

Universidade de Évora - Escola de Ciências e Tecnologia

Mestrado em Biologia da Conservação

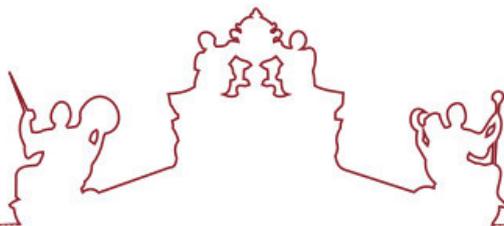
Dissertação

**Chimpanzee-Caregiver Relationships in Captivity: Impact on
Social Dynamics and animal welfare**

Miguel Tomás de Santas Brandão

Orientador(es) | Dietmar Crailsheim
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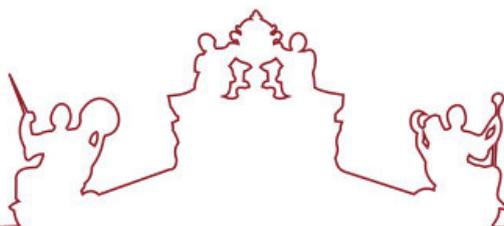
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A dissertação foi objeto de apreciação e discussão pública pelo seguinte júri nomeado pelo Diretor da Escola de Ciências e Tecnologia:

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Index

1. Introduction	1
1.1 Behavioral Ecology	3
1.2 Captive Management	4
2. Materials and Methods	6
2.1 Subjects and Study Site	6
2.2 Data Collection	10
2.3 Statistical Analysis	12
2.4 Social Network Analysis	13
2.5 Linear Mixed Models	14
3. Results	15
3.1 Occurrence of Social Interaction Types	15
3.2 Graphical Representations of Social Networks	19
3.3 Linear Mixed Models	22
3.3.1 Chimpanzee-Chimpanzee Dyads	23
3.3.2 Human-Chimpanzee Dyads	25
4. Discussion	28
4.1 Observed Behavioral Patterns	28
4.2 Dyadic Interactions	31
4.3 Study Limitation and Future Considerations	36
5. References	37
6. Annex	42

Figure Index

Figure 1- Chimpanzee’s subspecies current and historical distribution (from Barratt et al., 2021)	2
Figure 2- View of animal facilities, observation points and visitor’s viewpoints at Fundació Mona: respective animal enclosure labelled in red, green and purple; observation point labelled in dark grey; visitor’s view point labelled in light grey	7
Figure 3- Scaled visual comparison of overall occurrence of Affiliative and Agonistic behaviors.....	18
Figure 4- Social network representations of the 3 groups. Each network is based on one social interaction type (affiliative, agonistic, attention seeking, social vigilance social proximity). Edge weight is proportional to the weighted index value of the interaction pairs. The node layout is based on the force-directed). Edge weight is proportional to the weighted index value of the interaction pairs. The node layout is based on the force-directed algorithm “Spring-Embedded distribution”. Node shape represents specie of the individual (circle for humans and squares for chimpanzees) and the color represents the group (Mutamba is red, Bilinga is green and Sugus is purple). The node labels correspond to the individuals listed in Table 1.	21

Table Index

Table 1- List of biographical information on all chimpanzees housed at Fundació Mona.....	8
Table 2- Simplified ethogram: overview of analyzed behaviors (complete ethogram and definitions can be found in Table 3). Source: Definitions based on Mona Foundation established ethograms, except for “Attention Seeking” based on: (Nishida et al., 1999) and (Hopkins et al., 2006).....	11
Table 3 (Annex) – Complete ethogram with subbehaviors and defenitions. Source: Definitions based on Mona Foundation established ethograms, except for “Attention Seeking” based on: (Nishida et al., 1999) and (Hopkins et al., 2006)	43

Graphic Index

Graphic 1- Percentage of interaction directionality by type of behavior	16
Graphic 2- Percentage of interaction directionality by group	16
Graphic 3- Proportion of behaviors exhibited by each group	18
Graphic 4- Confidence interval plots of Social Proximity interactions and the significant fixed effects (Sex, Age, On-set and Infancy)	24
Graphic 5- Confidence interval plots of Agonistic behaviors and the significant fixed effects (Sex and On-set)	25
Graphic 6- Confidence interval plots of Affiliative behaviors and the significant fixed effects (Human)	26
Graphic 7- Confidence interval plots of Attention Seeking behaviors and the significant fixed effects (Human and Sex)	27

Resumo

Relações Chimpanzés-Tratadores em cativeiro: impacto na dinâmica social e no bem-estar animal

Em cativeiro, fornecer estímulos sociais e psicológicos que consigam garantir o bem-estar ideal para primatas socialmente complexos continua a ser um desafio. Especialmente na gestão de chimpanzés (*Pan troglodytes*), que possuem capacidades cognitivas mais desenvolvidas, há uma necessidade crescente de compreender as suas necessidades sociais quando mantidos em jardins zoológicos, centros de reabilitação, laboratórios e santuários. Os estudos sobre os impactos do cativeiro e as estratégias de enriquecimento têm sido amplamente desenvolvidos em diversas espécies de primatas, embora o papel e o impacto das interações humano-animal em cativeiro ainda não tenham alcançado um consenso na comunidade científica. Este estudo visa desenvolver a compreensão das interações humano-animal, num ambiente de santuário, considerando os humanos como parceiros sociais ativos e incluindo-os nas redes sociais dos chimpanzés. Foram recolhidos dados sobre as interações sociais de três grupos de chimpanzés (*Pan troglodytes*) com conspecíficos e humanos, dentro de cinco categorias comportamentais (Afiliação, Agonístico, Procura de Atenção, Vigilância Social e Proximidade Social) no santuário da Fundació Mona. Ao desenvolver redes sociais e modelos baseados em interações diádicas ponderadas, os resultados indicam que os humanos desempenham um papel numa quantidade significativa das interações sociais diárias dos animais e que os cuidadores integram a estrutura social dos grupos. Além disso, os resultados obtidos realçam o facto de os indivíduos se envolverem com os cuidadores em interações que variam em tipo e força, indicando traços de personalidade e níveis diferenciados de confiança. Estes resultados mostram que o cuidador deve ser considerado nas estruturas sociais de primatas em cativeiro e que esta abordagem pode apresentar-se como altamente benéfica para promover e apoiar a estimulação social no desenvolvimento de protocolos de manejo.

Palavras-chave: Bem-estar animal; Gestão de cativeiro; Interações Humano-Animal; *Pan troglodytes*

Abstract

In captive environments, providing social and psychological stimulation to ensure optimal welfare for socially complex primates remains a challenge. Specially when managing chimpanzees (*Pan troglodytes*), who possess more developed cognitive abilities, there is a growing need to understand their social requirements when housed in zoos, rehabilitation center, laboratories and sanctuaries. Studies regarding the impacts of captivity and enrichment strategies have been widely conducted in several primate species, although the role and impact of human-animal interactions in captivity has not yet reached a consensus in the scientific community. This study aims to further develop the understanding of human-animal interactions, in a sanctuary setting, by considering humans as active social partners and including them in the chimpanzee's social networks. Data was collected on the social interactions of three groups of chimpanzees (*Pan troglodytes*) with conspecifics and humans, within five behavioral categories (Affiliative, Agonistic, Attention Seeking, Social Vigilance and Social Proximity) in the Fundació Mona sanctuary. By developing social networks and models based on weighed dyadic interactions, the results indicate that humans do play a role on a significant amount of the animal's daily social interactions and that caregivers integrate the groups' social structure. Furthermore, our findings underline the fact that the individuals engage with caregivers in interactions that vary in both type and strength, indicating traits of personality and differentiated levels of trust. These results show that caregiver should be considered in captive primates' social structures and that this approach can present itself as highly beneficial for promoting and supporting social stimulations, when developing husbandry protocols.

Keywords

Animal welfare; Captive management; Human-Animal interaction; Pan troglodytes

1. Introduction

Chimpanzees (*Pan troglodytes*) is one of the two species belonging to the genus *Pan*, from the *Hominidae* family, with the other one being the bonobos (*Pan paniscus*), who previously were thought to be the same species but were later on distinguished as two distinct species via DNA analysis (Lobón-Rodríguez et al., 2016). This species has the highest genomic proximity to humans with up to 99% of shared DNA (Mikkelsen et al., 2005). The four recognised subspecies of chimpanzees (*Pan troglodytes*) are divided through their geographically distinct populations within their wide distribution area across equatorial Africa. The Western chimpanzee (*Pan troglodytes verus*), the Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*), the Central chimpanzee (*Pan troglodytes troglodytes*), and the Eastern chimpanzee (*Pan troglodytes schweinfurthii*) present very subtle physical differences but demonstrate specific culture variance in their socially learned behaviors, such as different tool uses and foraging strategies (Luncz & Boesch, 2014). They are present in a total of twenty two countries, although the majority of the estimated total population can be found in only two countries, Gabon and Congo (Butynski 2001; Cowlshaw & Dunbar 2000). Due to their broad distribution, chimpanzees live in a wide variety of habitats, from dry savannas to tropical rainforests, which translates to considerable adaptability to different available resources (Goodall, 1986). Despite their wide distributions, all four subspecies are considered either endangered or critically endangered majorly due to pressures such as habitat destruction and poaching (*The IUCN Red List of Threatened Species*, n.d.). This species have been found to live in altitudes up to 2000 metres and have a highly varied omnivorous diet, composed mostly of fruits and leaves but also including the consumption of other animals from insects to hunted mammals, like other primates such as species from the *Colobus* genus (Yamagiwa & Basabose, 2006). Moreover, chimpanzees have been observed consuming plants with low nutritional value but containing bioactive compounds, suggesting the intentional use of medicinal plants (Ohigashi et al., 1994; Wrangham & Goodall, 1989).

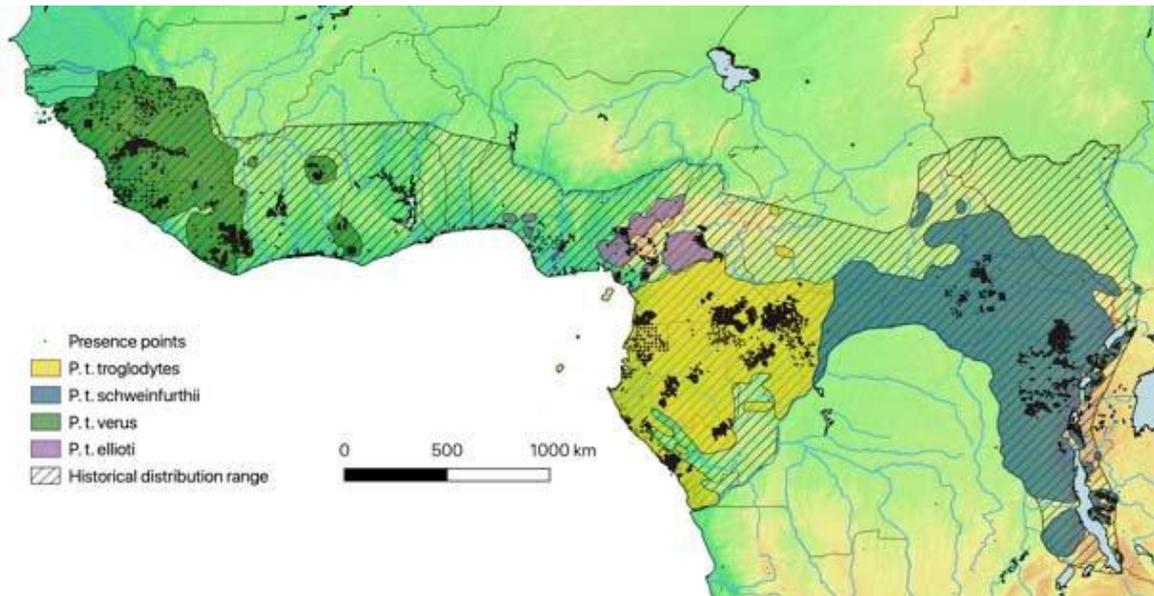


Figure.1. Chimpanzee's subspecies current and historical distribution (from Barratt et al., 2021).

Behavioral Ecology

This social species lives in groups of as many as 150 members. Male and female chimpanzees both possess hierarchies, with males competing for domination by displaying power and physical health. In encounters with other group members or intruders in their territories, violent hostility has been widely documented, leading to severe wounding or death of the intruding members (Manson et al., 1991). Chimpanzees live in patriarchy societies, with one alpha male holding his high-ranking position not only through displays, but also maintaining the support of females and creating alliances with other males in order to construct a well-structured community, where hierarchies are well-defined reducing possible conflicts (Foster et al., 2008). In order to express emotions and maintain relationships, chimpanzees have developed a wide repertoire of complex vocalizations, postures and facial expressions. This capacity to demonstrate individual traits and responses to a certain situations, has enabled this species to manage and even influence social environments with context-specific strategies, demonstrating intricate developed cognitive abilities. This is also demonstrated by the capacity to reconcile conflicts, ease accumulated stress and maintaining bonds via tactile communication such as grooming interactions (Nishida et al., 1999; Wittig et al., 2016).

Chimpanzees exhibit highly advanced social organisation based on fission-fusion dynamics, in which a troop divides itself into different parties whose membership changes depending on ecological, reproductive and social factors (Nishida & Hiraiwa-Hasegawa, 1986; Jones et al., 1996). This society allows individuals to possess dynamic association networks whose males are more social than the females and create larger parties and have high-level social interaction which comprises grooming, coalition formation, and cooperative dominance strategies (Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1985). Female, albeit more independent in the wild due to reproductive and offspring-rearing energetic costs, form strong affiliative relationships in captivity (Baker & Smuts, 1994; Goodall, 1986). Characteristics such as long-term social memory, individual identification, and adaptive bonding tactics, conditioned by life stage, reproductive status, and dominance status, demonstrate this social complexity, enabling chimpanzees to manage changing group membership and make connections which influence individual fitness and group cohesion (Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1986).

Captivity Management

The combination of the previously mentioned social organization factors, together with the advanced cognitive capacities of chimpanzees, adds considerable complexity in maintaining optimal welfare in accordance with the five domains of animal welfare. The five domains model is a framework for assessing animal welfare, evaluating nutrition, environment, health and behavior, which influence the overall mental state of an individual (Mellor & Reid, 1994), and therefore characterizing quality of life. This model was developed in response to the growing need to ensure a minimum standard of quality of life for captive animals and to enable its systematic monitoring, particularly as the number of individuals held in captivity increased throughout the twentieth century. In the case of chimpanzees, their similarity to humans created a big interest to visitors of zoos, circuses and fairs, where the animals were trained to perform, which led to their major centrality in zoological collections. Furthermore, their closeness to humans made chimpanzees highly sought-after subjects for scientific research, and as recognition of their physiological similarities expanded, their use as models for human health correspondingly increased (Ross, 2014). Consequently, the general demand for great apes for their use in medical studies and entertainment, fueled a highly profitable illegal trade of this species, with data from a seven years period (2005-2011) suggesting a minimum of 643 chimpanzees (*Pan troglodytes*), 48 bonobos (*Pan paniscus*), 98 gorillas (*Gorilla spp.*) and 1019 orangutans (*Pongo spp.*), were captured from the wild for illegal trade (Stiles et al., 2013).

In the present, the fascination for observing wildlife and its exhibition remains, specially with primates, particularly great apes, that continue to be one of the most popular animals in zoos (Moss & Esson, 2010). Currently deviating from a solely entertainment and profit orientated approach, zoos have been increasingly including education, welfare and conservation responsibilities in their primary objectives (Conde et al., 2011). With this transitioning perspective and an increasing number of studies on the impacts of captivity in wild animals, a growing concern on the animal's welfare has been rising. This leads to more detailed and well-structured husbandry practices and innovation on creating enclosures that can reproduce the animal's natural habitats and sustain a higher structural complexity, consequently improving the captive animal's physical and mental state (Azevedo et al., 2023). However, when managing social species, which rely on cooperation for many of their daily activities, an additional category of stimuli must be provided to adequately meet the species' behavioral needs. As many authors have documented and demonstrated, the lack of a social structure and

stimulation, can lead detrimental repercussions to the housed animal's mental state, such as significant increases in abnormal and/or self-harming behaviors (Khan, 2013). This can be particularly demanding when managing captive chimpanzees, especially in sanctuaries that rehabilitate individuals rescued from exploitation in entertainment, illegal pet trade, or biomedical research, where the animals are often deprived of such social mechanisms. Many arrive with significant emotional trauma, displaying behavioural pathologies such as social withdrawal, anxiety, or aggression (Visalberghi & Anderson, 1993). In such contexts, human interaction becomes an unavoidable, yet a possible solution to expand an individual's social environment in captivity. Several studies have indicated caregivers as significant social partners, shaping patterns of socialization and influencing the chimpanzee's daily interactions (Baker, 2004; Claxton, 2011). Furthermore, Funkhouser et al. (2020) demonstrated that chimpanzees form differentiated relationships with human caregivers, involving attention-seeking, greeting gestures and choosing proximity to familiar individuals, therefore providing source of social stimulation and possibly emotional regulation for individuals with disrupted early-life socialization. Given that chimpanzees are capable of forming mutually recognized and context-dependent relationships with humans, due to their advanced emotional and cognitive profiles (Campbell & De Waal, 2014), a nuanced and well-informed approach from caregivers is essential, as it is the monitoring for impacts of such interactions. Using the social networks analysis (SNA), the quantification and visualization of the social integration is possible and it can reveal patterns not easily observed through direct observation alone (Borgatti et al., 2002). By applying SNA to networks which include both humans (such as caregivers, staff or visitors) and chimpanzees, it is possible to measure and evaluate the outcomes of the influence of different types human-chimpanzee interactions on group social cohesion, identify socially excluded individuals and develop evidence-based protocol for human exposure.

This dissertation aims to further develop the literature regarding animal-caregiver interactions by examining the social roles of humans, particularly caregivers, within the chimpanzees social networks. In addition, the study intends to understand how that inclusion in the network, depending on the type of human and the inherent differentiated levels of familiarity and trust, modulates the social structures within the integrated captive chimpanzee groups. By analysing the social networks, through centrality and dyadic strength values, and modulating its behaviors depending on different individual characteristics of the chimpanzees, this study contributes not only to the field of applied ethology but also to the design of socially enriching captive environments

2. Materials and Methods

2.1 Subjects and Study Site

This study has been conducted at Fundació Mona, a primate rescue center that focuses its work on the rescue, rehabilitation and life-long care of primates which were removed from illegal and/or inadequate living conditions, since 2001. The center is located in Riudellots de la Selva (Girona, Spain) and it is a member of the European Alliance of Rescue Centers and Sanctuaries (EARS), housing at the moment of data collection a total of 17 animals, 3 barbary macaques (*Macaca sylvanus*) and 14 chimpanzees (*Pan troglodytes*).

The chimpanzees were divided in three groups (Mutamba, Bilinga and Sugus) with essentially the same daily routine. Each group had an habitat consisting in a outdoor and two to three indoor areas. During the day they are normally confined to the outdoor area with the possibility of having access to the indoors, depending on weather conditions and maintenance tasks. During this time, each group is able to have non physical interactions with each other, although only two of them due to the layout of the enclosures, and are also exposed to human visitors who are able to watch the animals from specifically located viewpoints. The exterior enclosures are composed by two adjacent but distinct areas measuring 2,420 m² and 3,220 m², respectively, with a combined perimeter of 191 meters. Both enclosures are secured by a perimeter steel fence and electrified wires to ensure safety. They are equipped with various climbing structures, including wooden platforms, towers and elements such as climbing ropes, environmental enrichment devices, hammocks, and ad libitum water dispensers. The more recent group, Sugus, was maintained in a smaller exterior, separated from the other two and weekly alternated to the biggest exterior, granting the same conditions. The enclosures maintain a naturalistic setting, preserving the original native Mediterranean vegetation, combined with a dense vegetative barrier, primarily composed of bamboo (*Phyllostachys puberula*) around the enclosures, allowing the animals to have the possibility to locate themselves in way which can increase their privacy and reduce visual exposure to visitors

(Figure 2). All visitor areas are separated by at least a two meter distance from the animal fencing, making physical interactions impossible.

During night time hours, individuals are confined to the indoor spaces where each group is granted access to shared dormitory. They can have the autonomy to select with who and where they want to sleep or be assigned to separate dormitories to mitigate potential conflicts in the absence of caregivers, in the case of the Mutamba group. Although visual contact is restricted, auditory communication remains possible, as individuals can hear one another across dormitory boundaries.



Figure 2. View of animal facilities, observation points and visitor's viewpoints at Fundació Mona: respective animal enclosure labelled in red, green and purple; observation point labelled in dark grey; visitor's view point labelled in light grey.

The 3 groups of chimpanzees (*Pan troglodytes*) housed at the sanctuary were observed, adding to a total of 14 individuals to the study population. The groups are composed by both females and males with no presence of infants or juvenile individuals, with ages ranging from 19 to 52 years old. In both the Mutamba and Bilinga groups there are 2 females and 3 males, with a mean age of 28,4 (SD:±7,37) and 35,4 (SD: ±7,77), respectively, and in the Sugus group there are 3 females and 1 male and a mean age of 35,25 (SD: ±13,87) years old. Depending on their age, each animal was considered either an adult, or a senior if their age was higher than 30 years old. Except for the Sugus group, all individuals have been in the center for at least ten years and are accustomed with the routines and being housed in proximity with other groups.

Most of the primates in the center were previously pets or used in the entertainment industry, before being confiscated and taken to Fundació Mona, as it can be seen in Table 1. Newly rescued individuals are initially housed in isolation from conspecifics for several weeks prior to the social integration. The duration required for adaptation to the new environment, physical rehabilitation, and successful integration into social groups varies according to individual needs. Personalized treatment and care protocols are developed for each subject based on their specific medical and behavioral requirements. The center has a strict hands-off policy, with physical contact limited exclusively to a select group of trained personnel for purposes related to veterinary care and rehabilitation.

Name	ID	Group	Age	Sex	Arrival at MONA (Year)	Social housing condition during infancy
Africa	AFR	Mutamba	26	F	2009	single
Bongo	BON	Mutamba	25	M	2002	social
Juanito	JUA	Mutamba	22	M	2003	social
Marco	MAR	Mutamba	41	M	2001	social
Waty	WAT	Mutamba	28	F	2002	social
Cheeta	CHE	Bilinga	39	F	2015	single
Coco	COC	Bilinga	31	F	2012	single
Nico	NIC	Bilinga	24	M	2004	single
Tom	TOM	Bilinga	40	M	2011	social
Victor	VIC	Bilinga	43	M	2006	single
Caline	CAL	Sugus	39	F	2023	social
Hugo	HUG	Sugus	31	M	2022	social
Mayumba	MAY	Sugus	19	F	2023	social
Suzie	SUZ	Sugus	52	F	2021	social

Table 1. List of biographical information on all chimpanzees housed at Fundació Mona.

Chimpanzees were fed a minimum of four times a day, with water provided ad libitum in both indoor and outdoor enclosures. Their diet primarily consisted of seasonal vegetables and fruits, boiled rice, various dried fruits, seeds, and protein-rich food items. A substantial portion of the food was dispersed and concealed within the outdoor enclosures to stimulate natural foraging behaviors. Environmental enrichment was routinely provided through diverse strategies to promote cognitive and behavioral stimulation. Interaction with familiar humans (staff members) was intentionally minimized and caregivers approached the animals only during feeding sessions or when performing essential management tasks, in order to avoid disrupting, and instead to promote, intra-group social dynamics.

Although human-animal interactions are intentionally minimized and limited to essential management tasks, distinct opportunities for interaction with different human groups occur at specific moments throughout the day. In the case of head caregivers (Xr) and caregivers (CRG) the interactions occurred mainly at the beginning and end of the day, when breakfast and dinner was given and the translocation between the inside and outside enclosures is done- tasks which represented the longest routine interaction periods. In addition to these regular interactions and the mid-day scatter feeding (performed by throwing food across the fence lines), there were occasional, non-daily procedures involving a substantial degree of interaction between the head caregivers and the chimpanzees, even though they occur at lower frequency. The head keepers and caregivers were differentiated by the level of familiarity with the animals, being that the head keepers all worked at Fundació Mona for more than 2 years and the caregivers are temporary volunteering workers, originating a difference in the behaviour of the animals and tasks carried out by each categorized human group. All other staff members of the sanctuary (OFI) were able to walk around the exteriors allowing the possibility for the interaction with them. In addition to the human groups considered familiar to the chimpanzees, the morning hours also included the presence of unfamiliar individuals, such as external workers or other unidentified human (OTH) and the daily visits (VST). At the sanctuary, only guided visits were allowed, permitting the public to observe the chimpanzees while minimizing potential disturbance. Unsupervised or free-roaming access by

visitors was strictly prohibited. During the study period, organized visits were conducted on weekdays for school groups and on weekends for families and other adult participants. All visitor-related activities were confined to the morning hours and carefully managed to reduce their impact on the animals. Trained guides accompanied each group, ensuring that visitor presence remained controlled and educational, and that the visitor protocol is followed.

2.2 Data Collection

Data on the behavior of the three groups was collected in the course of two months, from February to March 2025, adding to a total of 121 hours of observation with a mean of 40 hours to each group. The chimpanzees were observed throughout all the hours of the day included in the working schedule of the caregivers (9AM to 7PM), in order to record all of the different moments of possible interaction with humans. In the exteriors, where the animals spent most their time, the observations were conducted from two observation towers (Figure 2) providing the maximum visibility to the enclosures and guaranteeing that the presence of the observer would not influence the chimpanzees behavior. This procedure was applied in the two larger enclosures. In contrast, data collection in the smaller enclosure—alternately used by the Bilinga and Sugus groups—was conducted from ground level, maintaining a secure distance from the fence to ensure minimal disturbance to the animals. Behavioral data was also collected while the chimpanzees were in the interior enclosures, while husbandry procedures were carried out during the morning and at the end of the afternoon. During these moments the observer was located in front of each group's dormitory, within a safe distance, although animal interaction with the observer, in this case, was possible and registered more than once. This created the opportunity to record the interactions with the higher duration and closeness between the chimpanzees and the head keepers and caregivers, although there were also some moments of veterinary and welfare procedures where data was collected. A total of 37 hours of observation was conducted within the indoor enclosures.

Observations were carried out using a tablet device equipped with the data collection software Zoomonitor (Wark et al., 2019), where the established ethogram of only interactive behaviors was introduced (Table 2). Both All-Occurrence and Scan Sampling methodologies were employed concurrently through a multifocal approach (Altmann, 1974), in which all individuals within a single social group were observed simultaneously, including occurrences of intergroup interactions. In the All-Occurrence sampling method, all behaviors listed in the ethogram were recorded. A second entry of the same conduct was made, only if the focal chimpanzee exhibited a different behavior, regardless of whether it was included in the ethogram, before returning to the original behavior. In the case of Scan Sampling, behavioral data were recorded at one minute intervals for all individuals within the group, also noting the presence and type of human personnel present at each time point. This allowed for the calculation of either the frequency with which a given behavior occurred, or the probability of its occurrence. The two sampling methodologies were applied to allow for a subsequent evaluation of which would more accurately represent the occurrence of each behavior. This was necessary approach, given that certain behaviors tend to occur over very short durations, while others may be prolonged. Each observation session lasted 30 min, and sessions were equally distributed throughout the day and week.

Behavior	Abbreviation	Definition
Affiliative	AF	Socio-positive behavior directed and/or received by another member of the same group.
Agonistic	AG	Includes all aggressive or submissive behaviors directed and/or received by another member of the same group.
Attention Seeking	AT	Individual approaches the keeper maintaining eye contact, possibly extending the arm outside the fence. May occur at a distance and includes movements or repetitive sounds (e.g., swinging, clapping, hitting structures, short screams, hoots, lip splutter), usually reinforced by human response.
Social Vigilance	SV	Fixed gaze at someone. Includes looking at distant group members, other groups, and surrounding area. Human targets may include head keeper, caregivers, visitors, or other staff.
Social Proximity	SP	Not a behavior. Sharing space during inactivity or associated with other behaviors while being within a distance less than two times the upper limb's length. Only recorded between non-interacting individuals. For humans, proximity is considered relative to the closest point of the fence.

Table 2. Simplified ethogram: overview of analyzed behaviors (complete ethogram and definitions can be found in Table 3). Source: Definitions based on Mona Foundation established ethograms, except for “Attention Seeking” based on: (Nishida et al., 1999) and (Hopkins et al., 2006)

2.3 Statistical Analysis

Scan sampling was used to record affiliative behaviors and social proximity, as these typically involve longer durations and are well captured at regular intervals. In contrast, all-occurrence sampling was employed to efficiently record the exhibition of agonistic behaviors, attention seeking and social vigilance behaviors, which are usually brief and event-based. This dual method approach ensured accurate representation of both sustained and instantaneous behaviors, providing a reliable basis for statistical modeling and interpretation across different dyadic contexts.

In order to normalize the data, the proportion of scans was calculated by counting the number of times individual A was interacting or in social proximity with individual B and by dividing this value by the total number of scans where both individuals were actually present in the same enclosure, or in the adjacent one in case of intergroup interactions. For the all-occurrence dataset, the same approach was applied. However, instead of using the number of scans in which both individuals were present to estimate interaction potential, the total amount of time during which both individuals were simultaneously present was used. Thus, it was taken into account the time dyads actually had access to each other during the observations, as individuals occasionally would be absent for short amounts of time due to veterinary issues, veterinary training or other animal care management reasons. This was also necessary due to variations in which was the neighboring group in the outdoor enclosures.

2.3.1 Social Network Analysis (SNA)

The social network graphic representations developed consist in nodes (vertices) representing individuals (chimpanzees or humans) and edges (links) representing the extent (standardized rates) of observed interactions. Social networks were based on weighted dyadic interactions of each selected behavior, within the same group (intragroup) or different one (intergroup). A total of 5 interaction matrices were created, for the 3 groups and involved humans, based on affiliative, agonistic, attention seeking and social vigilance behaviors and also recorded social proximity.

The social network graphic representations were created using the program UCINET (version 6.806), using the integrated Netdraw (version 2.193) software for network visualization (Borgatti, Everett & Freeman, 2002; Borgatti, 2002). The layout setting was adapted, applying the Spring Embedding, which is a drawing technique that simulates physical forces to place nodes in a visually intuitive way, highlighting structure through spatial relationships. This option balances specific layout criteria, such as, node repulsion to prevent overlap, spring forces to reflect connection distances, and uniform edge lengths for an evenly spaced graphic. Thus, nodes were distributed based on the sum of the attractive and repulsive forces acting on each node (Golbeck & Mutton, 2005). The interaction matrices were then used to calculate a network measure for each previously mentioned interaction type. Eigenvector Centrality was used as a metric that measures how influential or important an individual (node) is within a network, based not just on the number of connections they have, but also on how well connected their connections are (Kasper & Voelkl, 2009). This metric was then calculated for each individual and used as a node attribute, while the weighted strength of dyadic interactions served as an edge attribute in the social network graphics. This allowed for a visual representation of the network structure, where more influential individuals appeared as larger nodes (reflecting higher centrality values), and stronger social bonds were depicted by thicker edges between individuals. In addition to value based attributes, nodes were also visually distinguished according to the identity of the individuals they represented. Human individuals were depicted as blue circles, while chimpanzees were

represented as squares, with the color of each square indicating the social group to which the individual belonged to.

2.3.2 Linear Mixed Models (LMM)

To assess the potential influence of individual chimpanzee characteristics, as well as the role of categorized human groups, on the occurrence of interactive behaviors, linear mixed models (LMMs) were employed. Fixed effects included age class (adult vs. senior), sex (male vs. female), length of time housed at MONA (≤ 5 years vs. > 5 years), and early social housing conditions (social vs. solitary), reflecting whether individuals were raised with conspecifics during infancy or not. For the analysis of human-chimpanzee interactions, humans were categorized into two groups: husbandry staff and educational staff, which includes office staff, visitors and guides. The LMMs were based on two separate datasets: one representing the dyadic strength of interactions between chimpanzees and humans, and the other including only dyadic interactions among chimpanzees. A total of 7 LMMs were run based on the same coding structure and only changing the dependent variable (dyadic interaction rates) : Affiliative, Agonistic, Social Proximity and Attention Seeking. Social Vigilance behavior was excluded as a dependent variable from all models, as it was not recorded in chimpanzee–chimpanzee interactions. Similarly, Attention Seeking behavior was not included in the chimpanzee–chimpanzee interaction models due to its extremely low frequency of occurrence.

As a way of controlling the distribution of the residuals' normal distribution, QQ plots were visually checked, revealing no violations of the assumptions of the LMMs. All models were run using the "lme4" package (Bates et al., 2015) in R statistical software (version 4.3.3) (R Foundation for Statistical Computing, 2018). Multicollinearity was tested between all fixed factors by calculating the variance inflation factor (VIF) using the "car" package (Field, 2009). The VIFs calculated for the five fixed factors used in the models ranged between 1.00 and 1.73, indicating that they were not correlated (< 2). In order to test if the full models (with

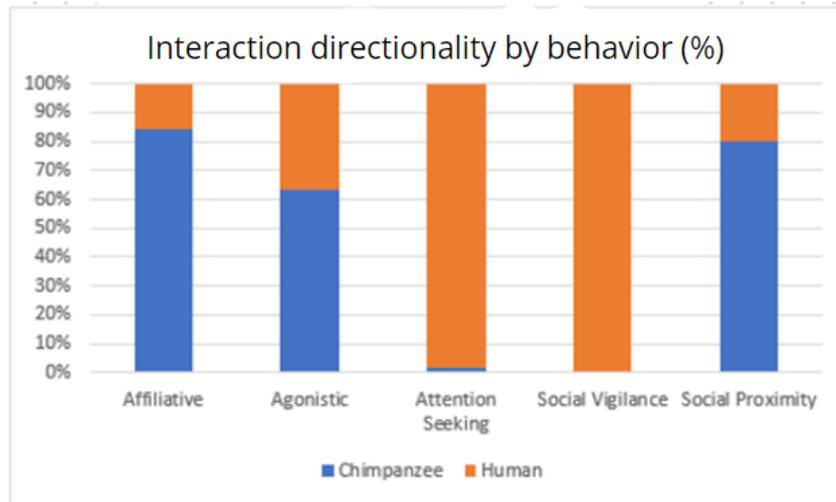
all fixed factors) were significant improvements over the null model (no fixed factors), the “ANOVA” function was used, ensuring that the fixed factors had a significant effect on the model outcome. If the full model presented significant improvement over the respective null model, the ANOVA function (type III analysis of variance) and post hoc analyses were conducted using the “glht” function to perform multiple comparisons of means with Tukey contrasts. P-values were adjusted using the Holm–Bonferroni method to control for multiple testing, allowing for further exploration of significant fixed effect.

3. Results

3.1 Occurrence of Social Interaction Types

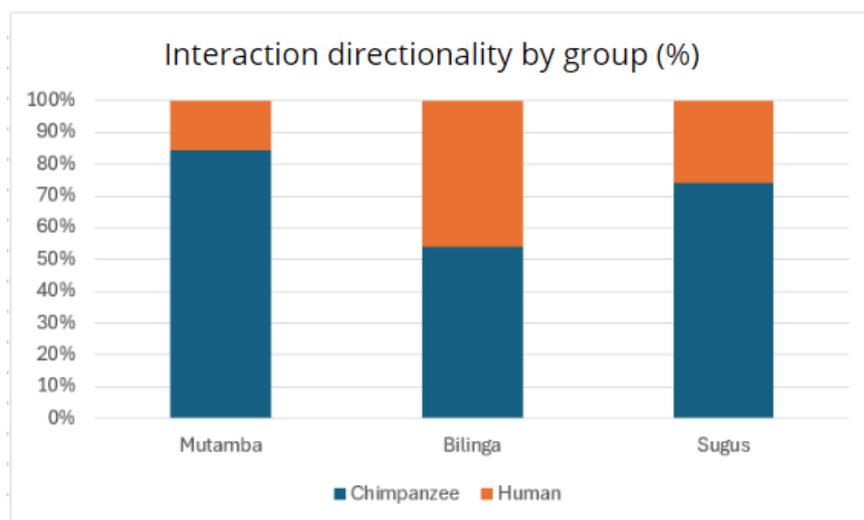
Over the course of data collection, a total of 983 affiliative behaviors, 148 agonistic, 117 attention seeking, 365 social vigilance behaviors, and 5078 occurrences of social proximity were recorded. Allogrooming represented 42% of all recorded affiliative behaviors, while within agonistic interactions, 65% were dominance and 35% submissive related behaviors. Thus, considering only the sub-categories of behaviors allogrooming was the most frequently observed behavior. When considering all four behavioral categories, 61% were related to affiliative interactions, 9% to agonistic, 7% to attention seeking and 23% to social vigilance.

As mentioned before, all of these behaviors and interactions could have been directed either to a chimpanzee, from the same or different group, or to a human. Social vigilance and attention-seeking behaviors were observed being directed toward conspecifics only once and twice, respectively, in contrast to the other recorded conducts, which were mainly directed to chimpanzees as it can be seen in Graphic 1.



Graphic 1. Percentage of interaction directionality by type of behavior.

The highest proportion of interaction with humans was found in agonistic interactions, with 38% of them directed to this group, representing 54 events, whilst in affiliative, only 16% were directed to humans but having representation of 155 events. Considering the category of social proximity, which is not a behavior but the sharing of a space without social interaction, humans had a considerable proportion of 20%, being that the amount of time possible to record this moment with humans is significantly lower than with conspecifics. More detailed information about the ethogram's sub-categories and recorded events can be found in Table 3.

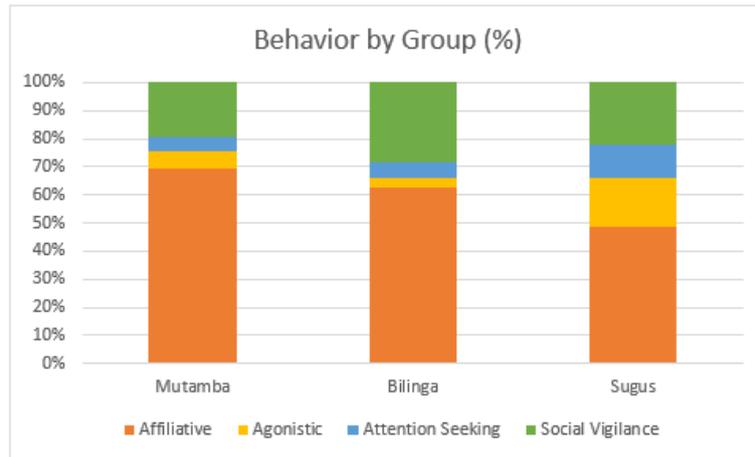


Graphic 2. Percentage of interaction directionality by group.

Major differences were found across groups regarding the frequency with each group was recorded performing a certain behavior and also the proportion of times it was directed to humans versus to conspecifics.

Within affiliative behaviors, the Mutamba group exhibited the highest values but the lowest directionality to human partners. In contrast, the Bilinga and Sugus groups showed approximately half the number of affiliative interactions compared to Mutamba. Notably, in the Bilinga group, 23% of these interactions were directed towards humans, representing almost twice the proportion observed in Mutamba. This may represent a more well-structured intragroup social dynamics in the Mutamba group. Regarding agonistic behaviors, the Sugus group was by far the one with the highest overall frequency among all groups, with two and six times more registered agonistic events than Mutamba and Bilinga, respectively. Interestingly, the Bilinga group was also the one with the highest directionality to humans in agonistic interactions. Furthermore, the sub-categories of this conducts were explored, and as expected, the males (in the 3 groups) were the ones performing the dominance-related behaviors (displays), whereas submission was performed mainly by females. In the social proximity scans conducted at one-minute intervals, the Mutamba group once again exhibited the highest number of recorded instances (almost twice as much), with only 10% of these involving proximity to humans, representing the lowest proportion among the groups. Maintaining the tendency described before, the Bilinga group was, once again, the one with the highest proportion of social proximity with humans (45%). The Sugus group had approximately the same number of recorded social proximity instances as the Bilinga group. However, it is important to consider that the Sugus enclosure is considerably smaller than the other two, which could have influenced the probability of two individuals remaining in social proximity, although it was not the case. The number of times social vigilance was recorded relatively consistent across all groups. Attention-seeking behaviors were considerably more frequent in the Sugus group. This may be attributed to the enclosure's location, facing the caregivers' primary working areas, which increases opportunities for human presence. Additionally, the more recent arrival of this group to the sanctuary, compared to the others, may

contribute to a heightened tendency to engage in such behaviors. Graphic 3 provides a more detailed overview of the proportions of behaviors exhibited by each group.



Graphic 3. Proportion of behaviors exhibited by each group.

Comparison of occurred Affiliative and Agonistic Behaviors

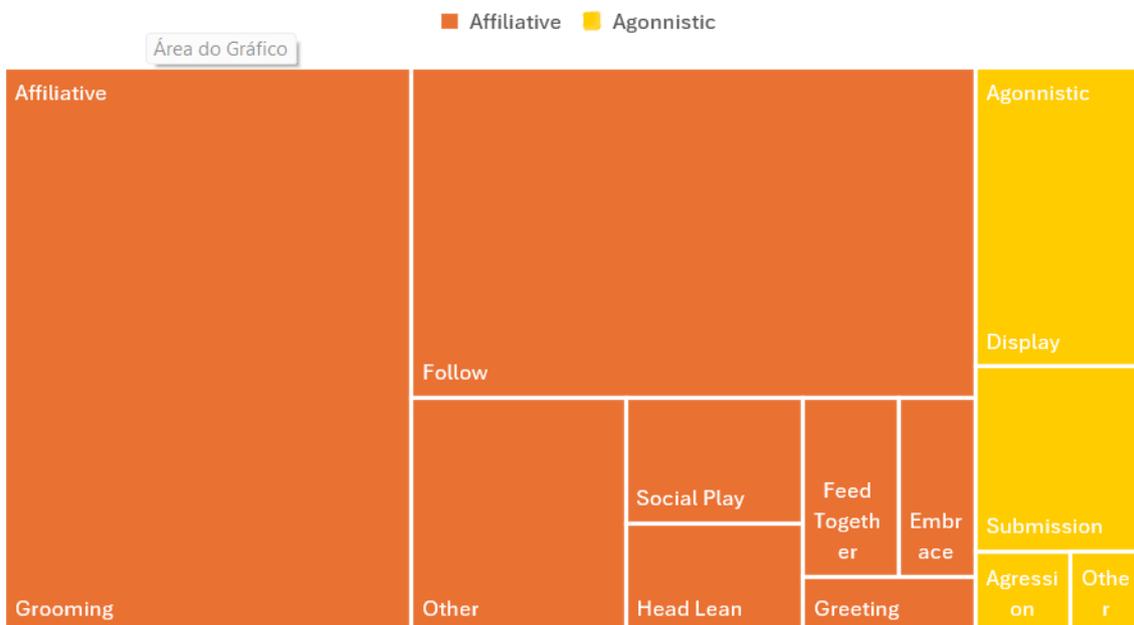


Figure 3 . Scaled visual comparison of overall occurrence of Affiliative and Agonistic behaviors.

3.2 Graphical Representations of Social Networks

The graphical representations of the weighted social networks of all four behaviors and social proximity are shown in Figure 4. These were created to demonstrate the complexity of the chimpanzees' social networks and to highlight the potential importance of humans in these networks, which translates to their impact on the animals' social dynamics. It is important to note that all five sociograms include individuals from the three chimpanzee groups, as well as the humans involved in the respective interactions. For this reason, each chimpanzee has the potential of establishing a social relationship with 13 conspecifics and up to 5 types of categorized humans.

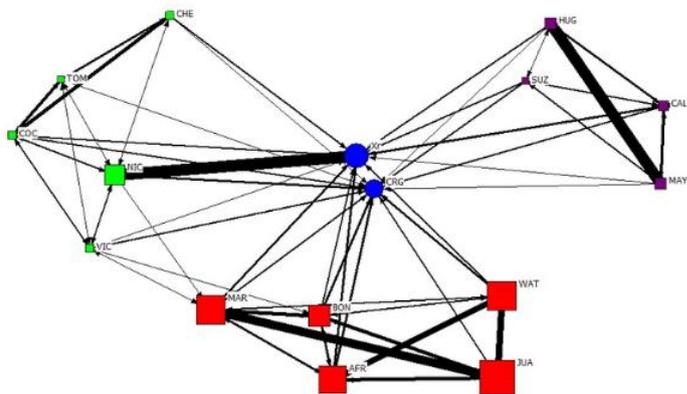
Networks based on affiliative behaviors and social proximity show a clear group separation even though intergroup associations are present. These connections only occurred between the Mutamba and Bilinga groups, mainly with two male individuals of each group (BON, MAR and VIC, NIC). As expected, the affiliative network revealed that the Mutamba group exhibited the highest levels of connectivity and eigenvector centrality, with significant sociopositive interactions with the head caregivers (Xr) and caregivers (CRG). In contrast, the other two groups display more segmented interactions, with strong but more isolated dyads and a lower overall cohesion, represented by strong edges (links) connecting only two to three individuals. It should be mentioned that all of the animals are connected to the husbandry personnel. It is important to note that the strongest dyadic interaction in affiliative behaviors is between Nico (NIC) and the head keepers (Xr). This is primarily due to medical requirements, as this member of the Bilinga group undergoes a brief daily veterinary procedure, leading to a mainly positive interaction integrated in his routine. In the graphic representation of the social proximity network a similar pattern can be observed, as the Mutamba group has lower values of eigenvector centrality, due to the fact that this individuals are mainly connected to themselves and not to other well connected individuals of the network, which once more reflects better cohesion levels in this group. In both graphical representations of the social networks, humans occupy a central position, with significantly stronger connection with some individuals. In this case, humans categorized as OFI, which were sanctuary staff members outside of the husbandry personnel, were the ones with the highest eigenvector

centrality value. This can be explained, not only by the fact that this particular node is connected to other well connected nodes but also by the way the weighted dyadic strength was calculated, dividing the strength value by the interaction potential between two nodes. Being that the node OFI, to whom the animals have considerable level of familiarity, was recorded as present a smaller number of times, its interaction potential was very low and therefore, its dyadic strengths was much higher also leading to a higher eigenvector centrality value.

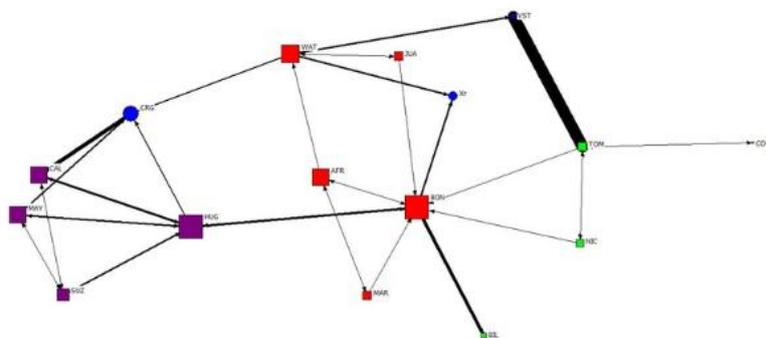
In the case of the attention seeking and social vigilance network representations, its clear that both of this behaviors were almost exclusively directed to humans, mainly to the husbandry personnel, as in both graphs the Xr is the node with the highest eigenvector centrality. Besides the similar directionality to the keepers and graph structure, it is noticeable that the more central animal individuals are females in both cases. Once more, this is evidence that the presence of humans may create differences in conducts performed by the housed chimpanzees.

Regarding the network representation based on agonistic events, it is possible to visualize that humans no longer play a central role in this network, although there is still some directed behaviors to the husbandry personnel (Xr and CRG) but mainly to the visits (VST). Recorded events directed to the Xr were very punctual and slightly more frequent towards CRG, almost entirely performed by the Sugus group. The human group categorized as VST shows a strong connection to Tom (TOM), a male from the Bilinga group, who frequently performs display behaviors, particularly in the presence of these individuals. The Mutamba and Sugus groups are more prominently represented in this graphic, with their respective high-ranking males occupying central positions and exhibiting the highest and second-highest eigenvector centrality values. Even though the Sugus group has a considerable amount of agonistic behaviors, they were mainly intragroup interactions, leading to a more clustered positions in the network. In contrast, the Mutamba group members have a more spread out positions due to higher number of intergroup interactions, specially with in the case of Bongo (BON) which performs recurrent displays to neighboring groups.

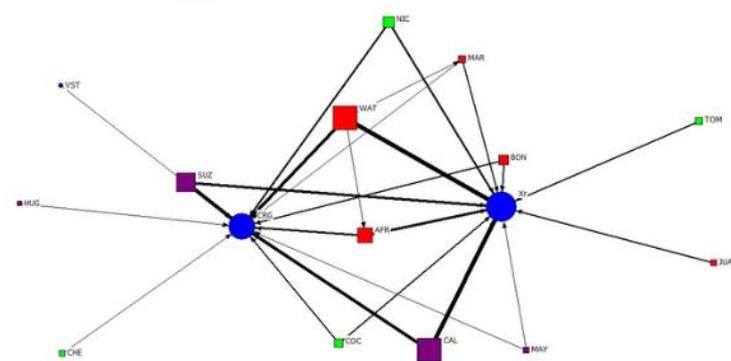
Affiliative



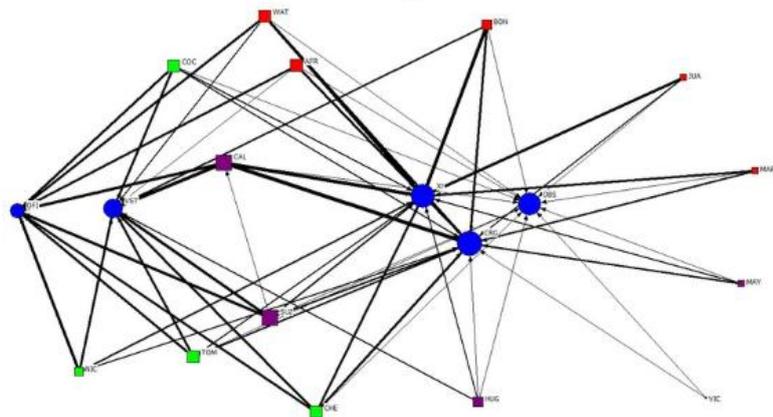
Agonistic



Attention Seeking



Social Vigilance



Social Proximity

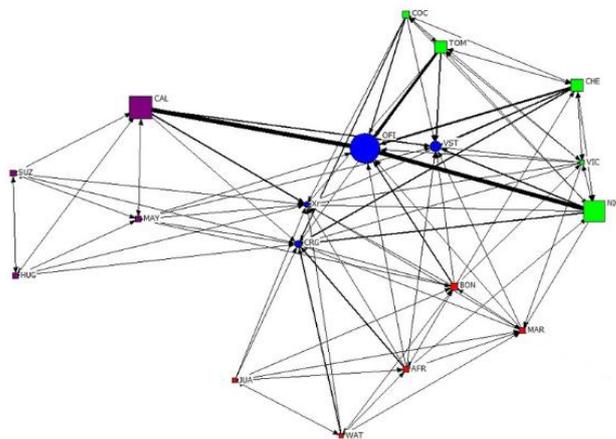


Figure 4. Social network representations of the 3 groups. Each network is based on one social interaction type (affiliative, agonistic, attention seeking, social vigilance social proximity). Edge weight is proportional to the weighted index value of the interaction pairs. The node layout is based on the force-directed algorithm “Spring-Embedded distribution”. Node shape represents specie of the individual (circle for humans and squares for chimpanzees) and the color represents the group (Mutamba is red, Bilinga is green and Sugus is purple). The node labels correspond to the individuals listed in Table 1.

3.3 Linear Mixed Models

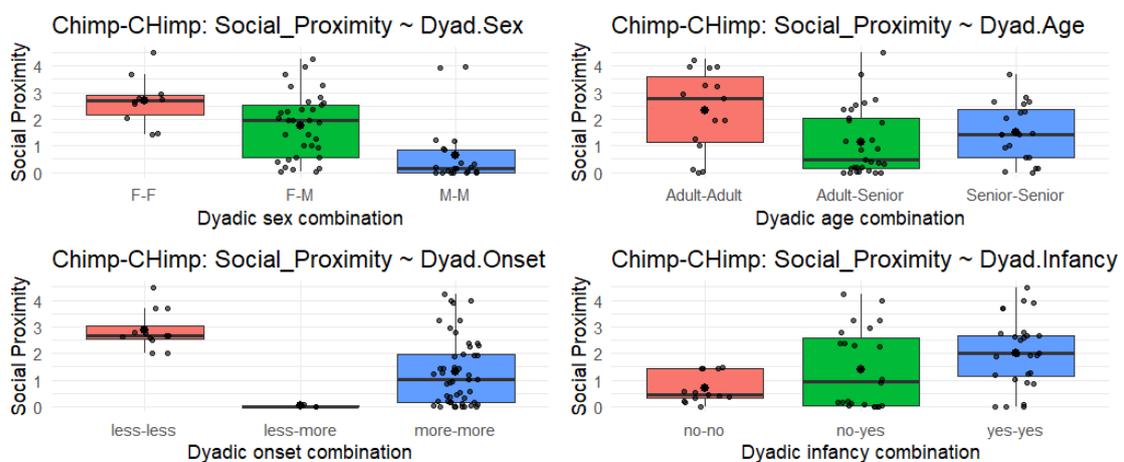
A total of seven LMMs were ran in order to analyse the impact of humans in the selected behaviors, as well as how the individual characteristics of the chimpanzees (fixed factors) potentially created a difference of outcome in the models. Three out of the seven models were not significantly improved by adding the predictors, and therefore none of them appeared to produce a meserable impact on the chimpanzees interaction patterns.

3.3.1 Chimpanzee–Chimpanzee Dyads

In the chimpanzee-chimpanzee weighted dyadic interactions models, three dependent variables were examined seperatly, although the Affiliative dyadic interactions outcome could not be explained by the the selected predictors, and therefore was discarded. Confidence interval plots regarding the significant fixed factors are shown in the graphics 4 and 5.

3.3.1.2 Social Proximity

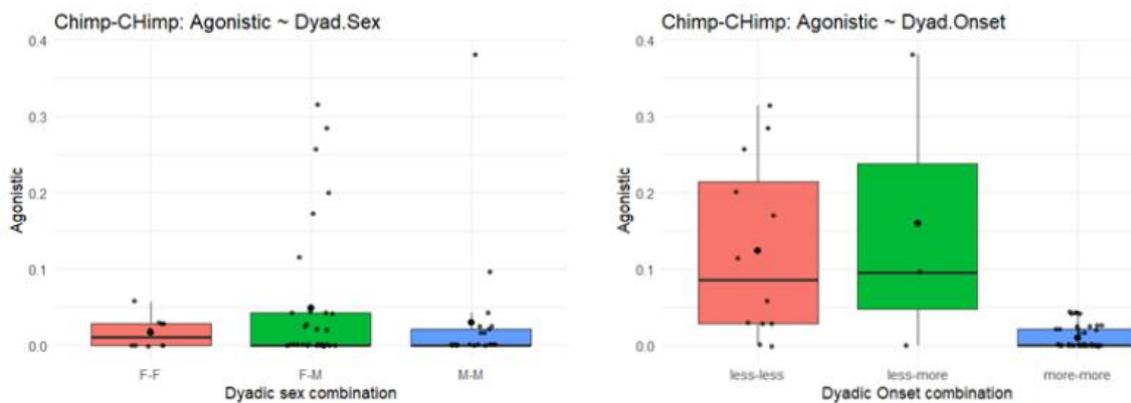
The comparison between the full model and the null model came out as significant ($p < 0.001$) meaning that the full model significantly explains the variation of values of Social Proximity dyads. The predictors (Sex, Age, Infancy, On set) were then tested and all four of them had a significant effect on the dependent variable ($p < 0.05$). Post hoc comparisons were made and within the predictor 'Sex' major differences were found between M-M and F-F dyads ($z = -1,291$, $p < 0.01$) and between M-M and M-F dyads ($z = -0.803$, $p < 0.01$). It can be concluded that same sex male dyads show less Social proximity then dyads including females. Within the predictor 'Age', there were significant differences between Adult-Senior and Adult-Adult dyads ($z = -1.037$, $p < 0.01$) and Senior-Senior and Adult-Adult ($z = -0.999$, $p < 0.01$), showing that dyads involving senior individuals (>30 years) present less social proximity the ones including adults. The analysis of the predictor 'On-set' revealed that dyads with similar lengths of stay in the sanctuary showed higher social proximity values, showing differences in all three dyad comparisons: Less-More - Less-Less ($z = -2.389$, $p < 0.01$), More-More - Less-Less ($z = -0.961$, $p < 0.05$) and More-More - Less-More ($z = 1.428$, $p < 0.05$). The last predictor 'Infancy', wich reflects if an individual was raised with conspecifics or not, revealed that the chimpanzees that were raised in a social environment tend to show higher level of Social Proximity: No-Yes – No-No ($z = 0.761$, $p < 0.05$) and Yes-Yes – No-No ($z = 1.020$, $p < 0.05$).



Graphic 4. Confidence interval plots of Social Proximity interactions and the significant fixed effects (Sex, Age, On-set and Infancy).

3.3.1.2 Agonistic

The agonistic behaviors in the chimpanzee-chimpanzee dyads were significantly influenced by the sex and length of time in the sanctuary of the individuals ($p < 0.001$). Post hoc comparisons were performed for both predictors. In the different 'Sex' dyads, major differences were found comparing F-M and F-F ($z = 0.053$, $p < 0.001$) and with M-M and F-F ($z = 0.059$, $p < 0.001$), revealing that dyads which include male individuals present higher values of agonistic behaviors. Within the predictor 'On-set', differences were found between More-More and Less-Less ($z = -0.118$, $p < 0.001$) and between More-More and Less-More ($z = -0.115$, $p < 0.001$), showing that dyads including individuals with more than five years in the sanctuary have less agonistic behaviors than dyads including individuals that have been in sanctuary for less than five years.



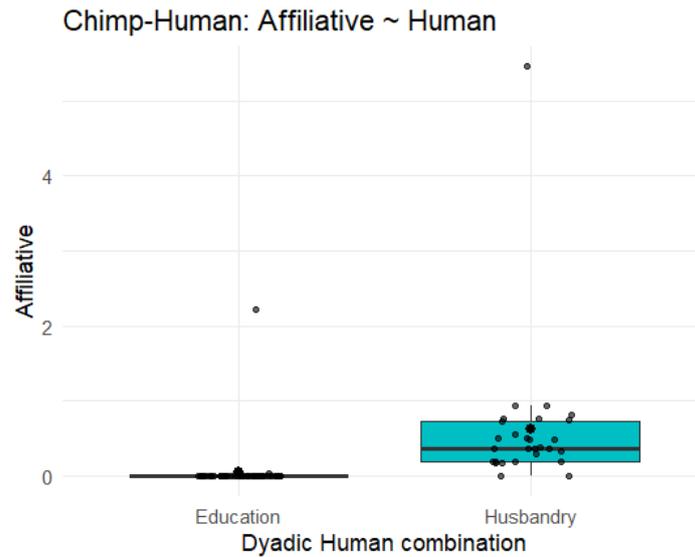
Graphic 5. Confidence interval plots of Agonistic behaviors and the significant fixed effects (Sex and On-set).

3.3.2 Human-Chimpanzee Dyads

In the human–chimpanzee interaction model, four dependent variables were initially tested to explain variation in interaction values. However, for two of these, social proximity and agonistic behaviors, the addition of predictor variables did not significantly improve the full model. As a result, these were excluded from further analysis. As mentioned before, in this case an extra predictor ‘Human’ was used, which categorized the staff of the sanctuary either as husbandry or education staff. Confidence interval plots regarding the significant fixed factors are shown in the graphic 6 and 7

3.3.2.1 Affiliative

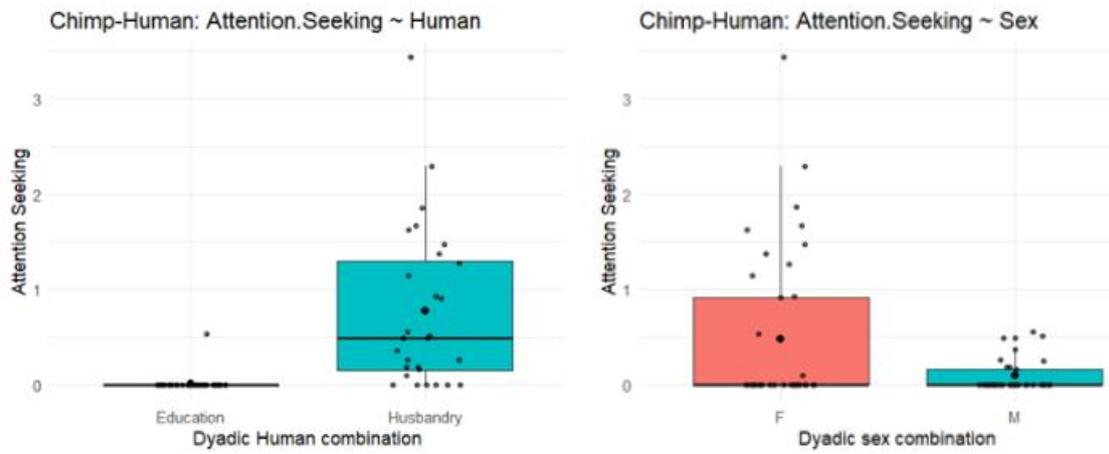
Using the affiliative behavior as a dependent variable in the linear mixed model, the predictor ‘Human’ was the only one which had a significant effect on the outcome ($p < 0.05$). Post hoc comparisons were performed, showing that the two levels of this predictor differ significantly ($p < 0.001$), being that the husbandry staff has considerably higher values of affiliative interactions with the chimpanzees. It should be noted that, although the difference was not statistically significant, within the predictor ‘Infancy’, the individuals who were not raised alongside conspecifics show a tendency to have more affiliative interactions with humans than individuals who were in contact with other chimpanzees during their infancy



Graphic 6. Confidence interval plots of Affiliative behaviors and the significant fixed effects (Human).

3.3.2.2 Attention Seeking

Attention Seeking as a dependent variable in the model, was significantly influenced by the predictors 'Human' and 'Sex' ($p < 0.001$), both of which had a meaningful effect on the model's outcome. Within the predictor 'Human', highly significant differences were found, as attention seeking interactions in dyads including education staff were close to 0 and, as expected, the values of this interaction with husbandry personnel were much higher. The same post hoc comparison was carried out for the fixed factor 'Sex'. The two levels of this predictor differ significantly ($p < 0.001$), showing that females perform much more attention seeking behaviors than males.



Graphic 7. Confidence interval plots of Attention Seeking behaviors and the significant fixed effects (Human and Sex).

4. Discussion

4.1 Observed Behavioral Patterns

This study examined the potential impact of humans, particularly husbandry staff, as extended social partners on the social dynamics of integrated captive chimpanzee groups. As expected, the collected data showed that humans do play a part on a proportion of the daily interactions of the animals housed at Fundació Mona, with 34% of the recorded behaviors directed at humans. This is also visible in the central position of nodes representing humans in the social networks graphical representations.

Through the recorded affiliative behaviors, it is possible to affirm that there is a majorly positive and socially cohesive environment in the study population, as this was the most recorded behavior, with a proportion of 61%. This is evident in the structure of the social network graphic, where three distinct clusters of nodes, corresponding to the different groups, can be observed, each displaying varying levels of internal cohesion. Within this behavioral category, allogrooming was the most frequently recorded interaction, a key factor in reinforcing bonds and reducing stress between conspecifics and therefore supporting the group's functionality (Lehmann et al., 2007). Notably, 16% of affiliative behaviors were directed towards humans, although almost exclusively to the husbandry staff (Xr and CRG), with only one and three recorded affiliative events towards visitors (VST) and observer (OBS), respectively. This confirms that, while the chimpanzees do have a considerable amount of positive interactions with humans, they are only maintained with people to whom the animals have a higher level of familiarity, as it has been shown with other great apes by Pedersen et al. (2019). This further supports the idea of husbandry personnel not being peripheral figures but rather strong social partners shaping the chimpanzee's social dynamics (Funkhouser et al., 2020).

Social proximity was another behavioral category which reflected a majorly positive interaction with humans, accounting for 20% of the recorded instances. This is a representative proportion, being that the potential of interaction with

humans in this category is much lower than with conspecifics. Furthermore, not only this reflects some level of trust to this dyadic partners (Crailsheim et al., 2020) but could also indicate that the chimpanzees actively seek for stimulation or affiliative interactions with humans, as in this context, within an enclosed environment, when the humans are present, the animals must be the ones approaching the fence lines in order to social proximity to be recorded. Through the social network analysis of this interaction, once more it is possible to recognize the contrasts in group cohesion, with the Mutamba group having lower eigenvector centrality values and less connected nodes, while the Sugus and Bilinga groups appear more connected to humans and not to same group social partners. This may be particularly concerning in the Sugus group, where a higher number of recorded social proximity instances was expected, given the fact that this individuals spent most of their time in a considerably smaller enclosure.

Attention-seeking and social vigilance behaviors were almost exclusively recorded towards humans. In a animal sanctuary context, where the focus lies of promoting species-typical behaviors and social integration among conspecifics, while minimizing human dependency, these findings require careful interpretation. To some degree, this could be considered as positive when seen as proof of humans being socially relevant partners for individuals lacking strong bonds (Funkhouser et al., 2020), although relying on humans for emotional or social needs not met within the group, does not go in accordance with a social rehabilitation approach. With that in mind, this two behavioral categories' impact on the effectiveness of social integration of an individual, should be taken into account, as it accrued marjorly directed to the husbandry staff (Xr and CRG) and could also be a result of the animals considering this social partners as a source of food and/or resources. Additionally, it is of importance to mention that social vigilance levels should more carefully be examined as this beahvior may reflect both information gathering or curiosity, as well as heightened state of alertness potentially linked to stress or social tensions (Kutsukake, 2007). Thus, for a more detailed evaluation of this behavior's impact on welfare, differentiated states of vigilance should stipulated.

Regarding agonistic behaviors, this was the least recorded of all five interactions categories with a representation of 9% of all recorded events. This might suggest a strong welfare conditions in the observed individuals (Honest & Marin, 2006). Looking further into this behavioral category, it is of importance to mention that 38% of this events were human directed, clearly showing that not all human-chimpanzee interactions are beneficial to the animals and may cause significant levels of stress to them. This can create highly impactful effects on individuals more susceptible to stress factors, as the disruption of an single chimpanzee's stability can create a cascade effect, not only increasing the number of agonistic behaviors on the other members of the same group but also on the neighboring group (Baker & Aureli, 1996), leading to a overall decrease in welfare. This highlights the importance of well established protocols not only for visitors but also to caregivers, being that this were the two human categories with the highest number of recorded agonistic behaviors directed at them, as it can clearly be observed in the graphic representation of the agonistic social network in figure 4. In the case of caregivers (CRG), this might be explained by the fact that these are temporary volunteers at Fundació Mona and consequently the animals do not present a high level of familiarity with this humans, who carry out management tasks with considerable level of interaction with the chimpanzees. As for the visitors, the majority of agonistic events directed at this group was performed by a male individual of the Bilinga group (Tom), who presents a higher susceptibility to the presence of visitors and this categorized humans did not show major impacts on the behavior of the rest of the study population.

It is possible to infer that there is a tendency for human-directed behaviors to be performed by individuals belonging to the less structured groups (Bilinga and Sugus), while at the same time having the highest number of agonistic behaviors and lowest number of social proximity instances, showing lower intragroup cohesion. On the other hand, the Mutamba group had the highest number of considered positive interactions (affiliative and social proximity) directed at conspecifics.

4.2 Dyadic Interactions

The Linear Mixed Models (LMMs) supported and statistically confirmed part of the behavioral tendencies previously observed in the chimpanzees. By running the human-chimpanzee dyadic interaction model, it was possible to confirm that the categorized humans have significant impact on the chimpanzee's behaviors. By analyzing the confidence interval box plots, it is possible to confirm that the husbandry personnel receives much higher levels of affiliative behaviors than the education staff. Although affiliative behaviors were used as the dependent variable in the chimpanzee–chimpanzee dyadic interaction model, none of the tested predictors showed a statistically significant effect on the model's outcome and therefore, could not be compared to the human-chimpanzee model. However, the social bonding observed between chimpanzee and husbandry staff reveals considerable levels of trust, which is of great importance to welfare and the ability of familiar human staff to manage and decrease negative effects of stressful situations (Morimura et al., 2010; Pedersen et al., 2019). It is important to note that, although the difference was not statistically significant (p -value = 0.09), within the predictor 'Infancy' there was a clear tendency for individuals who were not raised with other chimpanzees, to have more affiliative interactions with humans than the individuals who were raised with conspecifics. Moreover, in the chimpanzee-chimpanzee dyadic interactions, individuals who were raised with conspecifics also demonstrated higher social proximity values. This is consistent with the results presented by Crailsheim et al. (2020), demonstrating that individuals mainly raised without conspecifics during infancy, exhibited reduced levels of affiliative behavior and allogrooming compared to those who were housed with conspecifics. This reinforces the hypothesis that more isolated group members view familiar humans as relevant dyadic partners, thus developing management and human-animal interaction protocols based on the specific needs of the housed individuals and their past history is essential. This may prove to be a complex task, given that, in sanctuaries and rehabilitation centers, reducing human dependency is one of the main focus, and therefore, a typical approach is to reduce as much as possible human-animal interaction. However, some authors have shown that caregiver-chimpanzee interactions can be beneficial to welfare, specially when

carried out using species-typical behavior (Jensvold et al., 2010) or to isolated individuals who lack conspecific social partners (Morimura et al., 2010).

Attention-seeking behaviors were also notably influenced by human presence and, as expected, these interactions were much higher when directed towards the husbandry staff. At a surface level, these vocalizations and gestures could be interpreted as food-requesting behaviors directed at caregivers, given that a substantial portion of human-animal interactions in sanctuary settings are associated with feeding contexts. Nevertheless, this behavior was also recorded being directed at visitors (VST) and to the observer (OBS), both defined as unfamiliar social partners. Consequently, it is clear that getting food is not the only reason that drives chimpanzees to perform these behaviors. As shown in Leavens et al. (2005) and in Tomasello (2022), chimpanzees adapt their communication signs and attention-seeking gestures depending on the level of attention of humans, which is clear evidence of cognitive ability of intentional social interaction initiation. Considering this, it may be the case that the animals direct certain behaviors to humans, so that an interaction is started without the intent of receiving a reward but as social stimulation. Interestingly, females were found to carry out a much more attention-seeking behaviors towards human staff than male individuals. Analyzing the chimpanzee-chimpanzee mixed models, dyads including males were found to have much lower social proximity and higher agonistic values than dyads including female individuals. Considering this, the higher levels of attention-seeking displayed by females toward caregivers may represent coping strategies associated with social bonding tendencies, particularly given that, in both the Mutamba and Bilinga groups the sex ratio (three males to two females) could prompt females to seek additional positive social stimulation from husbandry staff. Females' higher attention-seeking levels were also found in the Sugus group, possibly due to lower group cohesion and not the sex ratio (one male to three females). Several studies have demonstrated that male individuals tend to exhibit higher levels of agonistic behaviors and lower levels of social proximity (Crailsheim et al., 2020; Clay et al., 2017). In spite the fact that behaviors which can lead to stressful situations and possible individual isolation, should be minimized, the ability of an integrated social group to handle such circumstances without substantial negative consequences should

promoted. Not only this minimizes the need of humans interfering in the chimpanzees' interactions, even if in a positive way, but also, further stimulates species-typical behaviors. Chimpanzees' sex have also been shown to differentiate behavioral patterns, specially while foraging, with females focusing movement patterns in feeding requirements and males integrating foraging with territorial defence (Bates & Byrne, 2009). For this reason, male individuals are expected to engage more frequently in patrolling, dominance displays, and other agonistic behaviors, which, in a well-structured social group, and in the absence of overt aggression, should occur without human interference. This is particularly relevant, given that, agonistic displays can be explained by the need of discharging build-up tension, and therefore, could be seen as a stress-relief strategy and not necessarily as major welfare concern (Duncan et al., 2013). Nonetheless, the caregiver's ability in potentially decreasing agonistic events by reducing tensions should not be overlooked, as Baker (2004) demonstrated that caregiver affiliative interactions show a tendency to reduce agonistic displays and tension-related behaviors.

Agonistic behaviors were also observed at a higher rates in dyads involving individuals that had spent less than five years at Mona Foundation's sanctuary, particularly when the length of stay differed substantially between the dyadic partners. This may pose a challenge when introducing new members to a structured group, specially in cases where the entire captive environment is unfamiliar. In this situations, reinforcing animal-caregiver affiliative interactions can present itself as possible solution to stimulate recently arrived individuals to positive and stress-relief interactions, being that, even in successful introductions building strong affiliative relationships with unfamiliar conspecifics is a very gradual process (Schel et al., 2012). Additionally, familiarity between humans and captive vervet monkeys has been shown to decrease neophobia and to support the search for new stimuli, and therefore, accelerating the habituation process to the captive environment (Forss et al., 2021). This is crucial step in the introduction of a chimpanzee to an integrated group, by decreasing or eliminating all other stress factors before putting two unfamiliar individuals in the presence of one another, as chimpanzees are highly territorial and can present extreme aggressiveness towards unfamiliar individuals (Schel et al., 2012).

In sanctuaries, reproduction is strictly prevented, as the focus lies on the lifelong welfare and rehabilitation of rescued individuals rather than increasing the number of captive animals. Consequently, sanctuary populations tend to age over time, which in turn modulates the chimpanzee's behavioral patterns (Baker, 2000). In the study population, age was found to influence social proximity, with dyads including senior individuals (>30 years old) showing reduced levels of this spatial association. This may reflect an increasing isolation or a growing selectivity in social partners in elderly chimpanzees, which has also been documented by Webb et al. (2019) and Rosati et al. (2020), respectively. In a husbandry and welfare management perspective, this can present obstacles to health monitoring, as lower social engagement can limit opportunities for caregivers to observe natural behaviors and physical indicators, which are crucial to assess mental, emotional and physical health. Once again, relying on trust-based human-animal bonds can possibly mitigate the complexity of some health monitoring tasks, if conditions are created so that the animals may perceive such interactions as positive and/or affiliative. The challenge lies in fostering bonds that enhance welfare without simultaneously generating undesired human dependency. With this purpose, positive reinforcement training has been demonstrated to increase welfare and facilitate husbandry tasks, while at the same time preventing over attachment to the caregivers. Studies made with zoo-housed primates revealed a significant decrease in abnormal, stress-related and agonistic behaviors and increase in affiliative behaviors following the implementation of a training program (Pomerantz & Terkel, 2009; Spiezio et al., 2017). Given that aggression events in primates occur more frequently directed at low-ranking group members (Shibata et al., 2022; Pasternak et al., 2013) and that the study also demonstrated that lower-ranked individuals presented a higher positive effect than the high-ranking ones, this highlights that structured interactions can provide a reinforced approach to those individuals and mitigate the undesired consequences of repeated agonistic events. Implementing this potential solution can promote positive and stimulating interactions between animals and their caregivers while also facilitating routine husbandry tasks. However, it is essential to clearly define the objectives and methodological approach in advance, as not all interactions between caretakers and captive animals are inherently beneficial for the animals. In unstructured interactions

based study done with great apes, an increase in agonism and a decrease in abnormal behaviors was reported. A careful interpretation must be taken, considering that higher agonism suggests arousal but lower abnormal behaviors is indicative of decline in stress and anxiety (Chelluri et al., 2012b). This underlines the importance of understanding the impact of all types of interactions by assessing possible outcomes at a group level, regardless of being considered as positive for the interacting group member.

Therefore, management and interaction protocols must consider the cognitive complexity and social managing abilities that chimpanzees have demonstrated in both wild and captive environments. Significant personality and emotional traits have been documented in distinct conditions involving resources and social responses. In a study comparing the reaction of captive chimpanzees to inequity in obtaining a reward, Brosnan et al. (2015) showed that some personality dimensions influenced significantly the reaction and sensitivity to unequal reward between two individuals. Furthermore, jealous behaviors have been documented and studied in chimpanzees, which demonstrates the perceptions of a threat in a relationship based on emotion. During a period of group introductions, chimpanzees were found to have more negative reactions, such as agonism and intervention attempts, towards dyads which included groupmates to whom they had valuable relationship, indicating the perception of a social rival (Webb et al., 2020). Applying this to a context where the caregiver is perceived as an integrated and relevant social partner, similar emotional and personality-driven reactions may arise, potentially influencing the quality of interactions and the expression of behaviors such as jealousy and competition. This findings underscore that viewing caregivers as integrated members of captive chimpanzee social structures can be highly beneficial for promoting social stimulations and supporting adaptation to new environments, although it entails a complex understanding of both group dynamics and individual personality traits.

4.3 Study Limitations and Future Considerations

While the study provided relevant insights to primate welfare management and the development of interaction protocols, some limitations were recognized. Mainly, the small sample size (14 individuals) and limited duration of data collection, constrained the data analysis. Specifically, it was not possible to directly compare the two dyadic interaction models (Human–Chimp vs. Chimp–Chimp) using the interaction behavior rate as the dependent variable. For future research on the topic of social species, we recommend the further consideration of impacts of human-animal interactions across different types of captive environments and time frames when including newly introduced members. In addition to the comparative approach within distinct settings, the inclusion of physiological stress indicators alongside the social network analysis should provide a more comprehensive understanding of the impacts of such interactions.

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6. Annex

Behavior	Abreviation	Definition
Affiliative Behaviors	AF	Socio-positive behavior directed and/or received by another member of the same group.
- Social Play	PL	Ludicrous behavior between two or more individuals, punctuated by playful indicators (e.g., play face, laugh, gallop, cartwheels, and pirouettes). Includes tag, catch and grab limbs or objects, tickles, muzzling, rough-and-tumble. These interactions do not require permanent physical contact.
- Follow	FL	Synchronized movement of walking behind or beside another individual, following the trajectory of one or several chimpanzees. Chimpanzees might touch occasionally but may also maintain big distances.
-Feed Together	FT	Two or more chimpanzees feed from the same source or forage in close proximity, sharing/allowing the collection of food within their reach by another individual, sharing food passively.
- Embrace	EB	An individual hugs or tries to hug another with one or both arms in the absence of an agonistic event or indicators such as aggressive or submissive mimics. This behavior can occur while stationary or in movement.
- Greeting	GT	Elements of reunion normally performed in the morning after release to the exteriors. Typically involves approximation with physical contact, head nods, and light pant-hooting vocalizations. Submissive behaviors can also occur in this context towards group leaders or higher-hierarchy individuals.
-Head Leaning	HL	Leaning head towards another individual while standing in very close distance, normally performed as a request or before another affiliative behavior.
-Direct Feeding	DF	Behavior received by chimpanzees from caregivers, with no physical contact, when specific drinks are provided, such as juices or teas, and given by taking a cup to the chimpanzee's mouth.
Grooming	GR	Body-cleansing behavior from one individual to another (includes mutual grooming), performed with the upper extremities or with the mouth.
Agonistic Behaviors	AG	Includes all aggressive or submissive behaviors directed and/or received by another member of the same group.
- Aggression	AGR	Behaviors relating to agonistic/display threat, direct aggression, wounding, chasing, displacement, and/or resource appropriation (including objects and social resources). It can be accompanied by vocalizations. The chimpanzee typically chooses a more dominant and impressive body posture to appear bigger and more threatening. Movements are broad and often contain drumming, swaggering, stomping, etc.
- Submission	SB	Behaviors indicating fear or subordinate intentions toward one or several other chimpanzees. The chimpanzee shows signs of fear directed at another individual in an agonistic context. It may include approaching and presenting vulnerable body parts to appease, or attempting to avoid or flee from an individual displaying aggressive behavior. It can include actions such as genital presenting, extending limbs, hand-to-mouth, finger-to-mouth, running away, avoiding, and is typically accompanied by a scared face and vocalizations such as yelling, screaming, crying, or pant-grunting.
- Display	DP	The individual shows off strength. May include vocalizations such as strong lip splutter, hooing, or hooting. Chimpanzees tend to be pilo-erected, running, swaggering, stomping the ground, throwing objects, or hitting elements and structures.
- Aggression	AGR	Behaviors relating to agonistic/display threat, direct aggression, wounding, chasing, displacement, and/or resource appropriation (including objects and social resources). It can be accompanied by vocalizations. The chimpanzee typically chooses a more dominant and impressive body posture to appear bigger and more threatening. Movements are broad and often contain drumming, swaggering, stomping, etc.
- Submission	SB	Behaviors indicating fear or subordinate intentions toward one or several other chimpanzees. The chimpanzee shows signs of fear directed at another individual in an agonistic context. It may include approaching and presenting vulnerable body parts to appease, or attempting to avoid or flee from an individual displaying aggressive behavior. It can include actions such as genital presenting, extending limbs, hand-to-mouth, finger-to-mouth, running away, avoiding, and is typically accompanied by a scared face and vocalizations such as yelling, screaming, crying, or pant-grunting.
- Display	DP	The individual shows off strength. May include vocalizations such as strong lip splutter, hooing, or hooting. Chimpanzees tend to be pilo-erected, running, swaggering, stomping the ground, throwing objects, or hitting elements and structures.
Social Vigilance	SV	Fixed gaze at someone. It includes looking at distant group members, other groups, and the surrounding area, where the receiver may be a head keeper, caregivers, observers, guides, visitors, and other staff.
Social Proximity	SP	This is not a behavior. Sharing space during inactivity, or associated with other individual behaviors, while the distance between individuals is less than two times the length of the upper extremity (includes physical contact). Social proximity is only recorded between animals that do not interact socially at the time. When recorded with humans, their position is considered as the closest point of the fence to them.
Attention Seeking	AT	The individual may approach a keeper while maintaining eye contact, extending an arm outside of the fence (when possible) towards the human, although this is not mandatory for all individuals. The behavior can also be performed at a relative distance from the receiver, creating a wider range of possible performances. This is normally accompanied by movements and/or sound productions, sometimes repetitive, such as swinging the body, clapping, hitting structures or elements, short screams and hoots, and lip spluttering, which can be reinforced by human response.

Table 3 - Complete ethogram with subbehaviors and definitions. Source: Definitions based on Mona Foundation established ethograms, except for "Attention Seeking" based on: (Nishida et al., 1999) and (Hopkins et al., 2006)