral items associated with the Greeting Ceremony during reunifications. Unrelated elephants only showed a few of those behaviors. Furthermore, related elephants showed significantly more affiliative behavior than unrelated elephants (p = 0.001), and unrelated elephants mostly expressed agonistic behavior (p = 0.001). Additionally, related females kept significantly smaller distances to the separating fence/animal than unrelated females (p = 0.038). Finally, related females had first contact with trunks after ~3.00 sec. In comparison, unrelated females showed first contact after ~1026.25 sec., and one pair of unrelated females did not touch at all during the first encounter (p = 0.034).

These findings testify that elephants under human care also display the species-specific social behavior of the Greeting Ceremony. As the related females of this study were all socialized in a zoo environment, they could not learn this social behavior from conspecifics in the wild. This suggests that this social habit is inherited.

The apparent display of affiliation and affection during reunifications after a long separation also accounts for the intense social bonds in African elephants, which is, therefore, also given in zoo elephants. Additionally, the results show that elephants have a long-term social memory.

3.3 Chapter III:

Running Head: Holding systems for *Loxodonta africana* calves under human care

Title: Behavior and social bonds of African elephant calves under different holding systems in European zoos

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Contribution: My contribution to this manuscript was 95 % and included idea, conceptualization, methodology, investigation, data analysis, visualization, funding acquisition, project administration, writing original draft, and writing review and editing.

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Article

Behavior and social bonds of African elephant calves under different holding systems in European zoos

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Abstract: The keeping conditions of elephants in zoos have been discussed for many years. The European studbooks for African and Asian elephants require the best husbandry conditions and the participating institutions constantly aim to improve those. To achieve this, housing, feeding, social constellation of the groups, and amount of human intervention with the elephants changed over the years. However, the decisions for adjustments of the husbandry conditions require empirical data to validate the benefits of such actions. This study evaluates possible differences in the social and general behavior of African elephant calves depending on the three management systems: *free contact*, *protected contact*, and *no contact*. The investigation included nine calves in four European zoos. For each calf, the interaction with the mother and other herd members was investigated and the social and general behavior was described, utilizing the next-neighbor method and an ongoing behavioral record applying an ethogram. Statistical analysis of the data was performed with a Kruskal-Wallis analysis. Results revealed no significant differences in the interaction of the calves with their mothers and the other herd members or the social and general behavior of the calves between management systems. Interestingly, the management system does not affect the calves' behavior, and therefore changes between management systems will most likely not influence calves' social and general behavior. However, general differences in the spatial distancing of calves in zoos and calves living *in situ* were found. The calves in the present study kept wider distances (up to >5 m) at an age of six to 48 months, while *in situ* calves of the same age are known to stay within reaching distance to the closest staying herd member. Data testify that choice of holding system does not influence social behavior or distance of calves. However, findings give reason for further investigations on possible differences in the development of calf's social behavior *in situ* versus *ex situ*.

Keywords: *Loxodonta africana;* zoo elephants; management systems; husbandry conditions; welfare; behavior.

Research Highlights: No significant differences in social behavior of African elephant calves between the three management systems in zoos were detected. However, compared to data from the wild, calves in zoos tend to maintain higher distances to their mothers or closest staying neighbors of the herd.

Graphical Abstract:

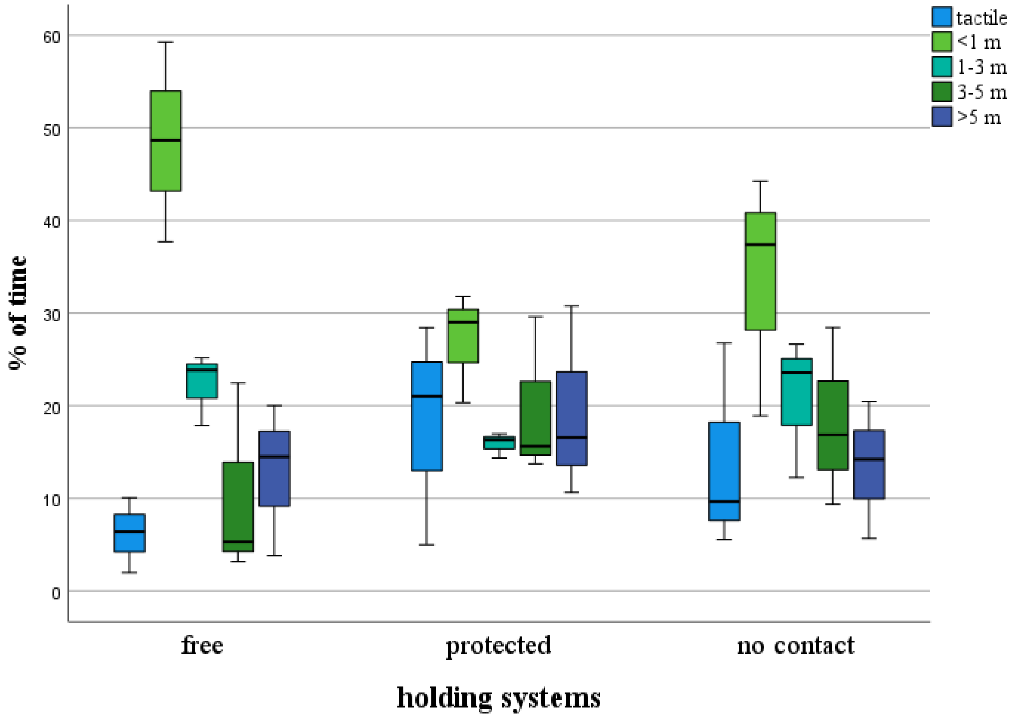

Figure I. Percentage of time calves spend in a distance category to mother, depending on management system. No significant differences between the three holding systems were detected. However, results alter from data known from the wild.

1. Introduction

1.1. Elephant Management Systems

There is a long history of keeping elephants in zoos and various management systems on how carers interact and treat elephants were applied over the last decades [Bechert et al., 2019; Clubb & Mason, 2002; Dale, 2010; Garaï & Kurt, 2006; Kowalski et al., 2010; Kurt, 1994; 2006; Meehan et al., 2016; Olson, 1994; Veasey, 2006; Williams et al., 2019]. Nowadays, there are three different management systems. The most frequent one is *protected contact*, less frequently *free contact*, and very rare, *no contact* [Bossy, 2019; EAZA, 2019; Meehan et al., 2016]. The three concepts differ in the way zookeepers take care of and interact with the elephants, also resulting in differences in the construction of the elephant enclosures [Olson, 2004; Proctor & Brown, 2015; Riddle & Christopher, 2011].

Free contact, also referred to as *hands-on*, is a management system in which zookeepers directly interact with the animals whilst entering the same space without barriers. The keeper acts as a dominant member of the social system of the elephants. There are no protective barriers between animals and humans during training and medical care. This gives the carers immediate access to the animals' different body parts, i.e. for medical treatment, ultrasound examination, or transport training [Bossy, 2019; Lundberg et al., 2001; Samson, 2000; Tanner, 2000]. Keepers lead the elephants in person and thereby direct them. However, as direct contact with these large animals has undeniable risks for the safety of the keepers, this management system requires intense training and perfect obedience by the elephants. Additionally, keepers are only allowed to enter the elephant enclosure carrying a so-called ankus, a stick with a metal spike at the top in most facilities, to defend themselves if beset or even attacked by an elephant. Additionally, keepers apply the ankus to lead the elephants and correct them during training. Albeit criticism of the ankus is widespread, as it is often regarded as an instrument that can potentially hurt the animals and cause stress for them. There is only a minority of zoos left that keep their elephants under *free contact* [Bossy, 2019; EAZA, 2019].

In 2019, the EAZA enacted that zoos have to stop keeping elephants in *free contact*. Several advantages of the two other management systems reasoned this decision. In the other management systems, elephants are free to move and react as they please and without human guidance. In addition, *free contact* is considered insecure for both, elephants and keepers and requires an excessive amount of strict training and obedience. Zoos that still handle their elephants in *free contact* are requested to switch to *protected contact* by 2030 [Bossy, 2019; EAZA; 2019].

For the management condition of *protected contact*, elephants are taken care of and trained through bars, a separating fence, or special training walls or cages. The main principle of *protected contact* is the voluntary work of the animals with the zookeepers during training sessions and medical care. Only operant conditioning is used to train the animals. Keepers are not allowed to enter the elephant enclosure at any time at the same time as the animals [Desmond & Laule, 1993; Harris et al., 2008; Laule & Whittaker, 2001]. This has the benefit that the risk for the keepers is reduced enormously. *Protected contact* is the most frequently used management system in European zoos.

The last of the three management systems is the *no contact* system. As the name already implies, there is no contact between zookeepers and elephants other than the provision of food and water and the cleaning of stables and enclosures. This also means that elephants are not being trained. Most zoos that practice this keeping condition let the elephants roam freely in their inside and outside enclosures and only open and close gates for feeding and cleaning purposes, to prevent that keepers and animals are in the same area [Laule & Whittaker, 2001]. In terms of human contact, this management system refers most closely to natural conditions. Nevertheless, due to disadvantages in the medical care of the animals and challenging logistics when animals have to be moved, this management system is the rarest of the three in Europe.

Elephants living in zoos are in general familiar with intense interaction with humans, while contact with humans *in situ* is much rarer and strongly differs. Additionally, the herd constellations in zoos may differ. Some breeding herds consist of unrelated females and their offspring and occasionally the offspring might only be related paternally. In both, *free* and *protected contact,* calves observe their mothers and the other herd members interacting with the keepers. They learn how their mothers react and adopt this behavior. In *protected contact,* calf training starts when they approach the fence and are willing to interact with the keepers. In *free contact,* on the other hand, calves must learn to respect humans as sensitive and vulnerable beings early in their lives. Later on, they will be trained in direct contact.

1.2. Development and Behavior of African Elephant Calves in situ

African elephants are known for their complex social structures and supportive social behavior and since many ethologists worked with elephants, the social behavior of African elephant calves is well understood [Douglas-Hamilton, 1972; Douglas-Hamilton & Douglas-Hamilton, 1989; Lee & Moss, 2011; Moss, 2001]. *In situ* African elephants live in matrilines and herd members display close (tactile) bonds with the calves [Lee & Moss, 2011]. This physical contact between mammals is important for their well-being, development, and future breeding success [Dunbar, 2010; Jablonski, 2021].

The physical and behavioral development of African elephant calves is classified by Lee & Moss [2011] into seven age stages: 0-6 months, 7-12 months (0.5 – 1 year), 13-24 months (1-2 years), 25-36 months (2-3 years), 37-48 months (3-4 years), 49-60 months (4-5 years), and 60-plus months (more than 5 years). At the age of four years, they are not referred to as calves anymore, but as youngsters. The upper age limit for a youngster is mostly set to 9 years, as most animals gain sexual maturity *in situ* around that age. Gender-specific differences in social behavior exist; however, these are not expressed significantly before the age of 4 years [Andrews et al., 2005; Archie et al., 2006; 2011; Lee & Moss, 2011].

The seven age stages are associated with several behavioral steps of the calves. They learn how to use their trunks within the first 12 months of their lives. They tend to expand their physical distance from their mothers within the first four years of their life. They display a peak in their playing behavior from the age of three to four years. Calves shift from milk to solid food as their main source of food around the age of six to nine months. They approach agonistic behavioral patterns at the age of four, and finally get mature at the age of six to nine, also practicing mating behavior [Andrews et al., 2005; Archie et al., 2006; 2011; Lee & Moss, 2011].

Calf survival strongly depends on its mother's care. If a mother dies while the calf is under 24 months old, its chance to survive is almost non-existent *in situ* [Archie et al., 2006; 2011; Lee & Moss, 2011; Moss & Colbeck, 2002]. Thus, the mothers are central individuals and calves are in frequent contact with them – visually, tactile, olfactory, and acoustically. During the first six months, calves spend approximately 56 % of their time in contact distance [Charif et al., 2005; Lee & Moss, 2011]. This reduces when calves become older, however, it is not until they are well over two years old that they start to strive at a distance of more than 5 meters away from their mothers [Charif et al., 2005; Lee & Moss, 2011]. During the first years of life, close contact between the calf and the mother is maintained by both sides. This shifts after two years, when the contact becomes less intense and is maintained more by the mothers. At this age, gender-specific differences such as different playing behavior arise as well [Charif et al., 2005; Lee & Moss 2011; 1986].

The close social bonds between elephants are also evident in the social distance of calves from other herd members. During the first two years, calves spend about 20 % of their time within contact distance from the next non-mother elephant, and only 10 % of the time at a distance of more than five meters from any other individual [Lee & Moss, 2011].

1.3. Aims of the Study

The three management systems, *free, protected,* and *no contact* are mostly discussed and compared in terms of human and animal safety [Bechert et al., 2019; Clubb & Mason, 2002; EAZA, 2019]. There are no studies on whether the different concepts have any impact on the social behavior of elephants as an indicator of welfare. From an ethological perspective, it seems vital to consider behavioral parameters to evaluate the influence of management systems on elephants. It is known that different keeping conditions affect mammal behavior [Bassett & Buchanan-Smith, 2007].

Elephants are highly intelligent, display unique senses, developed complex (social) behavior, and react very sensitively to their environment [Douglas-Hamilton, 1972; Douglas-Hamilton & Douglas-Hamilton, 1989; Estes, 1991; Moss, 2001; Pinter-Wollman et al., 2009; Schulte, 2000]. Naturally, this applies also to keeping conditions in zoos. While human-elephant contact is almost non-existent in the wild, a certain kind of relationship between keepers and elephants in zoos cannot be avoided. Therefore, it seems relevant to hypothesize, that different management systems and human-elephant contact, in general, may have an impact on behavior.

In this study, the three management systems for elephants in European zoos are compared in terms of their influence on social and general behavior as well as distance keeping in African elephant calves. Additionally, the elephants' behavior is also investigated under the parameter of space that is provided to the animals in the different facilities. Possible differences are evaluated and thereby assessed for their welfare in terms of species-specific behavior in zoo elephants.

2. Material and Methods

2.1. Animals

To compare the social behavior and development of African elephant calves in the three management systems, three elephant calves for each system were observed, resulting in a sample size of nine calves (n = 9). Calves were selected to represent a homogenous distribution in terms of age, sex, and number of playmates (calves of age suitable for playing). The age limit was drawn at four years because from this age on, gender-related behavioral differences become significant [Lee & Moss, 2011].

As the size of the elephant enclosures differs depending on the three management systems, behavioral data can also be applied to ethological differences in terms of the size of the enclosure.

Full information on the elephant calves of this study is shown in Table 1. Information is valid for the time of data collection.

Table 1. List of elephant calves.

Elephant	Sex	Management system	Size of enclosure in m^2	m^2 / elephant	Date of Birth	Age at data collection*	Number of playmates
Tu	F	Free contact	4,161	520.125	16-03-2016	47-48 month	2
Gu	M	Free contact	4,161	520.125	20-04-2019	11-12 month	1
Ts	M	Free contact	4,161	520.125	06-03-2020	6 month	2

Ch	F	Protected contact	1,442	240.33	14-04-2017	48 month	2
El	F	Protected contact	2,957	985.66	20-09-2019	11 month	1
Ku	M	Protected contact	1,442	240.33	05-04-2021	6 month	2
To	M	No contact	24,000	1,263.16	29-08-2018	47 month	2
Ma	F	No contact	24,000	1,263.16	22-02-2020	18 month	2
Ne	M	No contact	24,000	1,263.16	08-01-2021	7 month	1

*differences in age between the three sample groups were not significant: Kruskal Wallis analysis (p = .368)

2.2. Ethological Data Collection

Observations for this study were performed between 2020 and 2021. The observation time for each calf was a total of 15 hours, resulting in an observation time of 45 hours for each holding system. Data were only collected when keepers were not in the enclosure and not in contact with the elephants when elephants could wander of their free will within their entire enclosure. Observations were performed during the working hours of the keepers, spread over the day, covering all daytimes of the working hours of the keepers. The 15 hours of observation for each calf were spread over two weeks, observing approximately 1,5 hours a day. All observations took place during late summer and early fall.

For an ethological analysis of calf behavior, four categories were measured. Firstly, the calves' distance to their mothers was surveyed to investigate the calf-mother relation [Kappeler, 2020; Krull, 2000; Martin & Bateson, 2007; Naguib & Krause, 2020; Randler, 2018]. The distance was divided into five parameters: *tactile contact*, *<1 m*, *1-3 m*, *3-5 m*, and *>5 m* [Lee & Moss, 2011]. Data were recorded in an interval of 60 seconds.

Secondly, a next-neighbor analysis was applied to measure the calves' general distance to their closest neighbor, to evaluate the calves' bond to other herd members than their mothers [Kappeler, 2020; Krull, 2000; Martin & Bateson, 2007; Naguib & Krause, 2020; Randler, 2018]. Here, distances to their next-neighbor were measured using the distance parameters *tactile contact*, *<2 m*, 2-4 *m*, and *>4 m* [Lee & Moss, 2011] at an interval of 60 seconds. Distance categories were chosen wider and with fewer limitations, as the position of the next-neighbor to a calf is not as defined as the position of its mother [Lee & Moss, 2011].

Thirdly, the calves' behavior and relationships within the herd were evaluated by differing affiliative and agonistic contacts. The amount of affiliative and agonistic contacts was counted and it was noted whether the calves were the initiator or recipient of the respective contact. Categorization of the behavior was applied according to the ethogram of Poole & Granli, [2021], labeling the animal's behavior focusing on the initiating animal. Data were collected continuously during the whole observation time [Kappeler, 2020; Krull, 2000; Martin & Bateson, 2007; Naguib & Krause, 2020; Randler, 2018].

Finally, the general behavior of all calves was observed by applying an ethogram listing the eight behavioral items *eating, drinking, suckling, locomotion, locomotion trunk, comfort behavior* (meaning stretching, scratching, throwing sand and mud on oneself, and rolling in sand/mud), *sleeping*, and *playing*. Thereby, a behavioral profile of the calves in their different environments was generated [Kappeler, 2020; Krull, 2000;

Martin & Bateson, 2007; Naguib & Krause, 2020; Randler, 2018]. The ethogram was mainly extracted from Poole & Granli [2011; 2021]. Again, an interval of 60 seconds was chosen to collect the data.

All sets of data were classified numerically [Agresti, 2007; APA, 2013; Bortz & Döring, 2006; Naguib & Krause, 2020], and statistical analysis was performed using SPSS Version 29. As the graphical analysis showed that all sets of data were metrical and unevenly distributed, a Kruskal-Wallis calculation was performed to detect statistically significant differences between the three management systems (*free, protected,* and *no contact*) and the different space, elephants had in the four facilities where data was collected. In addition, an exact test (Monte Carlo Simulation) was calculated taking into account the small sample size [Adery & Hope, 1968; Cohen, 1988; Kubinger et al., 2009; Siegel & Castellan, 1988; Tomarken & Serlin, 1986]. As no significance was detected, post-hoc tests were not calculated [Benjamini & Hochberg, 1995; Hochberg, 1988]. The significance level was set to $p \leq 0.05$ [Fritz et al., 2012; Ryan, 2013].

3. Results

3.1. Distance to Mother

Figure 1 shows the distribution of contacts between calves and their mothers in all three management systems, none of which displays significant differences. Whilst the pattern of distance to the mothers was comparable in all three management systems, a notable result is the high amount of distance <1 m in *free contact* (nearly 50 %) and *no contact* (nearly 40 %) in comparison to *protected contact* (nearly 30 %). Yet of all distances observed, the dimension of <1 m was the most frequent in all three systems and even exceeded the tactile contacts.

The lowest variation in the frequency of all maintained distances was seen in *protected contact*. Calves kept higher distances (1-3 m, 3-5 m, and >5 m) to the mothers in all three management systems, even though, the bigger distance categories (3-5 m, and >5 m) were not observed as frequently. However, calves in *free contact* rather showed a higher percentage of >5 m than 3-5 m which was comparable in *protected* and lower in *no contact.*

Calves living in *free contact* tend to have less tactile contact with their mothers (mean of 6.16 %) than calves living in *protected* (mean of 18.15 %) or *no contact* (mean of 13.99 %). However, calves living in *free contact* spend most of their time in the second distance category *<1 m* (mean of 48.54 %), which is more than calves in *protected contact* (mean of 27.02 %) and *no contact* (mean of 33.52 %) do. Thus, the overall distance to the mothers is also small for calves living in *free contact*.

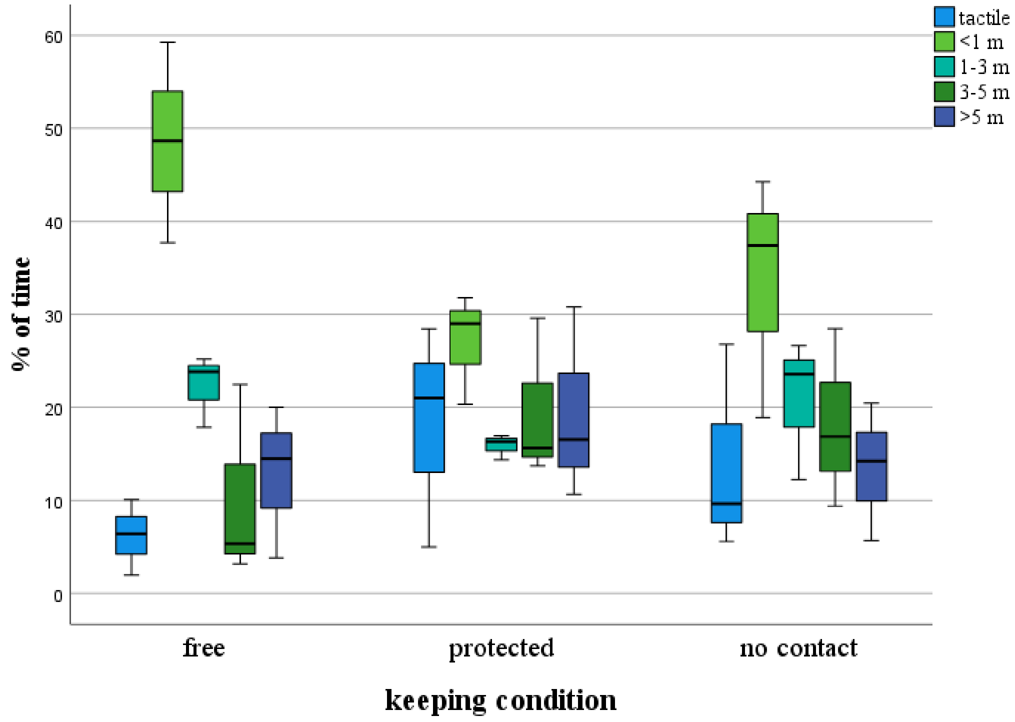

Figure 1. Percentage of time calves spend in a distance category to mother, depending on management condition.

Based on the five distance categories, the calves' position to their mothers was measured and statistically analyzed for differences between the management conditions and the space elephants had in the different enclosures. No significant differences were detected (see Table 2).

Table 2. Kruskal-Wallis calculation for the position of calves to their mothers, depending on different management conditions and depending on m²/elephant.

management condition			**tactile**	**<1 m**	**1-3 m**	**3-5 m**	**>5 m**
Kruskal-Wallis H			1.156	4.622	2.756	1.689	.622
df			2	2	2	2	2
Asymp. Sig.			.561	.099	.252	.430	.733
Monte Carlo Sig.	Sig.		.630	.099	.296	.510	.825
	99% Confidence Interval	Lower Bound	.617	.092	.284	.497	.816
		Upper Bound	.642	.107	.307	.523	.835
m²/elephant			**tactile**	**<1 m**	**1-3 m**	**3-5 m**	**>5 m**
Kruskal-Wallis H			2.956	4.622	2.655	1.889	2.422
df			3	3	3	3	3
Asymp. Sig.			.399	.202	.431	.596	.490
Monte Carlo Sig.	Sig.		.472	.195	.517	.704	.613
	99% Confidence Interval	Lower Bound	.459	.185	.504	.693	.601
		Upper Bound	.485	.205	.530	.716	.626

3.2. Next-Neighbour

In Figure 2 similar (non-significant) observations in the distance parameters of *tactile contact* and <2 *m* are seen in the data for the position of the mother. Again, calves living in *free contact* tend to have less tactile contact with their next neighbors than calves living in *protected* or *no contact*.

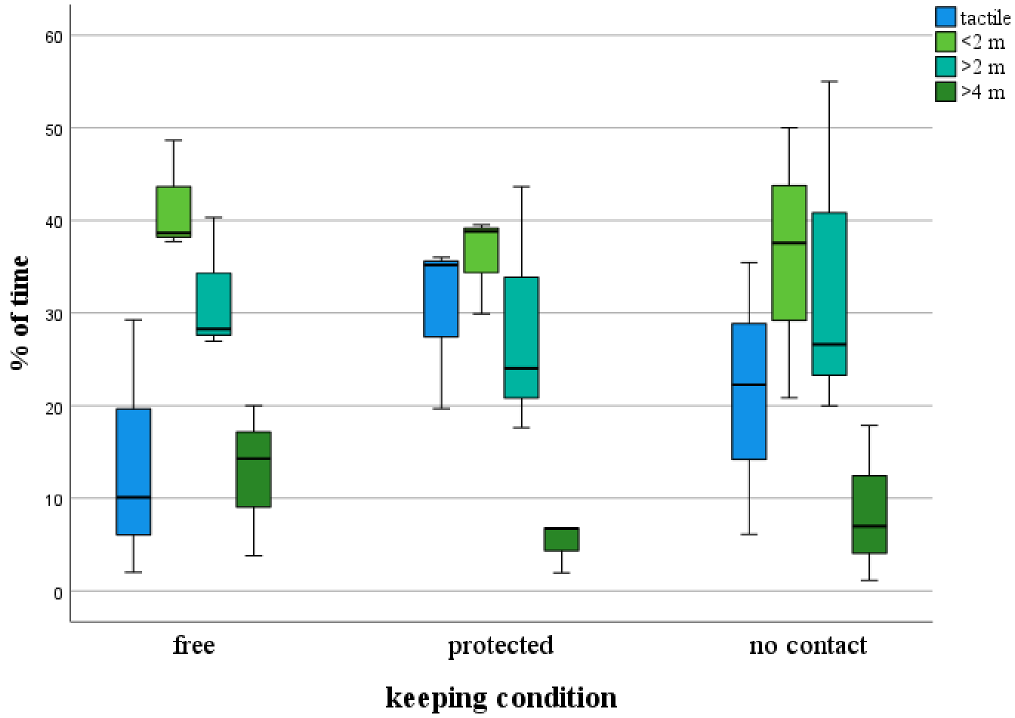

Figure 2. Percentage of time calves spend in a distance category to next-neighbor, depending on their management condition.

Table 3 summarises the statistical analysis for the data of the next-neighbor of the calves, which resulted in no significant differences for both, management conditions and space per elephant.

Table 3. Kruskal-Wallis calculation for next-neighbors of calves, depending on different keeping conditions and m²/elephant.

management condition			**tactile**	**<2 m**	**>2 m**	**>5 m**
Kruskal-Wallis H			2.222	.356	.800	1.422
df			2	2	2	2
Asymp. Sig.			.329	.837	.670	.491
Monte Carlo Sig.	Sig.		.378	.879	.716	.541
	99% Confidence Interval	Lower Bound	.366	.871	.705	.528
		Upper Bound	.390	.888	.728	.553
m²/elephant			**tactile**	**<2 m**	**>2 m**	**>5 m**
Kruskal-Wallis H			3.311	1.156	2.600	1.778
df			3	3	3	3

Asymp. Sig.			.346	.764	.457	.620
Monte Carlo Sig.	Sig.		.385	.859	.542	.716
	99% Confidence Interval	Lower Bound	.372	.850	.529	.704
		Upper Bound	.397	.868	.554	.727

3.3. Social Behavior

Figure 3 demonstrates the percentages of time of affiliative and agonistic behavior, dependent on whether calves mainly initiated and/or received affiliative and agonistic behavior between management systems. Results demonstrate that calves only initiated and received minor agonistic behavior but mainly initiated and received affiliative behavior, again without significant differences between holding systems or provided space.

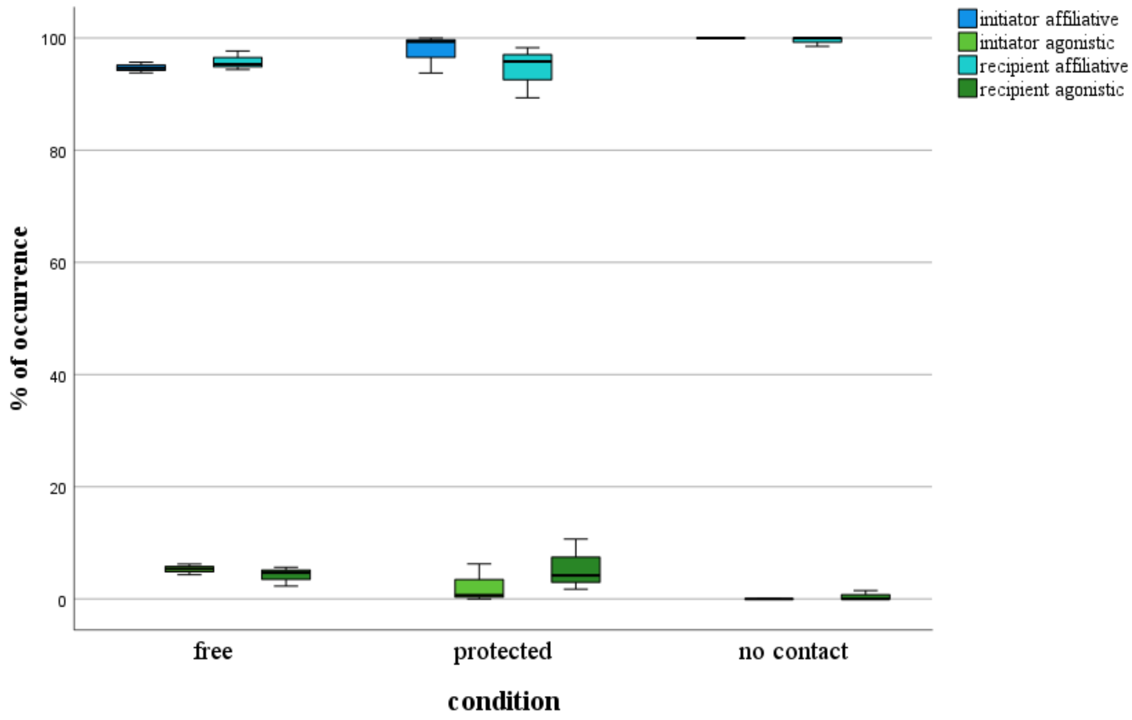

Figure 3. Percentage of affiliative and agonistic behavior initiated and received by calves, depending on management condition.

As the data analysis in Table 4 for the social behavior of the calves shows, the Kruskal-Wallis calculation did not determine any significant differences depending on keeping conditions or space per elephant in affiliative and agonistic behavior of the calves, neither from the initiator side nor from the recipient side.

Table 4. Kruskal-Wallis calculation for agonistic and affiliative behavior as initiator and recipient for calves, depending on different management conditions and m²/elephant.

management condition			**aff. initiator**	**aff. recipient**	**ago. initiator**	**ago. recipient**
Kruskal-Wallis H			4.582	4.582	5.468	5.468
df			2	2	2	2
Asymp. Sig.			.101	.101	.065	.065
Monte Carlo Sig.	Sig.		.130	.126	.066	.066
	99% Confidence Interval	Lower Bound	.121	.117	.060	.060
		Upper Bound	.138	.134	.072	.073
m²/elephant			**aff. initiator**	**aff. recipient**	**ago. initiator**	**ago. recipient**
Kruskal-Wallis H			4.636	4.636	6.902	6.902
df			3	3	3	3
Asymp. Sig.			.200	.200	.075	.075
Monte Carlo Sig.	Sig.		.179	.179	.014	.014
	99% Confidence Interval	Lower Bound	.170	.169	.011	.011
		Upper Bound	.189	.188	.017	.017

3.4. General Behavior

Statistics show no significant differences in any of the eight behavioral categories depending on the management system or space of the elephants in the respective zoos. The percentage of time that the elephant calves spent on a certain behavior are presented in Table 5. Many behaviors were only observed on few occasions for all three management systems. Prominent differences are only present in the major behavioral category of *eating*. The behavioral category *playing* tends to be less displayed in the management system with *no contact* and more frequently in the other two systems.

Table 5. Means of time behavioral categories were displayed in the three management systems and Kruskal-Wallis calculation for the general behavior of calves, depending on different management systems and m²/elephant.

management condition			**Eat**	**Drink**	**Suckle**	**Locom.**	**Locom. Tr.**	**Comfort**	**Sleep**	**Play**
Mean	Free		25.36	2.07	3.51	11.94	14.60	1.93	3.62	20.52
	Protected		28.52	0.68	5.01	11.12	17.01	1.52	1.25	16.19
	No contact		42.42	0.44	6.28	6.78	12.85	0.64	4.90	6.20
Kruskal-Wallis H			.325	3.493	1.412	3.389	.800	1.689	1.156	2.489
df			2	2	2	2	2	2	2	2
Asymp. Sig.			.837	.174	.494	.193	.670	.430	.561	.288
Monte Carlo Sig.	Sig.		.879	.191	.534	.236	.716	.510	.630	.336
	99% Confidence Interval	Lower Bound	.871	.180	.521	.225	.705	.497	.617	.324
		Upper Bound	.888	.201	.547	.247	.728	.523	.642	.348
m²/elephant			**Eat**	**Drink**	**Suckle**	**Locom.**	**Locom. Tr.**	**Comfort**	**Sleep**	**Play**

Mean	240.33		11.59	0.41	7.45	11.45	22.76	2.07	1.79	15.17
	520.125		36.98	0.81	3.78	10.95	14.14	1.25	0.97	16.7
	985.66		25.36	2.07	3.51	11.94	14.60	1.93	3.62	20.52
	1,263.16		42.42	0.44	6.28	6.78	12.85	0.64	4.90	6.20
Kruskal-Wallis H			1.156	3.854	1.866	3.489	1.000	2.778	1.511	2.844
df			3	3	3	3	3	3	3	3
Asymp. Sig.			.764	.278	.601	.322	.801	.427	.680	.416
Monte Carlo Sig.	Sig.		.859	.285	.720	.352	.875	.514	.784	.491
	99% Confidence Interval	Lower Bound	.850	.274	.709	.339	.867	.501	.774	.478
		Upper Bound	.868	.297	.732	.364	.884	.527	.795	.504

4. Discussion

4.1. Position to Mother

The results of this study demonstrate that management systems for the husbandry of elephants in zoos do not influence the spatial distance between mothers and their calves. In all three management systems calves stayed mainly at <1 m distance from their mothers. Thus, it can be assumed that the urge to stay close to the mother is present for calves in all three holding systems.

The analysis only demonstrated non-significant trends in the positions of mothers and calves between the three management systems. However, they are different from data known for calves living *in situ*, which agrees with previous studies on differences between calves *in situ* and *ex situ* [Webber, 2017]. In the wild, calves were observed to not walk farther than 5 meters away from their mothers, before they are two years of age [Lee & Moss, 2011]. In contrast, the six calves of this study that were under the age of two years spent an average of 10.9 % of the time at a distance of more than five meters to their mothers. This result is likely independent of the management system and suggests that these data are representative of calves living *ex situ*. Based on this difference between *ex situ* and *in situ* it can be argued that the lack of predators and perils in the zoo environment allows for a spatial detachment of calves from the mothers. The close (spatial) connection to the mother elephants that calves maintain *in situ* is crucial for their safety and food supply, and thus for their survival [Lee & Moss, 2011; Moss, 2001].

4.2. Social Distances

Data show that the management systems do not affect the social distances of the elephant calves and other herd members. The data demonstrate, that calves living in *free contact* have less tactile contact (mean of 13.77 %) than calves living in *protected* (mean of 30.3 %) or *no contact* (mean of 21.27 %). Calves in *free contact* spend most of their time at a distance of *<2 m* (mean of 41.67 %) from their next neighbor, which is more than calves in the other keeping conditions (mean of 36.09 % for *protected* and 36.13 % for *no contact*). Therefore, the overall distance for calves living in *free contact* with the other herd members is slightly, but not significantly, larger than in the other holding systems.

Interestingly, the data collected *ex situ* correspond with data from *in situ*. Lee & Moss [2011] describe, that calves living *in situ* spend approximately 20 % of their time at small distances from non-mother elephants and only about 10 % of their time at a social distance of more than five meters from other herd members. The data from the zoos show that the calves spend approximately 21.78 % of their time at small distances to non-mother elephants and about 8.85 % of their time at a distance of more than five meters. Hence, the social relationship to the herd in terms of keeping distance displayed by the calves in this study is equivalent to that of calves in the wild. This testifies a species-specific behavior of calves under human care.

4.3. Social Behavior

The affiliative and agonistic behavior of the calves is not different between the three management systems. According to the data at hand, both, the management system and the size of the enclosure do not seem to have an impact on the calves' general behavior.

The analysis of social behavior also emphasizes that relationships between calves and herd members are predominantly positive. These findings agree with other studies for zoo elephants as well as the social relationships known for calves in the wild, where young individuals are mainly treated with patience and care [Andrews et al., 2005; Douglas-Hamilton, 1972; Douglas-Hamilton & Douglas-Hamilton, 1989; Estes, 1991; Meehan et al., 2016; Moss, 2001; Pinter-Wollman et al., 2009; Schulte, 2000].

4.4. General Behavior

Although there was no significant difference in general behavior between management systems, minor differences for some of the parameters between systems as well as within the sample groups were evident (Fig. 4), e.g. in the category *eating*. These differences may be explained by the age distribution of the groups. The calves in this study ranged in age from six to 48 months. As described before, one of the stages of development in calves is to learn the use of their trunks and the development of normal eating behavior [Andrews et al.; 2005; Lee & Moss, 2011]. While young calves mainly suckle from their mother's breasts and spend only a minority of their time eating and drinking, older calves have to eat grass and hay and have to spend a considerable amount of time on food consumption, resulting in a different distribution of behavior patterns depending on the calves' age.

It can be hypothesized that the minor differences in the amount of playing behavior between the sample groups also depend on the age range because the older calves become, the more time they spend playing [Lee & Moss, 2011]. Also, whilst all calves of this study had company other than their mother, not all of them had the same number of playmates (see Table 1), which most likely has an impact on the amount of playing behavior, as well.

Management systems did not seem to influence locomotion, comfort behavior, suckling, and sleeping, indicating that time spent on those behaviors is determined genetically or not influenced by the management system.

Overall, the general behavior observed in the calves in this study resembles the behavioral patterns of calves living *in situ* [Andrews et al., 2005; Lee & Moss, 2011; Moss, 2001]. Therefore, neither the management system nor the general fact that the calves lived under human care showed an impact on the behavioral elements investigated in this study, admittedly with a low sample size.

5. Conclusions

This study offers empirical ethological data for African elephant calves in the three different management conditions *free*, *protected,* and *no contact*, under which elephants are kept in Europe. Spatial distances between calves and mothers and calves and other family members as well as social and general behavioral items were measured to detect possible differences holding systems might generate. No disparities in the social and general behavior of calves and their spatial distance from mother and non-mother elephants were identified in statistical analysis. No signs of hospitalism or inferior health conditions have been identified in all three elephant management systems. It seems that the elephant management system and provided space do not influence the behavior of elephant calves. This, in turn, leads to the conclusion that African elephant calf welfare and well-being are given under each of the three systems, as long as other welfare conditions are met. The choice of husbandry must focus on safety measures, as contact between elephants and humans is always risky with potential harm to humans [Bossy, 2019; EAZA, 2019].

Calves in zoos tend to hold bigger spatial distances to their mothers than *in situ*, a circumstance that would put them in danger if they were living in the wild with predators [Estes, 1991; Moss, 2001]. The reason for these larger distances might therefore be the knowledge of the mothers of the protective environment in the zoos, which also allows the calves to move farther away than calves in the wild are allowed. This difference displayed in the zoo environment most likely testifies to the cognitive abilities and adaptability of elephants under human care, as mothers adapt their behavior towards their calves to the environment in which they raise them.

At the same time, the results display less tactile contact between mothers and calves in *free contact*. Tactile contact with their mothers is highly important for the calves [Dunbar, 2010; Jablonski, 2021] and it remains uncertain, which impact the reduced contact might have on the long-term development of the calves. Further investigations on this issue are therefore important. Additionally, data suggest that carers should always reduce their direct contact with calves to the necessary minimum.

So far, this study solely supplies differences between calves under *in situ* and *ex situ* conditions with data from *in situ* only based on literature. For a reliable comparison, data collection *in situ* applying the same methods is required. In addition, long-term studies with higher numbers of research animals should shed light on possible ongoing differences in social behavior under human care of African elephant calves.

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Tables

Table 1A. List of elephant calves.

Elephant	Sex	Management system	Size of enclosure in m^2	m^2 / elephant	Date of Birth	Age at data collection*	Number of playmates
Tu	F	Free contact	4,161	520.125	16-03-2016	47-48 month	2
Gu	M	Free contact	4,161	520.125	20-04-2019	11-12 month	1
Ts	M	Free contact	4,161	520.125	06-03-2020	6 month	2
Ch	F	Protected contact	1,442	240.33	14-04-2017	48 month	2
El	F	Protected contact	2,957	985.66	20-09-2019	11 month	1
Ku	M	Protected contact	1,442	240.33	05-04-2021	6 month	2
To	M	No contact	24,000	1,263.16	29-08-2018	47 month	2
Ma	F	No contact	24,000	1,263.16	22-02-2020	18 month	2
Ne	M	No contact	24,000	1,263.16	08-01-2021	7 month	1

*differences in age between the three sample groups were not significant: Kruskal Wallis analysis (p = .368)

Table 2A. Kruskal-Wallis calculation for the position of calves to their mothers, depending on different management conditions and depending on m²/elephant.

management condition			**tactile**	**<1 m**	**1-3 m**	**3-5 m**	**>5 m**
Kruskal-Wallis H			1.156	4.622	2.756	1.689	.622
df			2	2	2	2	2
Asymp. Sig.			.561	.099	.252	.430	.733
Monte Carlo Sig.	Sig.		.630	.099	.296	.510	.825
	99% Confidence Interval	Lower Bound	.617	.092	.284	.497	.816
		Upper Bound	.642	.107	.307	.523	.835
m^2/elephant			**tactile**	**<1 m**	**1-3 m**	**3-5 m**	**>5 m**
Kruskal-Wallis H			2.956	4.622	2.655	1.889	2.422
df			3	3	3	3	3
Asymp. Sig.			.399	.202	.431	.596	.490
Monte Carlo Sig.	Sig.		.472	.195	.517	.704	.613
	99% Confidence Interval	Lower Bound	.459	.185	.504	.693	.601
		Upper Bound	.485	.205	.530	.716	.626

Table 3A. Kruskal-Wallis calculation for next-neighbors of calves, depending on different keeping conditions and m²/elephant.

management condition			**tactile**	**<2 m**	**>2 m**	**>5 m**
Kruskal-Wallis H			2.222	.356	.800	1.422
df			2	2	2	2
Asymp. Sig.			.329	.837	.670	.491
Monte Carlo Sig.	Sig.		.378	.879	.716	.541
	99% Confidence Interval	Lower Bound	.366	.871	.705	.528
		Upper Bound	.390	.888	.728	.553
m^2/elephant			**tactile**	**<2 m**	**>2 m**	**>5 m**
Kruskal-Wallis H			3.311	1.156	2.600	1.778
df			3	3	3	3
Asymp. Sig.			.346	.764	.457	.620
Monte Carlo Sig.	Sig.		.385	.859	.542	.716
	99% Confidence Interval	Lower Bound	.372	.850	.529	.704
		Upper Bound	.397	.868	.554	.727

Table 4A. Kruskal-Wallis calculation for agonistic and affiliative behavior as initiator and recipient for calves, depending on different management conditions and m²/elephant.

management condition			**aff. initiator**	**aff. recipient**	**ago. initiator**	**ago. recipient**
Kruskal-Wallis H			4.582	4.582	5.468	5.468
df			2	2	2	2
Asymp. Sig.			.101	.101	.065	.065
Monte Carlo Sig.	Sig.		.130	.126	.066	.066
	99% Confidence Interval	Lower Bound	.121	.117	.060	.060
		Upper Bound	.138	.134	.072	.073
m^2/elephant			**aff. initiator**	**aff. recipient**	**ago. initiator**	**ago. recipient**
Kruskal-Wallis H			4.636	4.636	6.902	6.902
df			3	3	3	3
Asymp. Sig.			.200	.200	.075	.075
Monte Carlo Sig.	Sig.		.179	.179	.014	.014
	99% Confidence Interval	Lower Bound	.170	.169	.011	.011
		Upper Bound	.189	.188	.017	.017

Table 5A. Means of time behavioral categories were displayed in the three management systems and Kruskal-Wallis calculation for the general behavior of calves, depending on different management systems and m²/elephant.

management condition			**Eat**	**Drink**	**Suckle**	**Locom.**	**Locom. Tr.**	**Comfort**	**Sleep**	**Play**
Mean	Free		25.36	2.07	3.51	11.94	14.60	1.93	3.62	20.52
	Protected		28.52	0.68	5.01	11.12	17.01	1.52	1.25	16.19
	No contact		42.42	0.44	6.28	6.78	12.85	0.64	4.90	6.20
Kruskal-Wallis H			.325	3.493	1.412	3.389	.800	1.689	1.156	2.489
df			2	2	2	2	2	2	2	2
Asymp. Sig.			.837	.174	.494	.193	.670	.430	.561	.288
Monte Carlo Sig.	Sig.		.879	.191	.534	.236	.716	.510	.630	.336
	99% Confidence Interval	Lower Bound	.871	.180	.521	.225	.705	.497	.617	.324
		Upper Bound	.888	.201	.547	.247	.728	.523	.642	.348

m^2/elephant		**Eat**	**Drink**	**Suckle**	**Locom.**	**Locom. Tr.**	**Comfort**	**Sleep**	**Play**
Mean	240.33	11.59	0.41	7.45	11.45	22.76	2.07	1.79	15.17
	520.125	36.98	0.81	3.78	10.95	14.14	1.25	0.97	16.7
	985.66	25.36	2.07	3.51	11.94	14.60	1.93	3.62	20.52
	1,263.16	42.42	0.44	6.28	6.78	12.85	0.64	4.90	6.20
Kruskal-Wallis H		1.156	3.854	1.866	3.489	1.000	2.778	1.511	2.844
df		3	3	3	3	3	3	3	3

Asymp. Sig.			.764	.278	.601	.322	.801	.427	.680	.416
Monte Carlo Sig.	Sig.		.859	.285	.720	.352	.875	.514	.784	.491
	99% Confidence Interval	Lower Bound	.850	.274	.709	.339	.867	.501	.774	.478
		Upper Bound	.868	.297	.732	.364	.884	.527	.795	.504

Figure Legend

3.3.1 Conclusive summary study III

Study III compared the social bonds of African elephant calves of the three holding systems practiced in European zoos and enclosures of different sizes. There are three holding systems for elephants in zoos that differ in how carers interact with the animals. Carers enter the elephants' enclosures in *free contact* and interact directly with them [Bossy, 2019; Lundberg et al., 2001; Samson, 2000; Tanner, 2000]. This requires a very high level of obedience by the elephants to ensure the carers' safety [Bossy, 2019; EAZA, 2019]. Carers must constantly carry an ankus as an additional safety target when entering the enclosure [Bossy, 2019; EAZA, 2019]. In *protected contact,* elephants are handled through a separating fence. All training and interactions are facilitated with this safety barrier between carers and animals [Desmond & Laule, 1991; 1993; Harris et al., 2008; Laule & Whittaker, 2001]. In the holding system of *no contact*, carers do not interact with the animals other than by opening and closing gates between enclosures [Laule & Whittaker, 2001].

This study collected ethological data for three calves of each holding system in four different facilities (n = 9). Their general behavior and their social behavior were observed. The distance to their mothers was measured, as well as their distance to their next neighbors. Statistical analysis was conducted with SPSS Version 29, using the Kruskal-Wallis calculation and the Monte Carlo Simulation [Adery & Hope, 1968; Cohen, 1988; Kubinger et al., 2009; Siegel & Castellan, 1988; Tomarken & Serlin, 1986].

No significant differences between the three holding systems or the size of enclosures were detected for any of the investigated parameters. Only minor differences were detected in the amount of tactile contact between calves and mothers displayed by individuals living in *free contact*. Calves of this holding system displayed less direct contact with their mothers than calves of the other two holding systems. However, tactile contact with mothers is vital for the social development of mammals and even influences their future breeding success [Dunbar, 2010; Jablonski, 2021]. Therefore, even if not significant, those results must be considered. A possible explanation is the dominant role carers have within the herd structures of elephants held in *free contact*. Their rank must be above the mothers and even the matriarch. Otherwise, secure handling in direct contact would not be possible [Bossy, 2019]. This might impact the calves' need for tactile contact with their mothers.

Nevertheless, the results indicate that the holding system does not impact African elephant calves' social behavior and mother-child bond. Therefore, a change in the holding system will most likely not affect the social bonds of the calves or their social behavior.

However, a comparison with studies of calves living *ex situ* showed that the calves observed in study III stayed farther to their mothers and their next neighbors than reported for calves living in the wild [Charif et al., 2005; Lee & Moss, 2011]. The most likely cause for those differences is the lack of predators and perils, such as losing the herd, in a zoo environment. This allows for a spatial detachment of the calves from their mothers. In the wild, the close spatial connection between calves and mothers is crucial for the calves' safety and food supply [Lee & Moss, 2011; Moss, 2001].

3.4 Chapter IV:

Running Head: Differences between *Loxodonta africana* calves *in situ* and *ex situ*

Title: Differences in social behavior and mother-child bond of *in situ* and *ex situ* living African elephant calves

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Article

Differences in mother-infant-bond and social behavior of African elephant calves living *in situ* and *ex situ*

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Simple Summary: In the wild, African elephant calves must stay close to their mothers and the family unit, as the African environment holds many threats. African elephant calves in zoos are raised in a protected environment. Therefore, we hypothesize that calves *ex situ* hold bigger distances and behave differently than *in situ*. Additionally, those differences are likely to increase with further zoo generations. This study used ethological research methods to compare the mother-calf bond of African elephant calves *in situ* and *ex situ* (first and second generation). The results showed that *ex situ* living calves of both generations maintain greater distances to their mothers and show a wider variation (positive and negative) in behavior than *in situ*. The detected differences indicate that calves *ex situ* can behave more freely as they are in a protected environment. Therefore, they can develop faster than in the wild, which agrees with similar findings on African elephant calf development and adult African elephants. The hypothesis that differences between *in situ* and *ex situ* increase with the zoo generations could not be verified. Hence, modifications in behavior under different environmental selection pressures may be adaptive.

Abstract: African zoo elephants live in safe environments with sufficient resources, are protected from threats, and have their health and body conditions cared for. Calves *ex situ* undergo the same developmental stages as *in situ* and are raised by the whole family unit. However, due to environmental differences, there might be behavioral modifications between calves *in situ* and *ex situ*. We hypothesize that these differences increase with ongoing generations. This ethological study compares social, general behavior and the distance calves kept to their mothers' between calves of the first (F1) and second (F2) zoo generation and the wild. Using ethological methods, data was collected for ~90 in situ calves and 16 *ex situ* (8 F1, 8 F2) between the ages of 0.5 to 4 years (120 observation hours per group). Results showed that *in situ* calves spent significantly more time close to mothers than of the F1 and the F2 zoo generations (F1/*in situ*: p = <.001; F2/*in situ*: p = .007). The behaviours of eating, drinking, trunk movement, washing and affiliative behaviours showed significant differences between in situ and ex situ calves. Amount and distribution of affiliative and agonistic behavior initiated and received by calves was displayed with a greater variety by *ex situ*. Ex situ calves not only performed affiliative but, in contrast to *in situ*, also agonistic behavior (F1/*in situ*: initiated $p = .002$, received $p = .010$; F2/*in situ*: initiated $p = .050$, received $p = .037$). The comparison of zoo generations suggests that differences did not increase with the generation. The more casual binding between mothers and offspring in zoos and the age-dependent improvement of social behavior of zoo-born calves are seen as a result of elephants' adaptation to secure zoo conditions. Results of this study agree with the faster development of *ex situ* African elephants, like earlier puberty and more frequent breeding patterns, as known from the literature.

Keywords: *Loxodonta africana*; zoo elephants; wild elephants; distance keeping; development; human care

1. Introduction

African elephants (*Loxodonta africana*) are known for their complex and close social bonds. Calves are born into stable families and cared for by their mothers, other females (allomothers), and older siblings [1-3]. The death of a mother during the first 24 months of life will leave the calf with almost no chances of survival *in situ* [4-6] and even in captivity [7]. Tactile, visual, olfactory, and acoustic contact between mothers and calves is essential [4-6]. This can be seen in data from the Amboseli population, representing the most complete long-term dataset in the demography of wild African elephants [6]. There, calves spend about 56 % of their time in close contact with their mothers during the first two years [6]. During this period, the close bond is maintained by both mother and calf but will loosen after two years and is then pursued more by the mother, as the mother is responsible for the calf's safety and survival [6].

Besides the contact with their mothers, during the first two years, the calves were observed to spend approximately 20 % of their time at a physical contact distance to the next family member [6]. Only about 10 % of the time, they were observed to be more than five meters away from their next neighbor [6]. Charif et al. [8] detected that close spatial bonds are even maintained by adult female elephants of the same bond groups (related family), which were found to have coordinated movement and preserve a distance of no more than 0.5 km for most of their time. African elephant calves' development is subdivided into seven stages, as listed in Table 1 [4-10].

Table 1. Developmental stages of elephant calves.

Age	Development
0-6 months	- Learn how to walk stable - Learn how to use the trunk for suckling
7-12 months	- Learn how to use the trunk for foraging - Main nutrition shift from milk to solid food
13-24 months	- First decrease in contact with mothers - Pick up on playing behavior
25-36 months	- Start to show more agonistic behavior, which is relevant for learning to compete in rivalries - Increase of gender-specific differences - Peak in playing behavior (way of learning social behavior)

37-48 months	- Classified as youngsters - Gender-specific differences in social behavior become more significant
49-60 months	- Social play (that is, among other functions, intended to prepare youngsters for breeding behavior, such as climbing and chasing others) increases significantly
60-plus months	- Classified as young adults - Males and females start to become fertile *in situ*, even though it still takes several years for them (especially the males) to mate successfully - Behavior shifts even stronger toward behavior related to breeding - Young bulls might already have left the natal family to socialize with bachelor groups

Calves in zoos possibly undergo the same developmental stages and are described by Andrews et al. [11], Webber [12], and Freeman et al. [13]. However, social constellations are different from the wild, and zoo family units are not necessarily related, as in the wild. Due to the increase in captive breeding, zoos are now at the F2 generation (second generation of zoo-born elephants, both parent animals being of the F1 generation), with very few even reaching the F3 generation (third generation of zoo-born elephants) [14]. This aspect is essential, as F1 calves (first generation of zoo-born calves) were born and raised by mothers imported from the wild, lacking their mothers' help and assistance. However, F2 calves are already born and raised by mothers who grew up in captivity and often in the presence of their grandmothers, which resembles the family structure from the wild [15].

It has been shown that elephants in zoos reach fertility at a younger age. Females start to show ovarian cycles at 6 to 7 years and can give birth for the first time at 8 to 9 years [16]. While data on the onset of the ovarian cycle in wild females are missing, first births are reported in cows mostly between 12 and 16 years of age, the earliest being reported at nine years old (± one month) [9-10; 17-18]. Males in zoos must not show musth to be able to breed [19] and can sire offspring as young as 9 to 10 years old [19]. Whereas in the wild, males reached musth for the first time around the age of 12-14 years and were observed to be accepted as mating partners by cows only at the age of 25 years [10].

If we are to suppose that African elephants in zoos reach puberty much earlier than in the wild. In that case, it is possible that African elephant calves in zoos also develop faster than those in the wild and most likely faster. Preliminary data were collected by Hoerner et al. [under review], who found that calves living *ex situ* tended to maintain greater distances to their mothers than reported for their conspecifics *in situ* as known from the literature [4; 6; 8]. Calves in zoos were observed to spend up to 31 % of their time at a distance of more than five meters from their mothers already at the age of three days [20-22]. This was observed in male and female calves and of the matriarch and sub-dominant cows. This spatial detachment was observed to increase with the age of the calves [20-22], whereas it is unclear if this feature will increase with future generations.

The new generations in the zoos (F2 and, most recently, F3) are no longer solely socialized by wild-born elephants but by zoo-born elephants. Additionally, the import of wild elephants is considered outdated [23]. Therefore, *in situ*-born elephants become less represented in zoos. Calves adapt the social and behavioral patterns of the relatives that raise them [9; 24-25]. This results in our two hypotheses: (1) Captive elephant calves keep bigger distances to their and show different social and general behavior than wild elephant calves. (2) Those differences between wild and captive elephant calves increase with the next zoo generations.

We tackled those hypotheses by combining ethological research *in situ* and *ex situ* to learn about possible differences in the behavior and distance keeping of calves brought up correspondingly. To investigate the second hypothesis, we collected data for ex situ calves' F1 and F2 generation.

2. Material and Methods

2.1. Animals

Data was collected for a total number of ~106 elephant calves of three different groups: (I) F1 generation *ex situ,* (II) F2 generation *ex situ,* (III) *in situ*. Within Europe, data was collected in four zoos for 16 African elephants – 8 of the F1 generation and 8 of the F2 generation. Calves from zoos had between 240 and 1,315 m^2/elephant of space. A possible impact of the varying enclosure size on the calves' behavior was eliminated in a previous study [22].

The animals observed *in situ* were selected to reflect the same age group and distribution as the F1 and F2 groups. The age of *in situ* calves was estimated by body size and confirmed by knowledge of local rangers. Calves of all data sets were further sampled by age group according to developmental stages [4-6]. Data for this group was collected in the Jafuta Reserve, the Zambezi National Park, and Hwange National Park in Zimbabwe. The areas in which family units were observed were sparse miombo woodland with nearby water sources. As no register for the family units in the observation areas was available, it could not reliably be determined whether the same families were observed on several occasions. Family units were followed by vehicles. The age limit for the sample animals was drawn at approximately four years, as gender-related differences in behavior become significant from that age on [6]. Family units of calves observed *in situ* had varying sizes between 4-26 animals, comprising family units with older daughter elephants, subadult males and allomothers.

Table 2 displays the information on the captive animals, valid for the time of data collection.

Table 2. List of elephants.

Generation /Origin	Elephant	Sex	Year of Birth	Age at data collection	Number of playmates	Total number
F1 / *ex situ*	Ts	M	2020	6 months	3	8
	Ku	M	2021	6 months	3	
	Gu	M	2019	12 months	3	
	Tu	F	2016	24 months	3	
	Jo	M	2014	36 months	3	
	Maj	F	2017	48 months	4	
	Ch	F	2017	48 months	3	
	Sa	F	2017	48 months	3	
F2 / *ex situ*	Ki	F	2020	6 months	4	8

	Ne	M	2021	6 months	1	
	El	F	2019	12 months	2	
	Mar	F	2019	30 months	2	
	Tora	M	2018	36 months	4	
	Tori	M	2018	42 months	4	
	Ta	F	2016	48 months	2	
	Ay	M	2016	48 months	1	
in situ	-	M & F	-	3 – 48 months	2 – 13	~90

2.2. Ethological data collection

The behavior of the calves was measured utilizing two research methods: the Social Distance Method and Focal-Animal-Sampling [26-28] and an ethogram extracted from Poole & Granli [29-30], listing 16 behavioral categories (Table 3).

Table 3. Ethogram for the data collection on the general behavior of calves (extracted from Poole & Granli [29-30]).

Label	**Behavior**
Eat	Eating food with trunk
Drink	Drinking water with trunk
Suckle	Suckling milk from the mother's breast
Walk	Walking at a slow pace, no more than one step per sec., with the purpose to go somewhere
Run	Running in an enhanced space, more than one step per sec., to run away from something or get somewhere fast for safety
Trunk movement	Moving either the tip of the trunk or the whole trunk for practice or to search the ground for food/objects
Washing	Washing the body with mud/water, sand bathing, rubbing the body on something to clean the skin, and protecting from mosquitos and sun
Sleep	Sleeping or resting in a lying or standing position with the eyes closed
Social play	Playing with one or more other individuals
Lone play	Playing individually with oneself or an object
Affiliative behavior	Behaving positively to other individuals (e.g., touching with the trunk, helping behavior)
Agonistic behavior	Behaving negatively to other individuals (e.g., pushing with trunk, tusk, or body)
Escaping	Running from something while showing signs of fear (screaming, low tail, head high)
Seeking rescue	Running towards other individuals in fear (e.g., screaming, low tail, head high) and hiding under/behind them for protection
Rescuing	Standing over/in front of other individuals for protection, after that individual ran towards them to seek rescue (see above)
Threatening	Pacing towards something, head, trunk, and ears high, sometimes trumpeting

The Social Distance Method measured the distance between calves and mothers, dividing the distance into five parameters: *tactile contact*, *<1 m*, *1-3 m*, *3-5 m*, and *>5 m* [26; 28; 31]. The distance was noted every 60 seconds using continuous sampling. This parameter was used to analyze the mother-calf relationship [6].

Utilizing the ethogram and Focal-Animal-Sampling, the general behavior of the calves was observed. This data was used to generate a behavioral profile of the calves of different origins [26; 28; 31-33]. Here again, the interval for data registration was 60 seconds using continuous recording.

Additionally, the calves' social behavior within the family units was measured. Therefore, all affiliative and agonistic contacts, either initiated or received by the calves, were measured. This data was collected using continuous recording [26; 28; 31-33].

Data collection in zoos took place between 2016 and 2021 and in the wild from February to March 2023. Each calf of the F1 and F2 *ex situ* generation was observed for 15 hours, resulting in an observation time of 120 hours for each sample group. For the *in situ* sample group, observation time was also 120 hours. However, here, calves were not observed for 15 hours but ~3-4 hours each, as the single individuals could not be tracked again reliably. Data *in situ* and *ex situ* was only collected when animals could behave freely without human interactions. During *in situ* data collection, observers held a significant distance from the family units (at least 200 meters). They used binoculars for a better view, ensuring that calves and family units were not influenced in their behavior by human presence.

2.2. Data analysis

For data analysis, all data sets were classified numerically by summing up all data to a joined maximum of 100 % [34-36]. Data for calves was additionally sampled according to age group for statistical analysis [4-6]. As all sample groups were chosen to be age matched in sample size, we did not include age as a variable. Statistical analysis was performed with SPSS version 29 (IBM SPSS Statistics 29). All data sets were tested for distribution with the Shapiro-Wilk Test and the Kolmogorov-Smirnov-Test [37]. As neither of the tests resulted in a homogenous or even distribution of the data sets, a graphical analysis of the Q-Q plots was used. All data sets were identified as non-parametric [38-39]. Therefore, the Kruskal-Wallis calculation detected significant differences between the three sample groups (F1 *ex situ*, F2 *ex situ*, and *in situ*). In the case of significances, a Post-Hoc Test was calculated to detect which sample groups showed differences [40-41]. For all calculations, the level of significance was set at $p \leq 0.05$ (normal significance) and $p \leq 0.001$ (strong significance) [42-43].

3. Results

3.1. Distance to mother

Statistical data analysis on the distance between calves and their mothers with the Kruskal-Wallis Test detected significant differences. We found that *in situ* living calves predominantly spend time in tactile contact with their mothers (M = 58.11 %), in comparison to *ex situ* of the F1 (M = 7.22 %) and F2 generation (M = 15.27 %) (Figure 1). Calves of the F1 and F2 zoo generations spent the majority of time in the distance category *<1 m* to their mothers (F1: M = 35.05 %, F2: M = 32.50 %). It can also be seen that calves living in the wild barely spend time at a distance further than 1 m from their mothers.

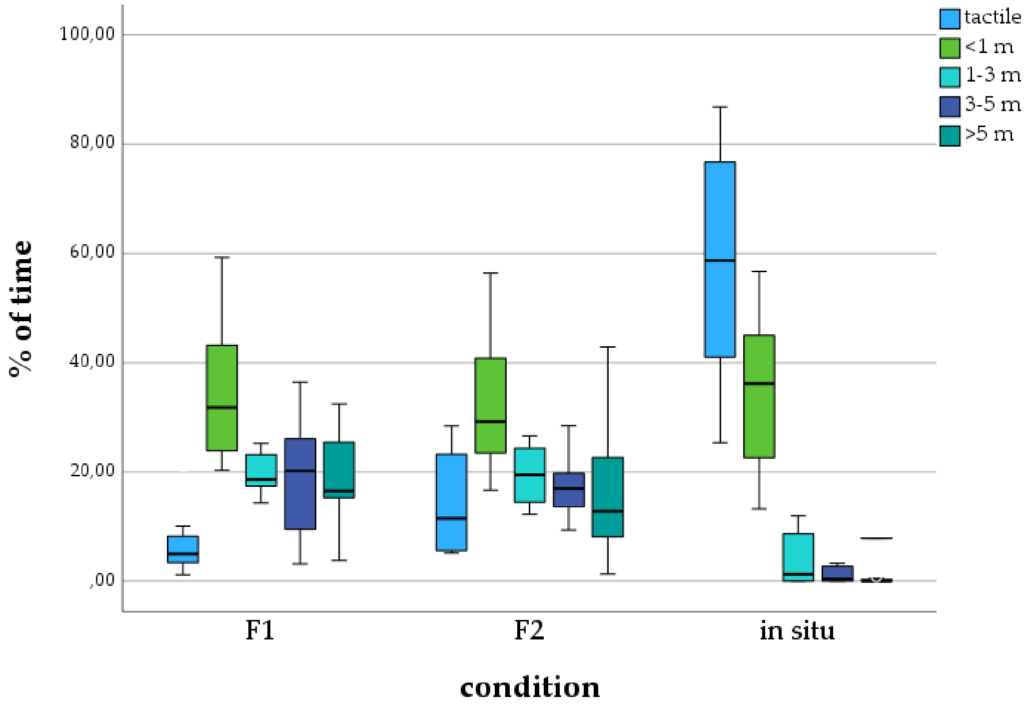

Figure 1. Percentage of time calves spend in a distance category to mother, depending on generation/environment.

Comparing the data of calves of the F1 zoo generation and the wild with the Post-Hoc Test, significant differences were detected in the distance categories *tactile, 1-3 m, 3-5 m,* and *>5 m*. The difference between the F1 zoo generation and wild calves was not significant for the distance category *<1 m*. Calves of the F2 zoo generation and the the wild also showed significant differences for the categories *tactile, 1-3 m, 3-5 m,* and *>5 m*. The comparison of the data on distance to the mother did not detect any significant differences between calves of the F1 and F2 zoo generations (see Tab. 4).

Table 4. Kruskal-Wallis calculation and Post-Hoc Test for the position of calves to their mothers, depending on generation/environment.

Kruskal-Wallis			**tactile**	**<1 m**	**1-3 m**	**3-5 m**	**>5 m**
Kruskal-Wallis H			15.495	.222	15.082	13.113	13.995
df			2	2	2	2	2
Asymp. Sig.			<.001	.895	<.001	.001	<.001
Monte Carlo Sig.	Sig.		<.001	.897	<.001	<.001	<.001
	99% Confidence Interval	Lower Bound	.000	.889	.000	.000	.000
		Upper Bound	.000	.905	.000	.001	.001

Post-Hoc						
Sig.	F1/F2	.224	.651	.819	.887	.570
	F1/*in situ*	<.001	.895	<.001	.002	<.001
	F2/*in situ*	.007	.740	.001	.002	.003

3.2. General behavior

Calves of the F1 and F2 zoo generation mostly displayed the behavior *eating* (F1: $M = 39.703$, F2: $M = 35.13$), followed by the behaviour *affiliative contact* (F1: $M = 12.435$, F2: $M = 14.944$) (Figure 2). *In situ* calves, on the other hand, mostly showed *affiliative contact* ($M = 48.22$). No other behaviour was recorded as often as the three categories mentioned above.

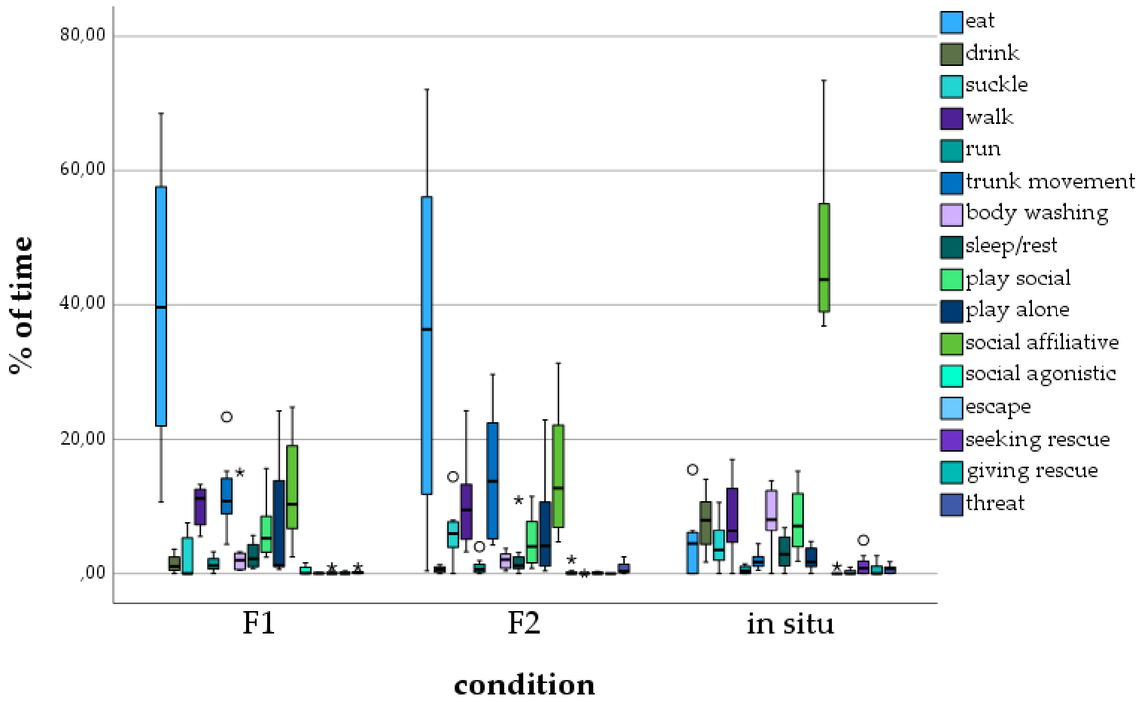

Figure 2. Percentage of time calves showed a certain behavior, depending on generation/environment. °= outlier, * = extreme outlier.

The statistical analysis (Table 5) of the amount the behavioural categories were shown (see Table 3) by calves of the F1 and F2 generation *ex situ* and living *in situ* revealed significant differences between calves of the F1 generation and *in situ* and also of the F2 generation and *in situ* in the five behavioral categories *eat* (*in situ<ex situ*), *drink* (*in situ>ex situ*), *trunk movement* (*in situ<ex situ*), *wash* (*in situ>ex situ*) and *affiliative behavior* (*in situ>ex situ*). For the behavioral categories *suckle, walk, run, wash, sleep, social play, lone play, escape, seeking rescue, rescuing,* and *threatening*, no significant differences were found between *in situ* and F1 *ex situ*, as well as *in situ* and F2 *ex situ*. Significant differences between the F1 and F2 generations were only detected for the behavioral category *suckle* (F1<F2).

Table 5. Kruskal-Wallis calculation and Post-Hoc Test for the general behavior of calves, depending on generation/environment.

Kruskal-Wallis			**eat**	**drink**	**suckle**	**walk**	**run**	**trunk move.**	**wash**	**sleep**	**social play**	**lone play**	**affiliative**	**agonistic**	**escape**	**seek resc.**	**rescue**	**threat**
M	F1		39.703	1.459	2.264	10.105	1.415	11.924	3.335	2.679	6.495	7.121	12.435	.453	.058	.164	.104	.236
	F2		35.13	.616	6.179	10.398	1.048	14.56	1.955	2.47	4.88	6.869	14.944	.31125	.004	.088	.0	.778
	in situ		4.566	7.713	4.3	8.032	0.536	1.939	8.431	3.206	7.884	2.225	48.22	.13	.225	1.273	.606	.653
Kruskal-Wallis H			12.026	14.443	3.879	.945	2.720	14.495	6.335	1.165	1.565	.665	15.405	3.569	2.658	4.648	3.063	1.682
df			2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Asymp. Sig.			.002	<.001	.144	.623	.257	<.001	.042	.559	.457	.717	<.001	.168	.265	.098	.216	.431
M.C. Sig.	Sig.		.001	<.001	.147	.647	.267	<.001	.039	.580	.474	.733	<.001	.156	.279	.101	.313	.447
	99%	L.B.	.000	.000	.138	.635	.256	.000	.034	.567	.461	.722	.000	.147	.267	.093	.301	.434
	C.I.	U.B.	.002	.000	.156	.660	.278	.000	.043	.593	.487	.744	.000	.165	.290	.109	.325	.460
Post-Hoc																		
Sig.	F1/F2		.620	.339	.049	.750	.327	.777	.860	.447	.437	.646	.832	.214	.103	.921	.100	.269
	F1/*in situ*		.001	.007	.299	.340	.101	.002	.037	.777	.646	.724	<.001	.064	.454	.056	.765	.254
	F2/*in situ*		.006	<.001	.352	.525	.510	<.001	.024	.297	.216	.416	.001	.541	.379	.069	.179	.972

3.3. Social behavior

The boxplots in Figure 3 demonstrate that calves of the F1 zoo generation initiated affiliative behavior of *M* = 91.41 % and agonistic behavior of *M* = 8.59 %. They received affiliative behavior of *M* = 83.65 % and agonistic behavior of *M* = 13.35 %. Calves of the F2 zoo generation initiated affiliative behavior of *M* = 94.61 % and agonistic behavior of *M* = 5.39 %. They received affiliative behavior of *M* = 85.78 % and agonistic behavior of *M* = 14.22 %. Calves living in the wild received and sent only affiliative behavior. The behaviour initiated by *in situ* calves was 100 % affiliative with no agonistic behavior. Additionally, they received affiliative behaviour of *M* = 98.73 %, with a single outlier.

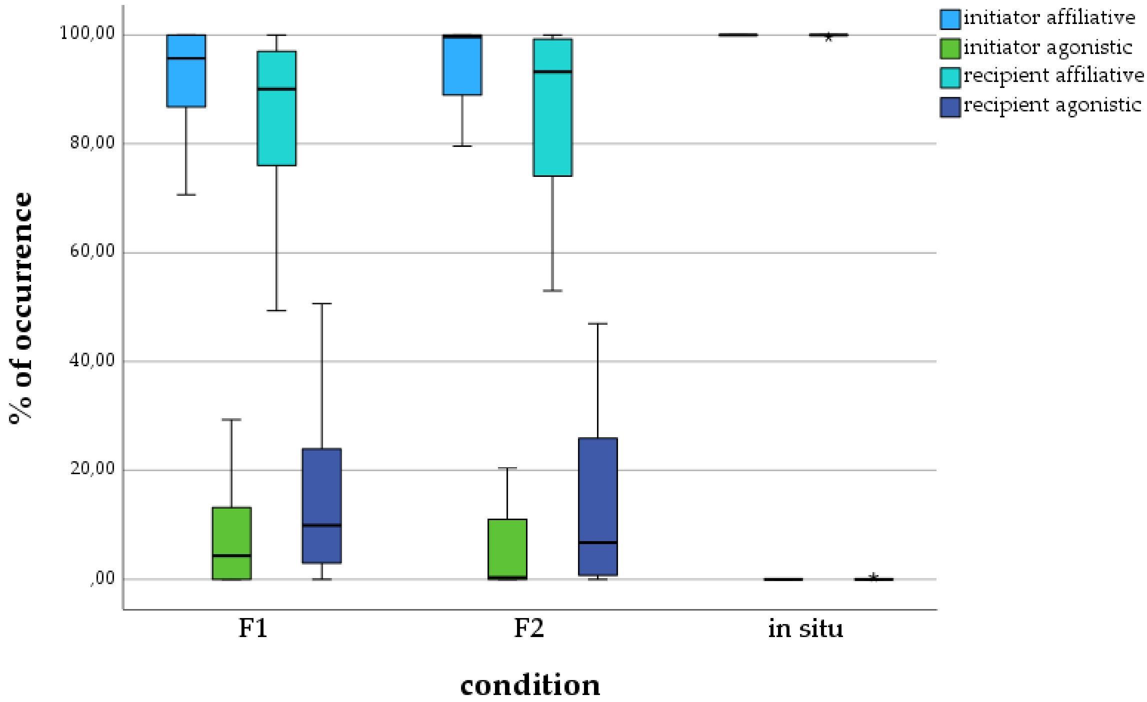

Figure 3. Percentage of affiliative and agonistic behavior initiated and received by calves, depending on generation/environment. * = extreme outlier.

The analysis of the social behaviour of the calves of the three test groups also showed significant differences between calves living *ex situ* and living *in situ* (Table 6). There were no significant differences between the F1 and F2 zoo generations. Significances were detected between the F1 generation and *in situ* calves in all four social behaviour categories. Significant differences were found in received affiliative and agonistic behaviour between the F2 generation and calves in situ.

Table 6. Kruskal-Wallis calculation and Post-Hoc Test for agonistic and affiliative behavior as initiator and recipient for calves, depending on generation/environment.

Kruskal-Wallis	affiliative initiator	affiliative recipient	agonistic initiator	agonistic recipient
Kruskal-Wallis H	6.105	6.105	7.581	7.581

df			2	2	2	2
Asymp. Sig.			.046	.044	.018	.019
Monte Carlo Sig.	Sig.		.046	.044	.018	.019
	99% Confidence Interval	Lower Bound	.041	.039	.015	.016
		Upper Bound	.051	.049	.022	.023
Post-Hoc						
Sig.		F1/F2	.649	.576	.649	.576
		F1/*in situ*	.022	.010	.022	.010
		F2/*in situ*	.050	.037	.050	.037

4. Discussion

The results of the distances between calves and their mothers confirm the first hypothesis that there are significant differences between African elephant calves living in the wild and zoo environments. Calves *in situ* spending a majority of time at a very close spatial distance to their mothers (*tactile* and *<1 m: M* = 92.78 %), which was significantly higher than for the F1 zoo generation (*tactile* and *<1 m: M* = 42.27 %) and the F2 zoo generation (*tactile* and *<1 m: M* = 46.78 %), agrees with former observations of Webber [12]. She states that *in situ* calves stay almost continuously at a close spatial distance to their mothers and that this is not valid for calves born in zoos. However, while comparing African and Asian calves *in situ* and *ex situ*, Webber only found this in Asian elephant calves living in zoos. Berg [44] also observed captive African elephant calves up to six months of age and observed that they spend 70-75 % of their time in body contact with other individuals. The data at hand first observed a spatial detachment for African calves living *ex situ.* A possible explanation for this spatial detachment between mothers and calves living in a zoo environment is the absence of possible threats (predators, losing the family unit, lack of water). In the wild, a close spatial bond with the mother elephant is crucial for the calf's survival [2; 6; 45].

The second hypothesis of this study that those differences might increase with the F2 zoo generation was not confirmed by data on the distance kept by calves from their mothers. The present study's data detected no significant differences between the distance keeping of the F1 and F2 generations. The significance level even decreases from strong to normal with the generations. We interpret the increasing spatial detachment between calves and mothers observed in zoos not as an issue of concern regarding elephant breeding in zoos. Furthermore, previous studies on adult F1 *ex situ* generation elephants detected species-specific social behavior and bonds that subsist over years and generations [46-47].

The data for general behaviour of calves living *in situ* collected in this study for 16 behavioural categories resemble those described by other researchers [2; 6; 48], as does the data for the calves from zoos [12; 49-51].

Other than the data on the distances between calves and mothers, the data on the general behaviour of the calves do not display as many significant differences between *in situ* and *ex situ* calves of both generations. The calves of the sample group *in situ* were observed to spend significantly more time drinking and washing. The observation spot can explain this, as data *in situ* were frequently collected close to a water hole when families moved out of dense bushe and could be easily observed. Hence, calves spent much time drinking and bathing on those occasions.

Calves *in situ* spent less time eating than calves of both generations *ex situ*. A possible reason is that animals must feel safe eating [2]. In the wild, calves were observed to be more anxious than in the zoos and, therefore, might spend less time eating than calves in zoos, which are constantly in a safe environment. Additionally, elephants in zoos have access to food almost continually and can eat without stress and fear [52-53]. *In situ*, elephants must feed in the open bush or grassland [17]. *Ex situ* calves of this study had constant access to food in the form of hay, branches, and occasionally fruits and vegetables. However, during our observation in the wild, calves also had constant access to food, such as grass and branches. As observations were made in March and April, the vegetation was dense due to the rainy season.

The behavioural category, *trunk movement*, was displayed significantly less frequently by calves living in the wild. A possible reason for calves living in zoos displaying this behaviour more frequently is that calves in an *ex situ* environment have more time to train their trunk instead of concentrating on following the mother and the family. It can be assumed that the protected environment leads to quicker development, as can also be noted by an earlier start of breeding [16; 19]. The more leisure behavior observed in this study's calves agrees with Webber et al.'s interpretations [54]. They observed that *ex situ* African and Asian elephant calves spend more time playing than *in situ* calves. They also conclude that this difference originates from the more peaceful zoo environment that gives calves more opportunities for playing behavior [54]. Another possible explanation for this difference is that calves *in situ* have more other occupations besides playing. In the wild, they must gain ecological and social knowledge and specific skills to ensure survival [4-6; 9]. This is not required in zoos.

The strongly significantly higher affiliative behaviour displayed by calves from the wild compared to the F1 and F2 generation in zoos indicates differing social behavior for calves living in these different environments. A possible reason for this the ever-changing presence of other elephants, independent of the family, in the wild. Zoo elephants live in generally stable family units that change less frequently than in the wild. The number of changes in nearby animals likely impacts the affiliative behavior of calves in the wild, which depends on the care and positive reactions of other elephants and, therefore, almost solely displaying affiliative behavior [2; 15].

Similar to the data for the distance between mother and calf, data on the general behaviour of the calves showed no trend of an increase in the differences between *ex situ* and *in situ* calves with the next generation of zoo elephants.

The amount of affiliative behaviour initiated and received by calves from the zoo in this study is significantly lower than that in the wild, where they are known to be treated with intense care and affiliative behavior by family members [2; 17; 45; 55-56]. Also, the distribution of affiliative and agonistic behavior between *ex situ* and *in situ* calves differs in this study, as the *in situ* sample group was barely observed to initiate or receive agonistic behavior. Nevertheless, the *ex situ* calves also initiated and received significantly more affiliative than agonistic behavior, corresponding to the wild's social behavior [2; 45; 55]. A possible reason for the lower amount of social behavior recorded for zoo calves is the enrichment and safety that the zoo environment supplies. While in the wild, calves must stay close, follow, and be in contact with their mothers almost constantly [2; 17; 45; 55]; the safe zoo environment allows them to devote themselves to other activities. This also enhances the faster development of elephants in zoos [16; 19].

Also, affiliative behaviour is less crucial for calves living in zoo environments, as they live in rarely changing social groups. Many young animals display more affiliative than agonistic behaviour in wild environments [57].

While many behavioural patterns of *in situ* and *ex situ* calves differ significantly in the study at hand, studies on adult African elephants of the F1 generation detected species-specific social behavior, with a strong majority of affiliative behavior initiated and received by family members, as stated before [46-47]. Hence, the question of whether differences in social behavior between *ex situ* and *in situ* living African elephants increase with the generations cannot be answered in this paper.

5. Conclusions

Despite the varying sample sizes and observation hours per animal, the present study found significant differences in the distance keeping, general and social behavior of *in situ* and *ex situ* African elephant calves to their mothers and other family units or family members. These findings agree with former findings on Asian elephant calves in zoos by Webber [12]. However, they did not make the same observations for African elephant calves [12].

Calves living in a safe environment are not hesitant to separate earlier from their mothers, as this involves less risk for them. *Ex situ* calves are less hesitant to contact other elephants with agonistic behavior. Additionally, instead of following their mothers and keeping social contact with the family members like in the wild, calves in a safe zoo environment have more time to observe, learn, play, adapt social behavior, eat, and compete and, therefore, can develop quicker. This faster development of *ex situ* calves corresponds with the earlier maturity and breeding of zoo elephants [16; 19]. African elephant calves *ex situ* are more independent than in the wild and spend more time eating and interacting with others, following the faster growth rate and the general pattern of enhanced development rates *ex situ* [16; 19].

If zoos continue to breed elephants to generate a self-sustaining population – which is necessary, as the import of wild elephants is considered outdated [23] – it needs to be ensured by ethological research that the elephants bred and socialized there show (social) behaviour that does not indicate a negative impact on their wellbeing. Social interactions and touch in captive elephant calves are highly relevant during early development and associated with prosocial behavior and elephant welfare [13]. Therefore, falsifying hypothesis two is essential, as this is reassuring for the *ex situ* breeding program, which seeks to establish an independent stock of zoo elephants living under the best welfare conditions [19].

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Data available statement: Please contact franziska.hoerner@uni-wuppertal.de for data.

Ethics approval statement: Not applicable, as the study required no interaction with the animals.

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3.4.1 Conclusive summary study IV

There is a broad field of *in situ* and *ex situ* research on African elephants and knowledge of both sides is frequently adapted [Andrews et al., 2005; Archie et al., 2006; Ortolani et al., 2005; Plotnik et al., 2014]. However, it was never investigated whether elephants of the two environments behave the same; hence, whether an adaption of information is legit. Study IV, therefore, intended to draw a basic comparison of the general and social behavior of African elephant calves living *in situ* and *ex situ* to close this research gap.

Additionally, African elephant calves' breeding in European zoos has increased with rising birth rates in the last fifteen years [EAZA, 2019]. Zoos have now entered the F2 generation of zoo-born African elephants, and the first calves of the F3 generation are already born [Rees, 2021]. However, pilot studies of this dissertation have detected differences in the social distances between calves living in a zoo environment and calves living in the wild [Hörner 2017; 2019]. This lead to the hypothesis that the differences between *in situ* and *ex situ* calves increase with the ongoing generations. Therefore, this study was also designed to detect possible differences between calves of the F1 and F2 generation and *in situ* calves.

120 hours of ethological data were collected for calves of each sample group for a total number of ~122 calves. Data for *ex situ* living calves' F1 and F2 generation were collected in four European zoos. Data for *in situ* living calves were collected in Zimbabwe. The calves' general behavior, social behavior, and the distance between calves and mothers were documented. Data were statistically analyzed with SPSS Version 29, applying the Kruskal-Wallis calculation and a Post-Hoc Test [Benjamini & Hochberg, 1995; Hochberg, 1988].

The results displayed a significant difference in the social distance to the mothers between *in situ* calves and calves of the F1 and F2 zoo generation (F1/*in situ* $p < .001$, F2/*in situ* $p = .007$). *In situ* living calves initiated and received significantly more affiliative and less agonistic behavior than *ex situ* calves (F1/*in situ* $p = .002, .010$; F2/*in situ* $p = .050, .037$). Differences in the general behavioral profile of the three sample groups were marginal.

No significant differences between the F1 and F2 generations of zoo-born African elephant calves were detected. Therefore, the hypothesis of an increase in differences with ongoing zoo generations can be rejected.

The spatial detachment of calves living in zoos might originate from the lack of perils and predators. Additionally, calves living in a safe environment also have more time to learn, observe, play, and show a broader range of social behavior, as observed in this study. Therefore, they also develop quicker. This corresponds with the early maturity and breeding of zoo elephants [EAZA, 2020; Oerke, 2004].

4 Discussion

4.1 Family Bonds in *Loxodonta africana* housed in zoos

The close family bonds and complex social structure African elephants are known for are crucial for this mammal's survival and breeding success with its extraordinarily long gestation period of 20 to 22 months [Moss & Colbeck, 2002]. Only a high survival rate of the offspring and ongoing breeding for a long lifetime can ensure the elephants' persistence [Douglas-Hamilton, 1972; Moss & Colbeck, 2002]. Their key feature to ensure a successful upbringing of their calves are their close and complex family bonds [Douglas-Hamilton & Douglas-Hamilton, 1989; Estes, 1991; Moss, 2001; Moss & Colbeck, 2002].

African elephants express these essential family bonds in various ways. They have an efficient protective strategy for their calves, the raising of the offspring is complexly divided by all members of the herd, and they show intense helping behavior for their conspecifics [Archie et al., 2006; Douglas-Hamilton & Douglas-Hamilton, 1989; Estes, 1991; Hanks, 1972; Lee, 1987; Mcdonald et al., 2009; Moss & Colbeck, 2002; Ortolani et al., 2005; Schulte, 2000]. However, it was never stated whether African elephants also show those family bonds by their olfactory abilities.

Study I, Chapter 3.1 of this thesis, gives empirical proof of olfactory long-term memory in *Loxodonta africana* of up to twelve years. This finding emphasizes how important family members are for elephants, as the memory of their scents is interlocked long-term in their memory. It also proves that African elephants use their sense of smell to maintain their family bonds and that scents can trigger an exclamation of those bonds. In the study, elephants' interest in the scent of their absent relatives exceeded their interest in new or unfamiliar scents. Von Dürckheim et al. [2018] made the same observation for *ex situ* elephants. It also agrees with similar findings by Bates et al. [2008], who stated that elephants living *in situ* mainly inspected olfactory samples of relatives and barely unknown scents. This is remarkable, considering that elephants encounter scents of unfamiliar and unrelated elephants in the wild daily [Bates et al., 2008].

As the environment in zoos strongly differs from the wild, differences in elephants' social and general behavior can arise [Kurt, 2006]. It would be alarming if zoo housing would endorse the loss of the close emotional connection female relatives usually have, as it is the basis for their breeding success [Estes, 1991; McComb et al., 2001; Moss & Colbeck, 2002]. However, the data of the intense behavioral reactions by the elephants in study I give evidence for close family bonds in zoo-housed and zoo-socialized African elephants, corresponding to the social bonds *in situ* [Archie et al., 2006; Payne, 2001].

Testing the social bond within a zoo environment is barely possible, as elephants live in fixed herds without contact with other elephants [Douglas-Hamilton & Douglas-Hamilton, 1989; Garaï & Kurt, 2006; Kurt, 2006; Moss & Colbeck, 2002], and chances to live in a fission and fusion structure are minimal. Therefore, observing the reunifications in study II was a unique opportunity to investigate those bonds in zoo elephants. After expressing the markedness of the close family bonds of zoo-housed *Loxodonta africana* caused by scent, the follow-up study on reunifications of female elephants gives evidence for those family bonds when elephants encounter the other individual. Performing an entire Greeting Ceremony reserved for close family members testifies to the elephants' closeness [Poole & Granli, 2021]. A picture of the Greeting Ceremony performed by two of the females in study II can be seen in Figure 4.1.

Fig. 4.1: Daughter elephant (left) and mother elephant (right) greeting on reunification after two years [Müller, 2020].

Checkups after the reunifications showed that the reunifications were successful in the long-term. The related females accepted each other as family members, and the mother elephants recognized their grandchildren as their offspring. In one case, the grandmother elephant tolerated its grandchild to allosuckle from her breast (see Figure 4.2), which testifies to the closest family bonds [Lee, 1987; Moss & Colbeck, 2002].

Fig. 4.2: Elephant family after reunification, with grandchild allosuckling from grandmothers' breast [Müller, 2020].

The study also shows that the zoo-housed females encounter their relatives with a significant amount of affiliative behavior, which is further evidence for close family bonds, as affiliative behavior is a characteristic of the social structure among elephant herds [Douglas-Hamilton & Douglas-Hamilton, 1989; Estes, 1991; Moss, 2001; Poole & Granli, 2021]. On the other hand, the reluctance to encounter unknown elephants demonstrates the significant difference in behavior between related and unrelated elephants [Moss & Colbeck, 2002; Poole & Granli, 2021].

An interesting observation concerning the different family bonds investigated in study I is that mother elephants reacted stronger to the scent of their absent daughters than vice versa. These findings indicate that the mother-offspring bond in African elephants is stronger than the offspring-mother bond. So far, there is no other study on elephants with similar observations. However, other mammals, such as chimpanzees living in a fission-fusion society with strong family bonds, display similar behavioral patterns [Kakinuma, 2016; Maestripieri, 2001]. A possible reason for this discrepancy in the reaction in elephants is the different relationships mothers and daughters have within the matriarchal group structure of elephants. While mother elephants seek to protect and keep their families together throughout their lives, it is natural for the daughters to survive their mothers [Moss & Colbeck, 2002]. It is a logical event for the daughters to lose their mothers at a certain point. Encountering remainders, even the scent of their mothers, should, therefore, not cause or motivate further reactions. Rediscovering a lost female offspring, on the other hand, might cause searching behavior and trigger a stronger behavioral reaction.

When observing the family bonds of zoo-kept African elephant calves in studies III and IV, the results show a different picture than study I and II. While no significant differences between the mother-child bond between the three holding systems and the size of the elephant enclosures were detected, results indicate a decrease of tactile contact between calves and mothers of the holding system *free contact* and a general decrease of tactile contact between *in situ* and *ex situ* calves. Tactile contact with the mother animals is essential for mammals' social and neurological development [Dunbar, 2010; Jablonski, 2021]. Hence, a decrease in tactile contact requires further attention. A possible reason for the minor tactile contact in the holding system *free contact* is the position of carers. Carers must be of the highest dominant rank to interact with the elephants in direct contact, even exceeding the matriarch [Bossy, 2019]. This rank and the amount of tactile contact the carers give may affect the calves' urge to be in direct contact with their mothers. The significantly lower amount of tactile contact between *ex situ* calves and their mothers detected in study IV likely origins from the lack of predators and threats in zoo environments. While *in situ* the close spatial bond to the mother elephant is essential for the calf's survival [Estes, 1991; Lee & Moss, 2011; Moss, 2001], this is not the case in zoos. Mothers and calves *ex situ* are unaware of threats and might loosen the close bond.

The investigations on family bonds in this dissertation give varying results. The adult females in studies I and II display strong family bonds, and the calves in studies III and IV show family bonds that differ from their conspecifics in the wild. A possible explanation for this is that the females in studies I and II were all either born in the wild or of the F1 generation of zoo-born elephants and might express social bonds equivalent to the bonds of African elephants in the wild. It is more likely that the differences detected for the calves in studies III and IV are not so severe that they will crucially influence their social bonds when they are adults. The finding of study I and II supports the hypothesis that adult females of the F2 generation also display close social bonds, as the females Tana and Panya (both elephants of the F2 generation) showed species-specific behavior during both studies [Hörner et al., 2021; Hoerner et al., 2023].

4.2 Species-specific social behavior of *Loxodonta Africana* in zoos

Ensuring that elephants living in zoos account for species-specific social behavior is essential for keeping and breeding them under human care [Andrews et al., 2005; Kurt, 2006]. The generic behavior of the animals is vital for zoos and part of their ethos, as noted in the EAZA statement [2019].

Data from studies I and II give positive findings regarding the species-specific behavior of zoo elephants. The elephants of study I are all zoo-housed. All of them reacted strongly to the familiar scent of their absent relative. They thereby gave credit to a close family bond in *Loxodonta africana* living *ex situ*, an essential species-specific element of the social behavior of the African elephant [Poole & Granli, 2021]. The elephants' indifferent reaction to the scent of unfamiliar elephants is equally species-specific. Wild elephants encounter unfamiliar scents (also of other elephants) daily, which is no incidence of concern [Bates et al., 2008]. Therefore, a reaction to those scents is not expected. Hence, the behavioral reactions to the various scents in study I all testify to species-specific behavior and are reassuring for the *ex situ* breeding program.

The related zoo elephants in study II performed an entire Greeting Ceremony on (re)unification. They displayed species-specific social behavior, as the Greeting Ceremony is a characteristic behavioral pattern of African elephants and was only been reported for wild elephants so far [Poole & Granli, 2011]. The elephants of the study were either zoo-born or lived under human care since they were two years old. They were mainly socialized in a zoo environment and had no opportunity to learn the behavior of the Greeting Ceremony in the wild. This indicates that the Greeting Ceremony is genetically determined in the species.

When wild elephants meet unknown conspecifics, they usually react cautiously and reluctantly when encountering those individuals [Moss & Colbeck, 2002; Poole & Granli, 2011]. Other herds are always resource competitors [Moss & Colbeck, 2002]. Social interactions are mostly limited to Bond Groups and clans [Estes, 1991; McComb et al., 2001]. Therefore, the reluctance and agonistic behavior of unrelated females in study II during unifications is species-specific.

4.3 Differences *in situ* and *ex situ*

Studies III and IV detected minor significant differences in the calf-mother bond and social behavior between African elephant calves living *ex situ* and *in situ*.

Compared with other studies on social bonds of *in situ* living calves, the results of study III display some differences in the tactile contact between *in situ* and *ex situ* living calves [Estes, 1991; Lee & Moss, 1986; Moss & Colbeck, 2002]. This finding was further investigated in study IV, where data for wild-living African elephant calves was collected firsthand. For some measured parameters significant differences in the mother-child bonds and the social behavior of African elephant calves living *in situ* and *ex situ* were detected here. According to the data, calves observed *in situ* spend significantly more time at a close distance to their mothers than calves of the F1 and F2 *ex situ* generations. This data agrees with similar findings by Webber [2017] and Freeman et al. [2021], who also registered a spatial detachment of *ex situ* elephant calves to their mothers. It is likely that this difference in the social bonds in the different environments is caused by the absence of threats in zoos, such as predators or the danger of losing the herd [Moss & Colbeck, 2002]. Maintaining a close spatial bond with their mothers and the rest of the herd is essential for the calves' survival *in situ* [Estes, 1991; Lee & Moss, 2011; Moss, 2001]. However, this necessity is not given in captivity and calves can roam more freely and independent from their mothers and under no perils.

In the wild, calves are treated with intense care and affiliative behavior by the rest of the herd and mainly initiate affiliative behavior themselves [Douglas-Hamilton, 1972; Douglas-Hamilton & Douglas-Hamilton, 1989; Estes, 1991; Moss, 2001; Pinter-Wollman et al., 2009]. Data from study IV show significant differences in the amount and distribution of affiliative and agonistic behavior initiated and received by calves *in situ* and *ex situ*. The total positive social interactions were significantly higher for calves living in the wild. Additionally, calves in the wild indicated and received significantly more affiliative and less agonistic behavior than calves in zoos. The most likely reason for those differences is the severe difference in the environment calves of the different sample groups live in. To this point, no other study registered such significant differences in the social behavior and social bond of *in situ* and *ex situ* living elephant calves. The safe zoo environment allows the calves to spend more time playing, interacting with other individuals, and practicing trunk movement [Webber, 2017], and also to display a wider range of social behavior. This can result in a faster development of *ex situ* calves, which is also displayed in their earlier maturity and breeding [Oerke, 2004].

The hypothesis that the detected differences in the social bonds of *in situ* and *ex situ* calves increase with the ongoing breeding of zoo elephants were not verified in study IV. No significant differences were detected in the mother-calve bond and the social behavior between the F1 and F2 generations. This finding is reassuring, considering the strongly significant differences between *in situ* and *ex situ* found in study IV. It is unlikely that the differences detected in study IV will have a long-term impact on the individuals social behavior, as all differences that were noted can be traced down to outward influences, such as the absence of perils and the safe environment. It can be hypothesized that the *ex situ* individuals of this study would show the same behavior as their conspecifics *in situ*, if released into the wild.

4.4 Olfactory long-term memory

Study I was performed with a small number of elephants. Nevertheless, the behavioral reactions of the elephants in this study prove that those females recognized their relatives' scent after two and twelve years of separation. Therefore, they give empirical proof of an olfactory long-term memory of up to twelve years. It is the first time such a long memory was empirically proven for the olfactory sense. von Dürckheim [2021], so far only gave evidence for an olfactory long-term memory in elephants for one year. Rasmussen [1995a] observed that a wild bull showed signs of recognition when smelling its mother’s feces after 19 years. However, this was a mere observation, not a test in a scientific setting, and it is unknown whether the bull had never encountered its mother or her scent in those 19 years.

From a scientific perspective, the findings of study I are extraordinary. Knowing that elephants have such a long memory sheds light on their cognitive abilities. This newly gained knowledge of their intelligence is essential for the handling and interactions with this species, which will be further discussed in Chapter 4.6.

4.5 Design of a new method: olfactory test and prediction for reunifications

The olfactory test designed for study I can be regarded as a practical tool in two ways. Firstly, it can be applied to test the olfactory abilities of elephants to gain knowledge of their skills and long-term memory. Secondly, the designed test can indicate the elephants’ reactions during (re)unification. The tested elephants of study I were all reunited shortly afterward, which was monitored in study II. The positive behavioral reactions to the scents of their absent relatives in study I was confirmed by their positive reactions during reunifications. Hence, the forecast of study I is proven right in study II.

Additionally, elephants showed a lack of interest in the unknown scent sample in study I. When meeting unknown elephants in study II, the elephants encountered those with reluctance and negative connotations. Here, the olfactory test could also forecast the elephants' reactions during unifications.

A new approach would be to use the olfactory test to familiarize elephants with the scents of unknown elephants before unification. Their reactions during unifications could not only be predicted, but the elephants might be less anxious during first encounters, as the scents would not be unfamiliar anymore.

4.6 Indications for holding in zoos

The gained information of the projects of this dissertation can be used as indications for the holding and handling of African elephants in zoos. As pointed out above, the olfactory test designed in study I can be used for further testing of the olfactory abilities and memory of elephants. It can also be used to forecast the elephants' reactions during (re)unification and be of practical use for the carers who facilitate (re)unification. If the previous olfactory test indicated that females are positively excited to see their relatives again, elephants are most likely not showing agonistic behavior during reunifications. Furthermore, the olfactory test can sensitize the elephants with unknown scents to reduce stress and agonistic behavior during unifications. However, further research is needed to test this hypothesis.

In a wild environment, it is not common for related females to be separated. Females usually stay together their entire lives [Moss & Colbeck, 2002]. Herds only split when they become too big or when resources are limited [Kurt, 1994a; Mcdonald et al., 2009]. However, even then, they still belong to the same Bond Groups and interact frequently [Archie et al., 2006; Moss, 2001; Payne, 2001]. When females are separated due to limited space in zoos, the separation is ultimate. This does not correspond to their natural social structure [Moss, 2001; Payne, 2001]. The two mother-daughter pairs of studies I and II displayed close family bonds throughout both projects. Those detected close family bonds give crucial indications for the handling of African elephant herds in zoos. The studbooks for African elephants should not separate related females, as their bonds are tense, and it can be assumed that those separations cause the animals' emotional disturbance [Moss & Colbeck, 2002; Poole & Granli, 2021]. As the European studbook for *Loxodonta africana* decided to avoid such separations of related females in the future, they already followed those indications [EAZA, 2019].

The behavior of the females during unifications in study II indicates that unifications need to be conducted with extensive caution to ensure the animals' safety and welfare. All females showed reluctance and negative agitation during unifications, corresponding to elephants' behavior in the wild, where unknown herds and elephants are regarded cautiously and can be considered competitors for resources [Moss & Colbeck, 2002]. Uniting and holding unrelated females together is an unnatural holding concept. Nevertheless, many zoos successfully hold merged groups, such as Zoo Wuppertal and Tierpark Schönbrunn.

Study III found no significant differences between social and general behavior and the mother-child bond, considering the holding system and enclosure size. Therefore, those results do not indicate which holding system is the best for the welfare of elephant calves. However, slight differences were detected in the amount of tactile contact between calves and mothers in the holding system *free contact*. As pointed out above, a possible explanation for this is the dominant position of the carers in this holding system [Bossy, 2019]. Therefore, carers of all facilities should reduce contact with the animals to a minimum. By 2030, this holding system shall be abandoned in all European zoos, as it is considered outdated [EAZA, 2019]. Those differences might not be of concern long-term. Nevertheless, the impact the change from *free contact* to *protected contact* might have on the social bonds of elephant calves requires further investigation.

Results of study IV detected significant differences in the spatial attachment of calves and their mothers and the social behavior of *ex situ* calves of the F1 and F2 generation compared to *in situ* calves. Calves of both zoo generations stayed less close to their mothers and showed less social behavior and social behavior with an agonistic connotation. Those differences might not affect their social behavior long-term, as the adult elephants of studies I and II that were socialized in zoos displayed species-specific social bonds and behavior. This hypothesis is supported by similar studies on the social behavior of zoo-socialized elephants [Pinter-Wollman et al., 2009; Schulte, 2000]. Also, no increase in the differences between *in situ* and *ex situ* was detected in the F2 generation.

Nevertheless, the results of study IV still give indications for the handling of African elephants in zoos that are similar to those of study III. Results of study IV support the indication that carers should minimize their tactile contact with the elephants. Studies have shown that holding and handling zoo animals similar to their natural environment is advisable as it increases their welfare [Andrews et al., 2005; Garaï & Kurt, 2006; Ortolani et al., 2005]. This would include a reduction of human interaction. Additionally, facilities should provide enrichment for the animals to prevent behavioral patterns that might lead to stereotypies, like the extensive locomotion of the trunk, as observed in *ex situ* calves of study IV [Elzanowski & Sergiel, 2006].

5 Conclusion

This thesis gives heterogeneous results on zoo-housed African elephants' family bonds and social behavior. Studies I and II testify to close bonds between the related females and species-specific behavior in interactions during unifications and reunifications. Studies III and IV indicate decreases in the spatial bonds between mothers and *ex situ* to *in situ* calves and, therefore, differences to the species-specific behavior known from calves in the wild. However, it is unlikely that the detected differences in the spatial attachment of the studied zoo calves have a long-term impact on their social behavior. Results of studies have shown that even calves of the F2 generation that were almost solely socialized by likewise zoo-born elephants show adequate social structures, behavior, and breeding success when they reach adulthood [Andrews et al., 2005]. Studies on primates detected that decreasing tactile and social contact during the animals' childhood has a negative impact on later breeding success [Dunbar, 2010; Jablonski, 2021]. This cannot be confirmed for elephants in zoos and the adult females of this project that show successful breeding [Andrews et al., 2005].

Additionally, the elephants in studies I and II likewise showed close family bonds, and they were also socialized in zoos. The analysis in study IV did not detect an increase in differences between *in situ* and *ex situ* calves. Hence, it can be assumed that those differences will not increase with future generations. Suppose the mother elephants keep showing affiliative behavior and maintain close family bonds, as detected in studies I and II, they will keep passing this on to their calves [Archie et al., 2006].

The detected decrease in social behavior shown by *ex situ* living calves and the shift towards more agonistic behavior in study IV indicate another non-species-specific behavior. However, as these changes also do not increase within the generations and mothers predominantly show species-specific behavior towards their calves, including a majority of affiliative contacts, it is unlikely that those differences will affect the elephants' behavior when they grow up. Nevertheless, close observations and long-time ethological studies on zoo-born elephants are required to rule out any development of atypical behavior.

Study I gives the first empirical evidence of an olfactory long-term memory of up to 12 years in *Loxodonta africana*, which gives new insights into this species' immense cognitive abilities. Study I also shows that elephants can recognize kin from non-kin just by scent. Also new is the finding that zoo-socialized African elephants perform a full Greeting Ceremony. This likewise proves the close family bonds and species-specific behavior of zoo-housed elephants, as this behavior was only observed in wild elephants so far [Poole & Granli, 2011].

A new and interesting finding is the stronger reaction of mothers in study I, which indicates stronger bonds from the mothers' side. This is the first observation of this kind made in *Loxodonta africana*. It agrees with social bonds known from other mammals [Kakinuma, 2016; Maestripieri, 2001]. It seems logical that mothers react stronger to the scent of an allegedly lost daughter, as the herd structure of elephants does not intend to separate mothers from their daughters [Moss & Colbeck, 2002]. Daughters, on the other hand, are expected to survive their mothers.

The olfactory test designed in study I is a new method for testing the olfactory abilities and memory of elephants. It can also familiarize elephants with the scent of new individuals before unifications, thereby reducing stress and agonistic behavior during unifications. However, studies to test this hypothesis are needed.

The results of this dissertation's four studies indicate the future handling and breeding of African elephants in zoos. The results of study I and II indicate that related females should not be separated, which complies with the social structures known from the wild [Estes, 1991; McComb et al., 2001; Shoshani et al., 1997; Wittemyer & Getz, 2007]. The results of studies I and II also indicate that separate living females should be reunited, as their behavior on smelling their relatives and reuniting was thoroughly positive. Fortunately, the number of related females living separately is deficient, and the studbook for African elephants made it their goal not to separate related females in the future [EAZA, 2019].

The results of study III give no empirical indication of which holding system initiates the best behavior in calves. However, slight differences between the management system *free contact* and the other two systems indicate that calves in direct contact have less tactile contact with their mothers. Therefore, this study's findings support the EAZA's decision to abandon *free contact* [EAZA, 2019]. Study III and IV's results detected strongly significant differences between *in situ* and *ex situ* living calves for several parameters. This also gives indications for the management of African elephants. To prevent significant decreases in the tactile contact between calves and mothers, carers should reduce contact with the animals to a bare minimum. Additionally, enclosures should provide as much space as possible to imitate the animals' natural habitat. Also, elephants should be provided with enrichment to give them further opportunities for occupation and physical development [Elzanowski & Sergiel, 2006].

As data from studies I-IV give ambiguous results on the similarities of social behavior and bonds of *Loxodonta africana in situ* and *ex situ*, the frequent adaption of data from both research fields is questionable. Data should never be considered valid for both sample groups, and researchers must be aware of the differences the two environments might cause.

The results of all studies conducted for this dissertation indicate that elephants under human care have good welfare conditions. Still, improving the management systems to prevent possible atypical developments in behavior is advisable. Also, long-term studies on the social behavior and development of zoo-born and socialized African elephants must investigate their development and ensure their well-being. If African elephants show behavioral patterns that stand for their welfare, zoos can hold those massive animals without concern. If negative differences in the behavior of their wild conspecifics arise, management needs to be adjusted. As important as the research and breeding of African elephants in zoos is for preserving this beautiful species, this can only be facilitated if the single individuals living under human care have the best welfare conditions and show healthy behavior.

„Die Elefantenhaltung in Zoologischen Gärten wird auch in Zukunft eine der schwierigsten Aufgaben sein, mit denen sich Zoologische Gärten beschäftigen. […] Ziel sollte es sein, natürliche Zuchtprojekte anzuvisieren und zu realisieren.“

(VDZ ,2005, 35)

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7 Appendix

Appendix I

Observation sheet for study I.

Animal:

Date/Time:

Category	Behavioral item	Frequency	Duration
Neutral	Walking around the enclosure		
	Locomotion trunk		
	Eating		
	Body care		
	Comfort behavior		
	Weaving		
Excitement	Folding, lifting, spreading, flapping ears		
	Raising trunk		
	Shaking trunk		
	Raising head		
	Shaking head		
	Raising tail		
	Shaking tail		
	Pacing		
	Pacing backwards		
	Acoustic signals		
	Defecating and urinating		
	Glandular secretion		
	Throwing feces		
	Intense weaving		
Mental processing	Freezing		
	Listening		
	Smelling air		
Sample examination	Sniffing on sample		
	Examining samples with trunk and feed		
	Squashing sample		
	Throwing sample		

Appendix II

Observation sheet for study II.

Animal:

Date/Time:

Ethogram

Affiliative	
Running towards the fence/animal	
Pushing against the fence	
Touching trunks	
Affiliative agitation	
Acoustic signals	
Defecating/urinating	
Agonistic	
Agonistic agitation	
Acoustic signal	
Pacing backwards	
Showing servility	
Showing dominance	
Neutral	
Eating/ drinking	

Behavior of Greeting Ceremony

Behavior	
Running towards elephant	
Clicking tusks and entwining trunks together	
Touching trunk	
Folding, lifting, spreading, and flapping ears	
Raising head	
Opening mouth	
Touching head	
Spinning round	
Lifting tail	
Acoustic signals	
Defecating and urinating	
Glandular secretion	

Distance to animal/fence

Category	
Direct	
> 1 m	
1 m	
2 m	
3 m	
4 m	
5 m	
< 5m	

Appendix III

Observation sheet for studies III and IV.

Date/Time:

Position to mother / Next-Neighbor

Distance		> 5m
tactile contact		
< 2 m		
> 2 m		
< 2 m		
> 2 m		
> 4m		
direct		
close		
middle		
far		

Social Contacts

Initiator positive		
Initiator negative		
Receiver positive		
Receiver negative		

Ethogram Date/Time:

Verhalten		
Nahrungs-verhalten	Fressen	
	Trinken	
	Allosuckling	
	Saugen	
Laufen	Gehen	
	Traben	
Lokomotion Rüssel		
Komfortverhalten		
Körperpflege		
Schlafen / Ruhen		
Spiel-verhalten	Sozial	
	Neutral	
Sozial-kontakt	Affiliativ	
	Antagonistisch	
	Neutral	
Beruhigen	Selbst	
	Andere	
Fluchtverhalten		
Schutz suchen		
Schützen		
Drohen		

List of Abbreviations

abs. n-kin	Absent non-kin
abs. kin	Absent kin
APA	American Psychological Association
Asymp. Sig.	Asymptotic Significance
BBF	Bundesinstitut für Bevölkerungsforschung
CI	Confidence Interval
CITES	Convention on International Trade in Endangered Species
d	Effect Size
df	Degrees of Freedom
EAZA	European Association of Zoos and Aquaria
EEG	European Elephant Group
EEP	European Endangered Breeding Programme
F	Female
F	Fisher-Value
F1/F2/F3 generation	First/Second/Third Filial Generation
Fig.	Figure
g	Gram
IUCN	International Union for Conservation of Nature
km	Kilometer
km^2	Square Kilometer
L.B.	Lower Bound
M	Male
M	Mean
m	Meter
m^2	Square Meters
Md	Median
n	Number
ng	Nano Gram
p	Significance
pres. n-kin	Present non-kin
s./sec.	Seconds
Sig.	Significance

Std.	Standard
t	t-value
t	Tons
U	Mann-Whitney-U-Value
U.B.	Upper Bound
VDZ	Verband Deutscher Zoodirektoren
WBG	The World Bank Group
Z	Standard Deviation of the Median
%	Percent
11-oxo-CM	11-oxo-eti-118 ocholanolone

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2021

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Hiermit erkläre ich, dass ich

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