WELFARE PROMOTING ENVIRONMENTS: ASSESSMENT AND MANAGEMENT IN SANCTUARY CHIMPANZEES

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DOCTORAL THESIS

WELFARE PROMOTING ENVIRONMENTS: ASSESSMENT AND MANAGEMENT IN SANCTUARY CHIMPANZEES

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Welfare promoting environments: assessment and management in sanctuary chimpanzees

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Dedication

To all wildlife housed in lacking captive environments.

To all primates I got to know and work with over the years.

To all those fabulous people caring for rescued primates,

tirelessly working towards improving their lives in their own ways.

To Tico, who after a difficult infancy

found a new life and family at MONA up till the last moments of his life.

Thank you for everything you taught and shared with me.

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List of Publications

This thesis is presented as a compendium of three scientific articles published in peer-reviewed international journals.

The articles included in this thesis are:

Crailsheim, D., Stüger, H. P., Kalcher-Sommersguter, E., & Llorente, M. (2020). **Early life experience and alterations of group composition shape the social grooming networks of former pet and entertainment chimpanzees (*Pan troglodytes*).** *PLoS ONE 15(1). e0226947*. doi: 10.1371/journal.pone.0226947

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López-Álvarez, J., Sanjorge, Y., Soloaga, S., Crailsheim, D. & Llorente, M. (2019) Looking for Visitor's Effect in Sanctuaries: Implications of Guided Visitor Groups on the Behavior of the Chimpanzees at Fundació Mona. *Animals 9*, 347. https://doi.org/10.3390/ani9060347

Accepts that Mr. Dietmar Crailsheim presents the cited articles as the principal author and as part of his doctoral thesis and that said articles cannot, therefore, form part of any other doctoral thesis.

And for all intents and purposes, hereby signs this document.

Glossary of Abbreviations

AZA – Association of Zoos & Aquariums

A.P.E.S. – Ape Population, Environments and Surveys

CITES – Convention on International Trade in Endangered Species of Wild Fauna and Flora

DEWD – Deviation from Edge Weigh Disparity

EARS – European Alliance of Rescue centers and Sanctuaries

EAZA – European Association of Zoos & Aquariums

GAIN – Great Ape Information Network

GAPIN – Great Ape Integrity

GRASP – Great Apes Survival Partnership

ICCWC – International Consortium on Combating Wildlife Crime

IUCN – International Union for Conservation of Nature

LAGA – Last Great Ape Organization

LMM – Linear mixed models

NAPSA – North American Primate Sanctuary Alliance

PASA – Pan African Sanctuary Alliance

PTSD – Posttraumatic Stress Disorder

QoL – Quality of Life

SNA – Social Network Analysis

SSC – Species Survival Commission

SWB – Subjective Well-being

USA – United States of America

VSC – Vertex Strength Centrality

WAZA – World Association of Zoos & Aquariums

WHO – World health organization

Summary

Primates, and great apes such as chimpanzees (*Pan troglodytes*) in particular, were and are still a matter of great interest to humans. As a consequence, we can find large numbers of captive chimpanzees all over the world housed in a wide array of living conditions. Chimpanzees can be found in zoos, sanctuaries and rescue centers, yet others might still be part of private unregistered animal collections, or held as pets or used in the entertainment industry. Living conditions in non-accredited housings and private homes are typically not regulated in any way to ensure minimum standards of safety and wellbeing and hence often inadequate.

Rescue centers, such as Fundació MONA, in collaboration with regional and international authorities strive to locate chimpanzees held in such illegal and/or species inadequate living conditions in order to relocate these animals to institutions that have the capacity and resources for rehabilitation and to provide lifelong care. Accordingly, most chimpanzees housed at sanctuaries and rescue centers have a history of adverse living conditions which may include traumatic events such as witnessing the death of their mothers and/or group members and prolonged social isolation, prior to their rescue. Considering the similar developmental trajectories of humans and chimpanzees, including the need for a safe base in early infancy, it should come to no surprise that we also share a certain vulnerability to trauma, reflected in the development of mental disorders and behavioral impairments caused by early traumatic life experiences.

Providing welfare promoting environments for captive chimpanzees can be very challenging considering their highly complex social and environmental demands. It is even more challenging in case of traumatized and behaviorally impaired chimpanzees, as such an environment should provide species adequate care and a habitat designed to reduce welfare compromising negative effects while eliciting welfare enhancing positive effects. Analyzing long-term behavioral data of former pet and entertainment chimpanzees housed at a primate

sanctuary, allows not only to explore the long-term impact of these adverse early life experiences on the behavior but also to evaluate the effects of sanctuary housing.

Most professional institutions housing chimpanzees entertain visitor activities with the objective to promote education and conservation programs. Yet the exposition to unfamiliar visitors is a factor that potentially may have a strong (negative) impact on the chimpanzees' welfare. Although many studies indicate a negative impact due to visitor proximity, crowding, noise and interactions, some studies provide contradicting evidence as well. As such it might not be the visitor activity itself, but rather how these visitors are granted access to the animals as well as what means the animals have to mitigate the presence of unfamiliar humans.

Based on behavioral data collected over more than 12 years, we could demonstrate that past adverse experiences during infancy produce a lasting impact on the social behavior of former pet and entertainment chimpanzees. Specifically, we found that chimpanzees who were predominantly housed without conspecifics during the first five years of their lives to spend less time on social grooming compared to those who were predominantly housed with conspecifics during infancy. We also found that wild-caught chimpanzees were significantly more selective regarding their grooming partners and spent less time grooming when compared to captive born chimpanzees. Regarding the impact of care management decisions, we found that alterations to the group composition (the integration of a new group member to as well as the removal of a chimpanzee from a group) produced a short-term effect on the allogrooming distribution from a more equal distribution during periods with a stable group composition towards a more unequal and selective distribution during unstable periods. Thus, we could demonstrate that the allogrooming networks of former pet and entertainment chimpanzees are shaped not only by long-term effects such as early life experience, but also by short-term effects such as alterations to group composition.

In a next step, by using multilayer social network analysis, we were able to analyze the sociability of these former pet and entertainment chimpanzees in more detail. For this we assessed and compared the similarity and information gain of four different social interaction types representing different levels of social stimulation from low to high: the toleration of stationary vicinity, affiliative behavior, allogrooming and the toleration of passive close proximity. By investigating these low-to-high level social interaction types simultaneously, we managed to improve our understanding regarding these chimpanzees' toleration of the different levels of social interaction. As expected, the results showed that some social interaction types were more similar to each other than other ones, yet each social interaction type imparted different information. Furthermore, we found the chimpanzees' early life experiences to affect the two middle to high social interaction types – allogrooming and affiliative behavior – in the long run.

Regarding the potential (negative) impact caused by the exposure to unfamiliar humans, we did not find visitor groups at the sanctuary to have any effect on the chimpanzees' behavior. We detected only a slight increase in locomotion and a decrease of inactivity during visitor activities, with chimpanzees exhibiting more interest towards groups of larger size. Thus, visitor activities that are severely restricting the visitors' possibilities to interact with or call the attention of the animals, as well as an enclosure design that guarantees the chimpanzees' privacy and control of being visible or not, may enable housing institutions to entertain educational visitor programs without producing a welfare compromising effect.

Each piece of information allows us to further improve our understanding of an ideal welfare promoting environment. It might also help to improve the evaluation of chimpanzees' behavior and welfare in future study designs and may serve caregivers to take even better decisions regarding the rehabilitation and social integration of severely impaired chimpanzees with their special needs.

Resumen

Los primates, y los grandes simios como los chimpancés (*Pan troglodytes*) en particular, han sido y siguen siendo objeto de gran interés para los humanos. Como consecuencia, podemos encontrar un gran número de chimpancés cautivos en todo el mundo alojados en una gran variedad de condiciones de vida. Hay chimpancés en zoológicos, santuarios y centros de rescate, pero otros pueden formar parte de colecciones privadas de animales no registradas, o ser mantenidos como mascotas o utilizados en la industria del entretenimiento. Las condiciones de vida en alojamientos no acreditados y hogares privados no suelen estar regulados y no garantizan unas normas mínimas de seguridad y bienestar, por lo que suelen ser inadecuadas.

Los centros de rescate, como la Fundació MONA, en colaboración con las autoridades regionales e internacionales, se esfuerzan por localizar a los chimpancés mantenidos en estas condiciones de vida ilegales y/o inadecuadas para su especie, con el fin de reubicarlos en instituciones que tengan la capacidad y los recursos necesarios para su rehabilitación con el fin de proporcionarles cuidados de por vida. En consecuencia, la mayoría de los chimpancés alojados en santuarios y centros de rescate tienen un historial de condiciones de vida adversas que pueden incluir acontecimientos traumáticos, como presenciar la muerte de sus madres y/o miembros del grupo y el aislamiento social prolongado, antes de su rescate. Teniendo en cuenta las trayectorias de desarrollo similares entre humanos y chimpancés, incluida la necesidad de una base segura en la primera infancia, no debería sorprendernos que también compartamos una cierta vulnerabilidad al trauma, reflejada en el desarrollo de trastornos mentales y alteraciones del comportamiento causadas por experiencias vitales tempranas traumáticas.

Proporcionar entornos que promuevan el bienestar de los chimpancés en cautividad puede ser muy difícil si se tienen en cuenta sus demandas sociales y ambientales, que son muy complejas. Es aún más difícil en el caso de chimpancés traumatizados y con problemas de

comportamiento, ya que un entorno de este tipo debe proporcionar una atención adecuada a la especie y un hábitat diseñado para reducir los efectos negativos que comprometen el bienestar, a la vez que provoca efectos positivos que lo aumentan. El análisis de los datos conductuales a largo plazo de chimpancés previamente usados como mascotas y en la industria del espectáculo alojados en un santuario de primates no sólo permite explorar el impacto a largo plazo de estas experiencias adversas en el comportamiento, sino también evaluar los efectos del alojamiento en estos centros.

La mayoría de las instituciones profesionales que albergan chimpancés organizan actividades para visitantes con el objetivo de promover programas de educación y conservación. Sin embargo, la exposición a personas desconocidos es un factor que potencialmente puede tener un fuerte impacto (negativo) en el bienestar de los chimpancés. Aunque muchos estudios indican un impacto negativo debido a la proximidad de los visitantes, la aglomeración, el ruido y las interacciones, algunos estudios también aportan pruebas contradictorias. Puede que no se trate de la actividad de las visitas en sí, sino de cómo se permite el acceso a los animales y de qué medios disponen éstos para mitigar la presencia de personas desconocidas.

Basándonos en datos conductuales recogidos durante más de 12 años, pudimos demostrar que las experiencias adversas durante la infancia producen un impacto duradero en el comportamiento social de los chimpancés previamente usados como mascotas y en la industria del espectáculo. Específicamente, encontramos que los chimpancés que fueron alojados predominantemente sin congéneres durante los primeros cinco años de su vida dedicaban menos tiempo al acicalamiento social en comparación con aquellos que fueron alojados predominantemente con congéneres durante la infancia. También se observó que los chimpancés capturados en libertad eran significativamente más selectivos en cuanto a sus compañeros de acicalamiento y dedicaban menos tiempo al acicalamiento en comparación con los chimpancés nacidos en cautividad. En cuanto al impacto de las decisiones de la gestión del manejo, encontramos que las alteraciones en la composición del grupo (la integración de un nuevo miembro del grupo, así como la eliminación de un chimpancé de un grupo) produjeron un efecto a corto plazo en la distribución del acicalamiento social, desde una distribución más igualitaria durante periodos con una composición estable del grupo hacia una distribución más desigual y selectiva durante periodos inestables. Así, pudimos demostrar que las redes de acicalamiento social de los chimpancés previamente usados como mascotas y en la industria del espectáculo están moldeados no sólo por efectos a largo plazo, como la experiencia vital temprana, sino también por efectos a corto plazo, como las alteraciones en la composición del grupo social.

En un siguiente paso, mediante el análisis de redes sociales multicapa, pudimos analizar con más detalle la sociabilidad de estos chimpancés domésticos y de entretenimiento. Para ello, evaluamos y comparamos la similitud y la ganancia de información de cuatro tipos diferentes de interacción social que representan distintos niveles de estimulación social: la tolerancia a una proximidad estacionaria, el comportamiento afiliativo, el acicalamiento social y la tolerancia a una proximidad pasiva. Al investigar simultáneamente estos tipos de interacción social de bajo a alto nivel, conseguimos mejorar nuestra comprensión de la tolerancia de estos chimpancés a los distintos niveles de interacción social. Como era de esperar, los resultados mostraron que algunos tipos de interacción social eran más similares entre sí que otros, aunque cada tipo de interacción social transmitía información diferente. Además, se observó que las experiencias vitales tempranas de los chimpancés afectaban a largo plazo a los dos tipos de interacción social media y alta: el acicalamiento social y el comportamiento afiliativo.

En cuanto al posible impacto (negativo) causado por la exposición a humanos desconocidos, no encontramos que los grupos de visitantes del santuario tuvieran ningún efecto sobre el comportamiento de los chimpancés. Sólo detectamos un ligero aumento de la locomoción y una disminución de la inactividad durante las actividades de los visitantes, y los chimpancés mostraban más interés hacia los grupos de mayor tamaño. Por lo tanto, las actividades de los visitantes que restringen severamente las posibilidades de interactuar o llamar la atención de los animales, así como un diseño de los recintos que garantice la privacidad de los chimpancés y el control de ser visibles o no, pueden permitir a las instituciones de acogida realizar programas educativos para visitantes sin producir un efecto que comprometa el bienestar.

Toda esta información nos permite seguir mejorando nuestra comprensión de un entorno ideal que promueva el bienestar de los chimpancés en cautividad. También puede ayudar a mejorar el diseño de futuros estudios de evaluación del comportamiento y el bienestar de esta especie, así como ayudar a los cuidadores a tomar mejores decisiones en relación con la rehabilitación y la integración social de los chimpancés con necesidades especiales.

Resum

Els primats, i els grans simis com els ximpanzés (*Pan troglodytes*) en particular, han estat i segueixen essent objecte de gran interès pels humans. Com a conseqüència, podem trobar un gran nombre de ximpanzés en captivitat en tot el món, allotjats en una gran varietat de condicions de vida. Hi ha ximpanzés en zoològics, santuaris i centres de rescat, però altres poden formar part de col·leccions privades d'animals no registrades, o ser mantinguts com a mascotes o utilitzats en la indústria de l'entreteniment. Les condicions de vida en allotjaments no acreditats i cases particulars no solen estar regulats i no garanteixen unes normes mínimes de seguretat i benestar, pel que solen ser inadequades.

Els centres de rescat, com la Fundació MONA, en col·laboració amb les autoritats regionals i internacionals, s'esforcen per localitzar als ximpanzés mantinguts en aquestes condicions de vida il·legals i/o inadequades per la seva espècie, amb el fi de reubicar-los a institucions que tinguin la capacitat i els recursos necessaris per a la seva rehabilitació i les cures per la resta de la seva vida. En conseqüència, la majoria dels ximpanzés allotjats en santuaris i centres de rescat tenen un historial de condicions de vida adverses que poden incloure esdeveniments traumàtics, com el presenciar la mort de les seves mares i/o membres del grup i l'aïllament social perllongat, abans del seu rescat. Tenint en compte les trajectòries de desenvolupament similars entre els humans i els ximpanzés, inclosa la necessitat d'una base segura en la primera infància, no hauria de sorprendre'ns que també compartim una certa vulnerabilitat al trauma, reflectida en el desenvolupament de trastorns mentals i alteracions del comportament originades per experiències vitals primerenques traumàtiques.

Proporcionar entorns que promouen el benestar dels ximpanzés en captivitat pot ser més difícil si es tenen en compte les seves demandes socials i ambientals, que són molt complexes. És encara més difícil en el cas dels ximpanzés traumatitzats i amb problemes de comportament, ja que un entorn d'aquest tipus ha de proporcionar una atenció adequada a l'espècie i un hàbitat dissenyat per reduir els efectes negatius que comprometen el benestar, a

la vegada que generi efectes positius que l'augmenten. L'anàlisi de les dades conductuals a llarg termini de ximpanzés prèviament utilitzats com a mascotes i en la indústria de l'espectacle allotjats en santuaris de primats, no només permet explorar l'impacte a llarg termini d'aquestes experiències adverses en el comportament, sinó també avaluar els efectes de l'allotjament en els santuaris.

La majoria de les institucions professionals que allotgen ximpanzés organitzen activitats pels visitants amb l'objectiu de promoure programes d'educació i conservació. Tot i això, la exposició a visitants desconeguts és un factor que potencialment pot tenir un fort impacte (negatiu) en el benestar dels ximpanzés. Encara que molts estudis observen un impacte negatiu degut a la proximitat dels visitants, les aglomeracions, el soroll i les interaccions, alguns estudis també aporten proves contradictòries. Pot ser que no es tracti de l'activitat dels visitants, sinó de com se'ls permet l'accés als animals i de quins mitjans disposen aquests per mitigar la presència de persones desconegudes.

Basant-nos en les dades conductuals recollides durant més de 12 anys, vam poder demostrar que les experiències adverses durant la infància produeixen un impacte perllongat en el comportament social dels ximpanzés prèviament utilitzats com a mascotes i en la indústria de l'espectacle. Específicament, vam trobar que els ximpanzés que van ser allotjats predominantment sense congèneres durant els primers cinc anys de la seva vida, dedicaven menys temps a l'empolainament social en comparació amb aquells que van ser allotjats predominantment amb congèneres durant la infància. També es va observar que els ximpanzés capturats en llibertat eren significativament més selectius en quant als companys d'empolainament i dedicaven menys temps a l'empolainament en comparació amb els ximpanzés nascuts en captivitat. En quant a l'impacte que tenen les decisions del maneig, trobem que les alteracions en la composició del grup (la integració d'un nou membre del grup, així com l'eliminació d'un ximpanzé d'un grup) van produir un efecte a curt termini en la distribució de l'empolainament, des d'una distribució més igualitària durant períodes amb una composició estable del grup cap una distribució més desigual i selectiva durant períodes més inestables. Així, podem demostrar que les xarxes d'empolainament dels ximpanzés prèviament utilitzats com a mascotes i en l'industria de l'espectacle estan modelats no només per efectes a llarg termini, com l' experiència de vida primerenca, sinó també per efectes a curt termini com les alteracions en la composició del grup.

En un pas posterior, mitjançant l'anàlisi de xarxes socials multicapa, vam poder analitzar amb més detall la sociabilitat d'aquests ximpanzés prèviament utilitzats com a mascotes i en l'industria de l'espectacle. Per a això, es va avaluar i comparar la similitud i el guany d'informació de quatre tipus diferents d'interacció social que representen diferents nivells d'estimulació social de baix a alt: la tolerància a la proximitat estacionaria, el comportament afiliatiu, l'empolainament i la tolerància de la proximitat passiva. A l'investigar simultàniament aquests tipus d'interacció social de baix i alt nivell, vam aconseguir millorar la nostra comprensió de la tolerància d'aquests ximpanzés als diferents nivells d'interacció social. Com era d'esperar, els resultats van mostrar que alguns tipus d'interacció social eren més similars entre si que d'altres, encara que cada tipus d'interacció social va donar informació diferent. A més, es va observar que les experiències vitals primerenques dels ximpanzés afectaven a llarg termini als dos tipus d'interacció social: l'empolainament i el comportament afiliatiu.

Pel que fa al possible impacte (negatiu) originat per la exposició al humans desconeguts, no trobem que els grups de visitants del santuari tinguessin cap efecte sobre el comportament dels ximpanzés. Només es va detectar un lleuger augment de la locomoció i una disminució de la inactivitat durant les activitats dels visitants, mostrant els ximpanzés més interès cap als grups més nombrosos. Per tant, les activitats dels visitants que restringeixen fortament les possibilitats d'interactuar o cridar l'atenció dels animals, així com un disseny dels recintes que garanteixi la privacitat dels ximpanzés permet a les institucions realitzar programes d' educació sense comprometre el benestar dels animals.

Tota aquesta informació ens permet seguir millorant la nostra comprensió d'un entorn ideal que promogui el benestar dels ximpanzés en captivitat. També pot ajudar a millorar el disseny de futurs estudis d' avaluació del comportament i el benestar d' aquesta epècie en captivitat així com ajudar als cuidadors per prendre decisions encara millors en relació a la rehabilitació i integració social dels ximpanzés amb necessitats especials.

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Personal motivation

A big part of my experience, working professionally with primates in captivity, is based on my tasks related to the rescue, rehabilitation and life-long care of former pet and entertainment chimpanzees. Thus, considering my original formation as a researcher and extensive experience in primate care, I consider myself a hybrid with the capacity to identify the strengths and shortcomings of both fields. I strongly believe that the collaboration between research and animal care staff is extremely important. It allows us to efficiently increase our knowledge regarding the species in our care and to improve our understanding of how to assess these animals as well as provide them with a welfare promoting environment in captivity.

My personal motivation is based on two main pillars: (1) Gaining insights to improve our understanding regarding care and rehabilitation strategies, specifically focusing on primates who suffered adverse living conditions in their past, while acknowledging the limitations of captivity compared to wild living conditions; (2) Extracting the full potential of captive research activities supporting animal care and welfare.

Professional Motivation & Justification

During the last few decades there is an increase in research regarding the human impact on primates in their wild habitats (Arcus Foundation, 2014, 2015, 2018). While I agree that this type of research is of utmost importance as it treats issues related to the species survival in the wild, human impact on captive housed primates is not to be underestimated. Considering the current limitations of laws and regulations regarding captive animal care and protection, conducting research demonstrating the negative impact of species inadequate care and human influence are greatly needed in order to improve their lives in captivity (Robinson & Weiss, 2023a) and to push towards improved laws and regulations (Brull, 2022). This includes improving our means to efficiently monitor and evaluate the primate’s welfare, discerning issues of captive care and environments, as well as validating strategies that seem to have a positive effect on the animals´ welfare. Furthermore, there is a growing body of information suggesting that capacities and requirements of primates vary greatly even within each species, depending on their past living conditions and experiences. Considering that in captivity nearly all decisions and choices regarding the primate’s lives are made by humans, taking into account how these decisions and human exposure impacts their behaviors and welfare seems to be crucial in order to establish welfare promoting care protocols and environments.

At Fundació MONA, we find chimpanzees who experienced varied scenarios of species inadequate living conditions (previous owners), who after being rescued remain in a captive setting being managed by humans (caregivers) and are exposed to unfamiliar human crowds (visitors). Furthermore, Fundació MONA as a primate rescue and rehabilitation center is eager to constantly improve strategies striving for improved primate welfare. Thus, it is the perfect site to conduct this thesis, aiming to (1) better understand how the chimpanzee’s adverse life history is impacting their behavior and capacities in the present; (2) as well as evaluating if visitor activities can be conducted at an institution housing former pet and entertainment chimpanzees without negatively influencing their behavior and welfare.

1. General Introduction

1.1 Life history and social organization of chimpanzees

Ontogenetic development

The developmental trajectory of chimpanzees is similar to that of humans (Goodall, 1986), and their cognitive (Lonsdorf et al., 2010; Matsuzawa, 2009), emotional (Kano et al., 2012) and social skills (Goodall, 1986) are highly complex (Bründl et al., 2021). The early developmental stages are significantly prolonged compared to smaller sized primate species and some aspects like lactation time and interbirth intervals even surpass the one of humans (Walker et al., 2018). Wild infant chimpanzees spend their first two to five years of life either attached to or in close proximity to their mothers (Bard, 1995; Goodall, 1986; Matsuzawa, 2006), and develop their social skills by interacting with their mother and other members of their group (Goodall, 1986; Plooij, 1984). As in humans, this is a critical time, in which the infant is extremely vulnerable and depends entirely on the care and protection of the mother (Goodall, 1973). During this stage the infant is acquiring an extensive array of skills, such as finding food, avoiding predators, development of gestural communication and handling complex social situations within its own group (Lonsdorf, 2013; Lonsdorf et al., 2012).

Offspring are weaned at around 4–5 years (Clark, 1977; Lonsdorf et al., 2019; Pusey, 1983), but will still remain as juveniles, despite the growing nutritional independency, in proximity to the mother for another 4 to 5 years (Goodall, 1986). Within that interval, apart from a somatic growth, they will practice and hone the necessary skills to survive as well as develop the social skill-set enabling them to become a functional part of the complex social dynamics of the group (Lonsdorf et al., 2012; Matsumoto, 2017; Pusey, 1983). This is being achieved by social learning from group members and practicing with peers and the mother (Goodall, 1986; Stanton et al., 2017). In average, at around 10 years of age, most chimpanzees start to spend most of their time away from their mother (Pusey, 1983).

Sexual maturation is prolonged and very variable (Walker et al., 2018), depending on many social and ecological factors. Females tend to reach sexual maturity between 8 and 13 years of age, emigrate from the natal group to another between 12 and 14 and give birth for the first time at around 16 years of age (Boesch & Boesch-Achermann, 2000; Nishida et al., 2003; Stumpf & Boesch, 2010; Sugiyama, 2004; Wallis, 1997). In continuation, a female may reproduce approximately every 4–6 years, typically giving birth to one infant at a time (Walker et al., 2018). Males on average tend to enter puberty a little later than females and reach sexual maturity at around 15 years (Hamada et al., 1996).

Life expectancy and mortality rates are continuously being updated, in the process becoming more and more realistic due to increasing data from long-term research sites. However, with populations differing in terms of habitat size and type (ranging from savanna to primary forest), population size, food availability and threats produced by predators, human activity and degree of coexistence (Hockings, 2009b), reports and estimates vary between study sites. Data from populations observed at the long-term sites of Bossou, Gombe, Kibale, Mahale and Taï suggest that the average life expectancy at birth for both sexes is around 14 to 15 years of age due to higher mortality rates of infants and juveniles (Hill et al., 2001). Yet individuals that surpass this age, on average reach the age of 30, with females having a lower mortality rate than males (Hill et al., 2001; Muller & Wrangham, 2014). That being said, several studies report individuals reaching a far higher age, with the oldest reported wild chimpanzee at Ngogo being estimated at 66 years of age (Wood et al., 2017).

Social Organization

Chimpanzees live in multimale-multifemale, fission-fusion communities with an average of 35 individuals (Goodall, 1973), but group size might range from 19 to 100 individuals (Langergraber et al., 2014). To date the largest community reported consists of 140–150 chimpanzees, located at Uganda (Mitani & Watts, 2005), though such a size is rare.

Although the total of individuals of one such community can be high, members separate into temporary subgroups called «parties» which vary in size and composition (Lehmann & Boesch, 2004). Parties range from 1 to 77 individuals (Hiraiwa-Hasegawa et al., 1984) with an average size of 6 chimpanzees per party (Goodall, 1968; Reyno & Reynolds, 1965). These variations are strongly influenced by ecological factors such as food quality and availability (Goodall, 1986; Itani & Suzuki, 1967; Matsumoto-Oda et al., 1998), predator pressure (Sakura, 1994) as well as socio-ecological factors such as the presence of receptive females (Anderson, Nordheim, et al., 2002; Boesch & Boesch-Achermann, 2000; Matsumoto-Oda, 1999).

Chimpanzee communities are characterized as polygyandrous (i.e., promiscuous) (Walker et al., 2017) and have a male dominance hierarchy, with males forming the stable core of a community (Bray et al., 2021). Communities are highly territorial, patrolling and defending their home range against neighboring chimpanzee communities, which can result in fatal encounters (Goodall et al., 1979; Martínez-Íñigo et al., 2021; Wilson & Wrangham, 2003) and typically only young sexually-mature females are seen to migrate between communities (Kahlenberg et al., 2008).

Navigating such complex social structures requires chimpanzees to acquire the necessary communication and social behavior skills, typically developed during their infancy by observing their mothers, peers and other members of their social group, imitating and practicing said skills (Bloomsmith et al., 1994; Lonsdorf et al., 2012; Matsuzawa, 2006). Besides its hygienic function (Grueter et al., 2013), allogrooming is one of the most used social behaviors to establish and maintain relationships, bonds, and coalitions (Goodall, 1968; Watts, 2000). Nevertheless, many more behaviors form part of their social behavior repertoire, including agonistic behaviors such as threat and dominance display behaviors (Soldati et al., 2022; Waller & Dunbar, 2005), behaviors to appease and show submission, reconcile or consulate (Fraser & Aureli, 2008) as well as social play behaviors (Cordoni &

Palagi, 2011; Flack et al., 2004) and behaviors to show affection such as hugging (Goodall, 1986). Yet besides, vocal and gestural communication as well as social behaviors, chimpanzees also use social proximity as means to interact and communicate social preferences (Clark, 2011; Mitani & Amsler, 2003).

1.2 Impact of human activities

Population decline in the wild

Humans and chimpanzees are similar in many ways, yet there is one crucial element that differs greatly. While the number of humans is increasing globally (Gross, 2023), chimpanzee populations in the wild are declining rapidly (Leroy et al., 2004; Molina-Vacas et al., 2023; Walsh et al., 2003). Both trends are closely connected, as human activities produce a negative impact on their natural habitat and populations (Caldecott & Miles, 2005). Thus, humans have to be considered a major threat as well as the biggest competitor for resources.

Chimpanzees (*Pan troglodytes*) can still be found in 18 countries across Equatorial Africa (Lester et al., 2021) and as such have the widest geographic distribution, compared to other African ape species. Over time they managed to continuously adapt to their natural environment, which allowed this species to strive and become the ape species with the most numbers. This wide geographic distribution and their adaptability resulted over time in a considerable genetic diversity, dividing chimpanzees into four subspecies including the Eastern chimpanzee (*Pan troglodytes schweinfurthii*); the Central chimpanzee (*Pan troglodytes troglodytes*); the Cameroon – Nigeria chimpanzee (*Pan troglodytes ellioti*); and the West African chimpanzee (*Pan troglodytes verus*) (Bowden et al., 2012; Fontsere et al., 2022; Gonder et al., 2011).

Yet, since the early 19th century the anthropogenic environmental changes in Africa advanced at an unparalleled speed, modifying and drastically reducing their natural habitat rapidly. Most African environmental issues are human induced, affecting African endemic life both directly and indirectly. Chimpanzee habitats became increasingly subject to degradation and fragmentation by logging, agriculture, mining activities (Arcus Foundation, 2014) and the expansions of human settlements (Arcus Foundation, 2018). By now this habitat destruction is affecting most chimpanzee populations, with human population growth and consumption trends being the major drivers (Arcus Foundation, 2018). The human population growth in Africa creates a need for more accessible and usable terrain, yet the global human increase also increases the amount of food production. Furthermore, richer countries tend to over-consume, importing these resources often from poorer countries such as Africa (Arcus Foundation, 2015).

Due to human encroachment of wildlife areas and progressive appropriation of chimpanzee habitats with roads and infrastructures being planted in or close to wildlife areas, the separation which originally helped to protect each other is greatly reduced or eliminated completely (Devaux et al., 2019; Lindsey et al., 2013). As a result, chimpanzee population became even more vulnerable to human-chimpanzee disease transmission (Negrey et al., 2019; Ordaz-Németh et al., 2017) as well as more susceptible to fall victim to hunting and poaching activities (Poulsen et al., 2009; Wilkie et al., 2011).

Chimpanzees are listed in CITES Appendix I and since 1996 are categorized as endangered (critically endangered in case of Western chimpanzees) on the IUCN Red List (Humle et al., 2016). An exact census is not available, but the IUCN provides estimates, based on pooled sources, published in the red list assessments every few years. The latest report from 2016 (Humle et al., 2016) estimates that there are approximately 140.000 Central chimpanzees (*Pan troglodytes troglodytes*), 18.000–65.000 Western chimpanzees (*Pan t. verus*), 181.000–256.000 Eastern chimpanzees (*Pan t. schweinfurthii*), and only about 6.000–9.000 Nigeria–Cameroon chimpanzees (*Pan t. ellioti*) left in the wild. Due to the difficulty of accessing their habitats, tracking the animals and pooling data from different study sites, the estimation range for each subspecies tend to be very broad. Furthermore, as populations are estimated to follow a declining trend, we have to expect even lower numbers today (i.e., in 2023).

Due to the recent Covid-19 outbreak, once more have we been reminded that disease transmission between species (zoonosis) is not only dangerous for wildlife, but humans as well (Llorente, 2020). Yet, despite this risk, hunting activities and in continuation the consumption of bush meat is being practiced throughout the areas where chimpanzees can be found (Milner-Gulland et al., 2003). Especially in remote and/or impoverished areas, bush meat represents an essential source of animal protein, particularly if livestock and fish are not accessible or affordable (Brashares et al., 2004). For some, bush meat also represents an important economic resource, which becomes especially urgent in periods of economic hardships, i.e.,, crop failures (Loibooki et al., 2002; Schulte-Herbrüggen et al., 2013). These hunting activities partly consist of bush meat acquisition to satisfy the protein demand, but also includes the extraction of life wildlife to be sold and exported for private and/or commercial purposes (Jeffries, 2006; Stiles et al., 2013).

Chimpanzees living in a captive setting

Great apes and in particular chimpanzees triggered a curiosity in humanity since early times and their possession was often associated with wealth and status (Duncan, 2019). Descriptions and trade activities regarding these species have been documented in ancient scripts such as the Bible and Egyptian hieroglyphs, typically describing how they were displayed as a curiosity to entertain and amuse the rich and wealthy (Kisling, 2000). During the age of exploration between the 15th and the 17th century, Europeans rediscovered these exotic animals once more during the process of expanding their territories on the African continent. Due to improving means of travel and transportation at that time, more and more chimpanzees were killed or captured in order to be brought back to Europe (Kisling, 2000). In the following two centuries, great apes as well as other exotic species were specifically targeted to be imported to Europe. Great apes soon became one of the most popular attractions at circuses, entertainment parks, zoological gardens, private collections or to be sold as pets (Kisling, 2000; Moss & Esson, 2010). From the 1930s onwards, the close genetic relationships and general resemblance to humans resulted in the widespread use of chimpanzees in invasive biomedical and behavioral research conducted by medical facilities (Institute of Medicine and National Research Council, 2011; Johnsen et al., 2012; Peterson & Goodall, 2000).

Due to the animal welfare and care practices lacking knowledge, resulting in inadequate and limited living conditions, chimpanzees showed a high mortality rate and short life span in most of these captive settings. This lead to continuous replacement and importation of more individuals (Baratay & Hardouin-Fugier, 2004; Benbow, 2004; Jamieson, 2008). Over time, by learning more about animal behavior and the effects of captivity and husbandry practices on behavior and physiology, it became possible to increase the life expectancy of chimpanzees and breed them in captivity, reducing the need of continuous importation (Seal & Flesness, 1986; Wolfle, 1999). In the beginning of the 1970s the legal capture and import of wild chimpanzees covering the demand of zoos and research facility greatly decreased (Institute of Medicine and National Research Council, 2011; Kabasawa, 2011), with the last wild chimpanzee to arrive at a zoological garden in the 1980s. By now, legal trade of great apes has ceased completely, being replaced by breeding and exchange programs.

In the end of the 19th century and the beginning of the 20th century, several initiatives, such as the International Consortium on Combating Wildlife Crime (ICCWC), the Conservation on International Trade in Endangered Species of Wild Flora and Fauna (CITES), the Great Ape Survival Partnership (GRASP), the Last Great Ape Organization (LAGA) and the Great Ape Integrity (GAPIN) emerge in order to control the legal and illegal trade in great apes. Regardless the efforts made, illegal trade business of exotic fauna, i.e.,, great apes remains one of the most profitable and active criminal activities today (Stiles et al., 2013).

As a result, chimpanzee can be found in a variety of different settings and legal situations in captivity all around the world, ranging from privately owned pets, laboratories, side road zoos, circuses to accredited zoos such as AZA/EAZA member zoos, sanctuaries and rescue and rehabilitation centers. These settings differ widely in their care and housing standards and guidelines.

When comparing aspects of captive and wild chimpanzees it is of outmost importance to take into account the large differences of their respective social and physical environments as well as implications of human control and impact on their daily lives. Wild chimpanzees have large day ranges (Baldwin et al., 1982; Basabose, 2005; Herbinger et al., 2001), varied vegetations within a three-dimensional complex environment (Chapman & Wrangham, 1993), live in a complex fission fusion social society (Lehmann & Boesch, 2004) and, need to invest a big part of their daily activity budget in travel, forage and feeding (Potts et al., 2011). Human interference can globally be broken down in «encounter humans» (Hockings, 2009a), mostly responded by ignore, monitor, intimidate, threat, retreat or flight (McLennan & Hill, 2010) and «competing for resources», as chimpanzees can at times be seen to raid crops (Bessa et al., 2015; Hockings et al., 2009; Krief et al., 2014; McLennan, 2013). While the human presence and activities in or close to chimpanzee habitats produce a major impact on their lives, humans are not directly controlling their day-to-day activity. Compared to the wild, captive chimpanzees, tend to inhabit far smaller areas/enclosures, lacking such highly complex climbing structures, and in many cases with little to no access to arboreal and terrestrial natural substrate (Pruetz & McGrew, 2001). Their social environment is controlled by humans, including social aspects such as group size and composition, with typically far less variety of group members over time (Fultz et al., 2022). In many cases, neither the physical nor the social environment enable chimpanzees to exhibit activity levels and a behavioral range comparable to wild ranging conspecifics. It is important to understand, that this is not meant as a critic regarding specific captive settings, but rather trying to underline the immense difference between the wild and captive environments. As mentioned before, chimpanzees are highly flexible and adaptive animals, thus will adapt their behavioral repertoire and activity levels to their living conditions. Thus, it has to be expected that the chimpanzees themselves in many aspects, be it physically (Lewton, 2017), socially or behaviorally (Inoue & Shimada, 2020) are difficult to compare as well. This becomes even more apparent, if we take into account how varied and different environmental aspects and influencing conditions can be even between different captive settings. Depending on the site, chimpanzees living in captivity can be found in barren unnaturalistic environments as well as spacious enclosures consisting of the same vegetation they would find in their natural habitat; the degree of freedom and control regarding their environment can range from extremely restrained to flexible/amendable; and professional care and management can range from following the latest suggestions of best practice manuals or be non-existent. Therefore, we must distinguish between primates housed by a recognized professional institution, such as a licensed zoo, scientific institution, sanctuary or rescue/rehabilitation center (i.e. institutions dedicated to research, education, conservation and/or rescue activities), and privately owned primates kept as pets for leisure or as a hobby or entertainers used for non-educational displays or exhibits (Hevesi, 2023).

Although there are differences in how social and ecological factors affect different wild populations, we are still able to provide a global description, conceptualizing the chimpanzees’ life in the wild and their interaction with their habitat. Yet doing the same for chimpanzees living in captivity is far more difficult and ill-advised, as the captive circumstances and environment can be extremely dissimilar depending on the purpose, philosophy and financial situation of the housing organization/owner. Thus, in the same manner as we do not expect wild and captive chimpanzees to develop and behave exactly the same way, we should consider this to be as well the case when comparing chimpanzees living in different captive settings. For example, chimpanzees kept as pets in a human household and those living in a primate care institution specialized in animal care are likely to receive very different treatments and inhabit drastically different housing facilities, yet both live and might have been raised in captivity.

Additionally, we have to take into account the consistency of the upbringing and life conditions. Wild chimpanzees may spend up to 30-40% of their time traveling on average between 2 to 4 km every day, but remain generally in their home ranges (Ross & Shender, 2016) or in case of adolescent females (after reaching sexual majority at 11-13 years of age) emigrate to neighboring populations (Thompson, 2013), yet the environment stays the same or is at least comparable. Yet captive chimpanzees and especially those illegally obtained, are likely to change owners, locations and/or their purpose over time (Freeman & Ross, 2014; Peterson & Goodall, 2000). These animals might have been breed in captivity or been caught in the wild, to be sold and transported to their new owners. Even if being apprehended and confiscated due to the efforts of the authorities and/or professional animal housing organizations, the chances to go back to life in a wild habitat are very slim (Hannah & McGrew, 1991). In most cases, if rehabilitation and re-release into their natural habitat are not possible, their best option is to be cared for in a sanctuary or zoo. Nevertheless, the destination, changing for better or worse, each stop remains part of their life history potentially influencing their development, capacities and limitations.

Current situation in captivity

Although modern communication means greatly improved worldwide information flow, putting an exact number on captive populations still remains very complicated. This is due to several reasons. Although some major organizations such as AZA, EAZA, WAZA and GAIN, to name a few, maintain registers and studbooks, updating these records depends greatly on the collaboration and desire to participate of each housing organization. Another reason is the unavailable information regarding illegally held chimpanzees, as reliable records tend to only include chimpanzees housed at accredited zoos, research facilities, sanctuaries, and laboratories (Che-Castaldo et al., 2021). Yet privately owned chimpanzees used as mascots, in the entertainment industry or for breeding are unlikely to be included in any publicly available lists (Arcus Foundation, 2021). Even known cases may not being included in these lists, mainly due to the difficulty of gathering reliable information and data consistency.

As such, we are only able to provide some indicative numbers on a regional level. Arcus Foundation and Project Chimp Care estimate around 1300 chimpanzees to live in North America (ChimpCare Licoln Park Zoo, 2023), GAIN lists 297 chimpanzees in Japan (Great Ape Information Network, 2023) and the latest Studbook provided by EAZA (Carlsen et al., 2022) registered 1059 chimpanzees in Europe. We refrain from listing any more sources as they are either outdated, do not seem fully reliable or work on a too small regional scale to be meaningful. Yet the above-mentioned numbers of legally housed chimpanzees in captivity, already show the great number of chimpanzee population that can be found in captivity these days. However, in the following chapters we will concentrate on said chimpanzees that are typically not registered or cared for based on recommended best practice guidelines, i.e. pet and entertainment chimpanzees.

Visitor programs and unfamiliar human exposure

Most institutions housing wildlife depend on the income produced by visitor programs to cover the expanses of housing the animals in their care (Godinez & Fernandez, 2019). Furthermore, other objectives such as environmental education and conservation projects often require to invite the audience/visitors to come to the housing institution, seeing animals on display (Baker & Farmer, 2023). The presence and actions of unfamiliar humans such as visitors may produce welfare challenges for many species (Fernandez et al., 2009). Studies regarding human-animal interactions in zoos reported varied results, suggesting that visitors may produce a positive, negative or neutral impact (Hosey, 2023; Hosey, 2005). However, specifically in primates the majority of studies suggest a negative impact on the animal welfare (Hosey, 2005) mostly expressed by increased agonistic or stereotypical behaviors and decreased intra-group affiliations or time spent in exploration (Cooke & Schillaci, 2007; Davis et al., 2005; Mitchell et al., 1991; Sekar et al., 2008). Several studies suggest that by offering larger, more naturalistic and well planned enclosures, negative welfare impacts of visitors can be strongly reduced (Coe, 2003; Maple & Perdue, 2013).

1.3 Effects of adverse life experiences

When working with rescued animals, the term «a fresh start» frequently comes up, referring to the animal's arrival at a professional housing organization, dedicated to their rehabilitation. This however is far from reality, as «a fresh start» stipulates ignoring the past and starting from zero without being influenced or tainted by previous events and circumstances. While the new housing organization might strive to maximize efforts to help the rescued animals recuperate, past experiences may have strongly shaped the animals to their current state (Bogart et al., 2014; Clay et al., 2018; Reimers et al., 2007). Thus, all decisions and efforts from this point of time onwards, may guide and influence the current being, yet will not erase the past itself, i.e., reset to a time before traumas occurred or damage started to build up. Thus, the animal's past should be considered a crucial piece of information in rehabilitation and care management decisions.

Chimpanzee's perception of people

Pet and entertainment chimpanzees tend to establish strong (but not necessarily always positive) relationships with humans, due to their use as companions and entertainers. This intense human exposure is likely to result in a specific perception of humans, which due to their capacity to remember events from their past (Lewis et al., 2019) may remain even after the chimpanzee has been moved to a more species adequate environment. As a result, we might find chimpanzees with such an adverse history to respond with extreme reactions towards humans, such as extreme wariness, excessive aggression as well as heightened interest or even the preference of human company and interaction over that of conspecifics. Leavens and Hopkins (1998) also reported male chimpanzees with higher human exposure during their first year of life to act more aggressively towards humans as adults, compared to those with less human exposure. The widespread occurrence of agonistic and affiliative interactions directed at people should not be considered as problematic, as these are species typical means of communication and interaction with others and some might even argue that humans are part of their social network (Funkhouser et al., 2020). Yet if such behaviors are exhibited in high frequencies or during every human encounter, they should be considered a serious problem. During the first weeks after arrival at a new environment, behaviors related to fear and wariness may be considered as an appropriate response due to the fact that both the environment and the people are strangers to the chimpanzees, in which case, the intensity and frequency should diminish over time (Miller et al., 1990). The relationship between captive chimpanzees and the caregivers is a critical aspect of captivity, which potentially can improve or impair the chimpanzee's quality of life (Baker, 2004; Jensvold, 2008). Caregivers have several tools at hand to improve said relationship, such as positive reinforcement training (Darren et al., 2011; Pomerantz & Terkel, 2009) and adapting care management aspects permanently or temporarily.

Physical consequences

Even though every rescue case is different, former pet and entertainment chimpanzees were usually kept in poor environments lacking professional care, which could have led to physical problems that may vary depending on how long they were exposed to harmful or lacking living conditions. Malnutrition, obesity, arthritis, diabetes, bone structure malformations, muscle loss, untreated bone fractures, advanced teeth deterioration, hair loss, skin infections, injuries, and problems with essential organs such as heart, lungs, liver and kidneys are typical deficiencies exhibited by rescued chimpanzees (Arcus Foundation, 2021). Once diagnosed, most of these health issues may be treated or greatly improved, although at times requiring lifelong treatment and frequent health check-ups (Hevesi, 2023). By providing professional care and an adequate environment to strive and recuperate, veterinarians and caregivers may be able to promote and maintain a desired health state. However, up to date, there is no information published in official journals regarding the conditions these animals arrive at rescue centers, and thus information needs to be extracted from veterinary or caregiver reports.

Psychological impact

Humans and chimpanzees share an array of psychological qualities, such as consciousness, self-awareness (Davis, 2008), compassion (Hirata, 2020), social bonding (Roberts & Roberts, 2019), strategic thinking (Hare et al., 2000; Martin et al., 2014), memory (Inoue & Matsuzawa, 2007; Kawai & Matsuzawa, 2000) and even humor (Picton, 1889), to name a few. However, they also share a vulnerability to trauma (Padrell et al., 2021; Reimers et al., 2007). In the early 2000 after discussing if chimpanzees and other apes might suffer traumas and could benefit from psychotherapeutic treatments (Brüne et al., 2004; Brüne et al., 2006), more researchers started the focus on mood and anxiety disorders in chimpanzees (Bradshaw et al., 2008; Ferdowsian & Merskin, 2012; Ferdowsian et al., 2012; Ferdowsian et al., 2011; Úbeda et al., 2020).

The combination of adverse circumstances and traumatic or intrusive events, particularly during early stages of development, is likely to have lasting consequences and can even result in symptoms that can be defined as Post-Traumatic Stress Disorder (PTSD), as typically identified in individuals who have experienced traumatic events (Briere & Spinazzola, 2005; Herman, 1992; Kolk et al., 2005). Such symptoms are typically identified and assessed according to diagnostic systems such as the DSM (American Psychiatric Association, 2013). Brüne (2006) states that assessing psychopathologies in great apes to be rather difficult due to the absence of verbal self-reports and comparisons to moral standards are inadequate for non-human primates. Thus, we are left with measuring the deviance in form, content, or frequency and the functional outcome of the behaviors we can observe (Brüne et al., 2006).

Such long term effects and deviances from the norm can be observed in the form of the occurrence of stereotypical behavior and other abnormal behaviors, alterations in the animals stress responses as well as the reduced or incapability to bond and form normal social relationships, the inability to copulate and incompetent maternal behavior (Brent, 2001; Brent et al., 1989; Kraemer, 1997; Walsh et al., 1982). Although stereotypical and other abnormal behaviors can disrupt and interfere with a normal life, even leading to serious physical health issues in case of self-harming (Kummrow, 2021), we are focusing here in the deviance from the norm and maladaptive consequences regarding their social skills and abilities. This includes the chimpanzee's capability to take advantage of improved living conditions, adapt and live in a social setting, as well as the exposure to humans in a captive setting. Troisi (2003) emphasized the necessity, in both human and non-human primate psychopathology, to include the criteria of maladaptive consequences of behaviors, which interfere with the individual's biosocial goals such as mating, infant raising, coalition forming and social bonding, to name a few. In 1969 experimental research in laboratory chimpanzees described social and environmental deprivation as during early life as having clear detrimental effects, such as reduced drive to interact socially, reduced and infrequent play, reduced learning speed and frequent exhibition of stereotypical behaviors to name a few (Turner et al., 1969).

Chimpanzees, being highly social animals, typically acquire the most essential social and survival skills from their mothers and peers during infancy and adolescence, in order to function in a social group setting and increase their fitness as adults (Fragaszy & Mitchell, 1974; Murray et al., 2014). This includes both solitary behaviors such as foraging, including identifying, locating (Rapaport & Brown, 2008) and processing of food and nest building (Videan, 2006), and social skills such as agonistic behaviors, recognizing dominance indicators, establishing and maintaining relationships through affiliative interactions, communication skills, grooming and mothering (Lonsdorf, 2013; Lonsdorf et al., 2012; Watts & Pusey, 2002). This requires both an adequate physical environment providing the situation to promote these natural behaviors as well as the social component, of having their mothers and other adults to learn from and peers to practice with (Hayashi & Matsuzawa, 2017). Bloomsmith et al. (1994) reported in a study regarding juvenile and adolescent behavioral development in complex natal groups (i.e., all juvenile and adolescent chimpanzees were born and raised in those groups), that the social behavior patterns observed resembled those of wild populations, rather than those of captive chimpanzees raised in peer groups, i.e., missing mothers and other adult group members. These similarities to wild chimpanzees highlight the importance of an appropriate rearing environment, promoting a species-typical social development. i.e., the presence of a diverse social group including the mother, adults and peers.

Rehabilitation and recovering from their past lives

Once we agree on chimpanzees suffering long term effects from adverse living conditions and traumatic experiences during their infancy, the question still remains if and how they can partially or fully recover once cared for adequately. Professional care institutions are dedicated to provide favorable conditions for these animals to recover and rehabilitate. Rehabilitation can be understood as the process in which captive primates receive medical treatment until they regain health, are weaned from excessive human contact and social dependence, while being gradually integrated in an social environment with conspecifics and are being helped to acquire the necessary skills to cope with future challenges and living conditions while developing their behavioral and social skill set (Llorente et al., 2015). In this context, the aim is to recuperate a physical, psychological and emotional state which allows these animals to be re-released or in case in release is no option anymore, being able to live a life worth living in captivity (Borner, 2009; Humle et al., 2011). This rehabilitation process can be very complex and lengthy (ranging from a few months to several years), depending on the chimpanzee's age and individual traumatic experiences, typically associated with the capture, maternal deprivation and/or mistreatment received (Hannah & McGrew, 1991).

To date, research on the rehabilitation process, its effectiveness and potential successes is greatly lacking, with few exception being projects that aim for re-release into their natural habitat (Ongman et al., 2013) or case studies with small sample sizes (Feliu et al., 2022; Llorente et al., 2015). Due to the complexity and often long duration of the rehabilitation process, most chimpanzees end up living in sanctuaries or zoos rather than being re-released (Hannah & McGrew, 1991).

1.4 Concepts of Animal Welfare

The most controversial issues in animal welfare are related to the way humans treat animals in captivity and the way how those animals respond to said treatment (Hevesi, 2023). On the other hand, animal welfare scientists carry the heavy burden of finding the most objective and efficient way to assess and measure the animal's welfare.

Five Freedoms

Although, there are records of both philosophers and scientists reaching back as far as to the ancient Greeks, treating topics regarding the relationship of humankind to animals, their sentience, awareness and capacity to feel, it was not until the second half of the 19th century that these topics were addressed (Duncan, 2019). One of the initial keystone events might be the publication of the book «Animal Machines» (1964) written by Ruth Harrison, which described in detail the cruelty of methods and conditions used in the cattle industry. Her criticism regarding the suffering and negative subjective state these animals were experiencing, lead to a surprisingly strong reaction by the general public, which in turn forced the British Government to act and form a Committee of Enquiry. The resulting «Brambell Report» (Brambell, 1965) concluded that there was indeed some cause for concern about animals in intensive production systems, but due to a lack of scientific evidence it was not possible to draw a firm conclusion. Thus, this report stated, *"Welfare is a wide term that embraces both the physical and mental well-being of the animal. Any attempt to evaluate welfare, therefore, must take into account the scientific evidence available concerning the feelings of animals that can be derived from their structure and functions and also from their behavior"* (Brambell, 1965). At that time the scientific approach to animal welfare was strongly orientated towards negative welfare, i.e., evaluating the pain, suffering and stress, animals in the livestock production experienced. In an attempt to incorporate subjective experiences, the health and behavior in animal welfare, the Five Freedom concept (Farm Animal Welfare Council, 1993) was formulated. This concept is based on a series of fundamental principles to enforce right actions and standards including the freedom from thirst, hunger, malnutrition, thermal and physical discomfort, pain, injury, disease, fear, distress and the freedom to express normal behavior. However, over time, due to the rising popularity of animal ethics and improved understanding of animal needs and awareness, many other concepts, often much more complex and detailed, emerged (Robinson & Weiss, 2023b).

Although originally focused on farm animals in the production industry, these concepts eventually extended their appliance to other animals held in captivity, such as pets, zoo animals and laboratory subjects (Broom, 2011).

Five Domains

Originally established in 1994, the Five Domain Model for animal welfare was updated seven times in order to incorporate the most recent authenticated understanding and developments in animal welfare science (Mellor, 2016). The earliest versions focused on the detection and assessment of welfare-compromising negative effects, but later included welfare-enhancing positive effects (Mellor & Beausoleil, 2015) and eventually progressed to incorporate the interaction between physiological mechanisms and the generation of particular subjective experiences, i.e.,, affective states (Mellor et al., 2020). The principal purpose of the domains is to detect and assess both internal states and external circumstances animals may experience, which are producing a negative (limiting) or positive (enhancing) effect on their lives. The first three domains concentrate on animal care-related inputs on welfare, i.e., nutrition (imbalances and opportunities), physical environment (unavoidable and enhanced conditions) and health (negative and positive conditions). The fourth domain focuses on the behavioral output of the animals as an indicator of the animals´ perception of their external environment (physical environment). The fifth and last domain was designed to capture the overall mental state, taking into account all impacts considered within the first four domains, evaluating what the animal was likely to experience subjectively.

Five Domains, including human-animal interaction

The latest update of the Five Domains Model, published in 2020, is focused on the presence of humans in the animals' vicinity, i.e., emphasizing the importance of including the impact and interactions of humans (Mellor et al., 2020). The previous model included and differentiated to some degree between interactions with the physical environment and other non-human animals, yet human-animal interactions were not yet included. This latest update highlights that humans play an influential role in the animal’s environment, and human-animal interactions have the potential to produce welfare-compromising negative but also welfare-enhancing positive effects.

Latest tendencies in animal welfare views

There is a great variety of opinions regarding how animal welfare should be measured and what needs to be included. Some attempts concentrate purely on the behavior, taking special note of abnormal behaviors, anxiety related behaviors and making a clear differentiation between species-appropriate and inappropriate behaviors (Lutz & Baker, 2023). Recent developments have led some scientists to focus on psychological well-being, applying «cognitive bias» paradigms to assess the animals’ emotions. They describe how emotions such as anxiety and depression are associated with changes in the way the brain processes information, i.e., measuring the interaction between emotion and cognition in nonhuman primates (Bethell & Pfefferle, 2023). Physiological measures such as hypothalamic-pituitary-adrenal, sympathetic-adrenal-medullary, cardiovascular and immune functions may also provide insights into the animals´ welfare (Capitanio et al., 2023), although often relatively costly and limited to a one point in time measurement.

During the last few decades, the use of quantitative questionnaires allowed us to obtain an estimate of animals´ well-being, health, behavior, and personality. Similar to the evaluation conducted on non-verbal human infants, the information has to be obtained as objectively as possible from other human sources, typically being the animals’ caregiver. This method allows covering a broad assessment of the animal’s physical, psychological, emotional state, including information regarding the environment and living conditions while being economically efficient and non-invasive (Gartner, 2023).

Regardless of the method used, each methodology is able to provide information the others cannot and the issue remains that animal welfare is extremely difficult to measure (Mason & Mendi, 2023). Furthermore, there is an ongoing lack of definition universally agreed upon when it comes to welfare. Although the philosophical base tends to be the same or at least similar there is much confusion regarding the terms welfare, wellbeing, subjective well-being (SWB), quality of life (QoL), happiness and how these should be assessed and discussed (Haynes, 2011; McMillan & Yeates, 2020).

1.5 Welfare promoting environment

Starting from the premises that their natural habitat remains the most suitable environment for these animals, living conditions in the wild might be harsh, survival is not guaranteed and human activities have an increasingly strong impact on wild populations (Haynes, 2011; Littleton, 2005). Depending on the species and the individual's circumstances, in some cases captive primates can be successfully re- or introduced to their natural habitat (Cheyne, 2009; King et al., 2012; Marsden et al., 2006). However, for most primates born in captivity, or when caught in the wild at an early age and growing up in captivity for a prolonged period of time, re-introduction is most likely not an option (Goossens et al., 2005).

As previously mentioned, chimpanzees should not be held captive for the purpose of personal leisure, entertainment or economical profit, but should be cared for by institutions focused on rescue, rehabilitation, education, or conservation (Hevesi, 2023). An institution focusing on the latter respects the integrity of each animal, providing a safe and nurturing environment in specifically designed enclosures, adapted to the species' and individual's needs, while prioritizing the individual's welfare at all times (Doyle, 2017).

Based on the most recent views about animal welfare (Robinson & Weiss, 2023a) and insights from welfare assessment tools like the Five Domains Model (Mellor et al., 2020), a welfare promoting environment can be understood and defined as a professional care institution providing captive chimpanzees with a species adequate habitat and care designed to reduce welfare-compromising negative affects while eliciting welfare-enhancing positive effects. However, the identification of factors producing a welfare-compromising or enhancing affects is an ongoing process, thus needs to be treated carefully and requires continuous updates. Hence, an institution, aiming to provide a welfare promoting environment to the chimpanzees in their care, needs to continuously strive to integrate newly acquired knowledge regarding the animal's care and welfare requirements. This may partly be achieved by consulting and implementing best practice guidelines that have been established and validated by multidisciplinary professionals (Ross, 2020). Yet even within one species, complying with the welfare needs of each individual is a significant challenge due to the many differences that might occur due to sex, age, health status and especially the individual life history.

In conclusion, a welfare promoting environment can be provided and is defined as an institution that (a) houses chimpanzees under the premises of rescue, rehabilitation, education and/or conservation and (b) strives to provide the highest levels of welfare by considering the individual's limitations and requirements, by continuously updating and improving the facilities and care strategies, based on validated guidelines and professional counseling.

1.6 Research Objectives

In this thesis, I examine the short and long-term impacts of past and current living conditions on the behavior of former pet and entertainment chimpanzees (*Pan troglodytes*), housed at the primate rescue and rehabilitation center Fundació MONA. I aim to study the social capacities and preferences of chimpanzees that suffered varied level of adverse living conditions in their past (Kalcher-Sommersguter et al., 2011) by combining long-term observations and detailed multi-level social network analysis (De Domenico, Porter, et al., 2015) based on behavioral and social proximity interactions between social group members.

Furthermore, I also aim to study if controlled educational visitor activities are producing a short-term impact on the behaviors of former pet and entertainment chimpanzees (Fernandez et al., 2009). By analyzing the individual chimpanzees' behavioral tendencies and responses, I intend to provide a holistic understanding of the behavior of former pet and entertainment chimpanzees within the greater context of considering their traumatic and/or adverse life history, expanding on the current scientific knowledge that to date, has been mostly limited to former laboratory or zoo chimpanzees. Specifically I am to provide insights that may serve to further update welfare assessment models such as the Five Domains Model (Mellor et al., 2020). For this, I address the main research questions below, which focus on the chimpanzees' behavioral activity– especially their affiliative behavior – found in two social groups of captive housed chimpanzees by considering their living conditions during infancy. Hypotheses that are more specific to each topic are given in each article.

This thesis is organized into four chapters. In the **first chapter**, I provide additional information regarding chimpanzees' development, requirements, and information related to their welfare that has not been presented in any of the studies forming part of this compendium. In the **second chapter**, I discuss the study site and population and outline the general methods used in this thesis. However, methods that are more specific to each article are given in each article. In the **third chapter**, I present all three articles, which have been published in peer reviewed journals in the formatting style of this thesis. Although the content is identical, as all three articles have been published in an open access format, they can be consulted in the original formatting style of each respective journal (open access links are provided to facilitate the quick access).

Chapter 3 – Article A is based on long-term behavioral observations and relates to short-term impact of alterations to their social group composition and long-term impact of adverse living conditions during infancy on the chimpanzees grooming behavior. I attempt to study their individual grooming activity and distribution depending on the stability of the group composition, by comparing stable and unstable time periods (i.e., where alterations to group composition occurred) during a period of 12 years. Furthermore, I attempt to classify the former pet and entertainment chimpanzees based on their origin (wild-caught vs. captive born) and social housing condition during infancy (predominantly housed with vs. without conspecifics during infancy). Once their adverse past has been established, their grooming strength and distribution are examined, in an attempt to identify how adverse living conditions during infancy correlates with the chimpanzees grooming patterns. The general research questions in this article are:

1. Are early life adversities producing a detectable long-term impact on the grooming activity of former pet and entertainment chimpanzees, even after being introduced and living within a social group of conspecifics for years? We expect prolonged housing without access to conspecifics during infancy to have a negative impact on the respective chimpanzee's grooming activity, as social behaviors, such as grooming, develop very slowly in infant chimpanzees. We expect to find wild-caught chimpanzees to exhibit less and more restricted grooming activities compared to captive born chimpanzees, as they mostly likely experienced traumatic life events during the poaching and transportation might have impacted the grooming competences of wild-caught chimpanzees in the long run.
2. Do care management decisions, i.e., alterations to the group composition, provoke a short or long-term impact on the chimpanzees grooming activities? And are chimpanzees impacted differently based on their adverse living conditions during infancy? We expect to find differences between stable and unstable time periods, as the addition or loss of potential allies is likely to require a certain modification of the social strategy. However, we expect the modification of their grooming activity to last

only during a short period of time, until already existing relationships have been reconfirmed and new ones established.

Chapter 3 – Article B is exploring the utility of using highly detailed analysis based un multi-layer social network analysis to gain insights regarding the chimpanzees' social activities. I attempt to determine if different interaction types (allogrooming, affiliative behaviors, passive social proximity and stationary vicinity) may provide new insights and thus should be considered when assessing the social activity of former pet and entertainment chimpanzees. More specifically, I aim to demonstrate that each social interaction type imparts different information and attempt to examine how the chimpanzees past adverse living conditions may impact some or all of the analyze analyzed social interaction types.

1. Does analyzing different social interaction types impart new information and provide a more realistic understanding regarding the chimpanzees' social activity, compared to traditional mono-layer social network analysis, i.e., typically limited to allogrooming networks? I expect some interaction types to be more similar than others, yet each type to impart different information, allowing us to achieve a more realistic understanding of the complex social functioning of chimpanzee groups.
2. Do the past adverse living conditions of the chimpanzees impact their social activity equally across all analyze analyzed social interaction types? I expect more intense social interaction types, such as allogrooming and other affiliative behaviors to be impacted by the chimpanzees' adverse past and to generally find differences on an individual level.

In **Chapter 3 – Article C**, I assess several aspects of controlled visitor activities on two groups of former pet and entertainment chimpanzees in an attempt to: (a) expand on the current scientific knowledge that to date, has been mostly limited to human-animal interactions in a zoo setting; (b) analyze the impact of strictly controlled visitor presence, i.e.,, where visitors are restricted regarding their behavior and proximity towards the chimpanzees; (c) examine if factors such as group size and group type as well as the timing, i.e.,, the behavior while a visitor group is present or after the visitors have left, are impacting the behavior of former pet and entertainment chimpanzees.

1. Is it possible to conduct educational visitor activities at an institution housing former pet and entertainment chimpanzees, without producing a detectable negative impact on the animals´ behavior? I expect, that strictly controlled guided visitor activities may produce no or at least no undesired impact on the chimpanzee’s behaviors.
2. Do different types of visitor groups produce a different impact on the chimpanzees´ behavior? I expect that as long as the visitors’ behavior is controlled and limited, differences regarding the composition of visitor groups are not affecting the chimpanzees’ behavior differently.

Finally, in **Chapter 4**, I summarize my major findings and discuss their broad implications in the context of chimpanzee welfare in former pet and entertainment chimpanzees.

2. General Methodology

In the following chapter, we aim to provide a general overview regarding the study population as well as the approaches and methods applied throughout all three studies related to this thesis. Specific details regarding each article can be found in the individual methodology section of the corresponding publications, yet here we will provide a global summary and additional explanations.

2.1 Study site: Fundació MONA

Fundació MONA is a private non-profit organization registered in the Department of Justice of the Generalitat de Catalunya, with its facilities located in the North of Spain in Riudellots de la Selva (Girona, Catalonia). The center is a member of the European Alliance of Rescue Centers and Sanctuaries (EARS) since 2011 and functions as a primate rescue and rehabilitation center providing lifelong care to chimpanzees (*Pan troglodytes*) and barbary macaques (*Macaca sylvanus*) since 2001. Although the Foundation was originally established purely as primate sanctuary, over time several other objectives emerged:

- **Rescue & Rehabilitation and life-long care** remains to this day the central pillar of the foundation, as many more primates are still in need to be relocated and cared for by professionals in this field.
- **Conservation, Education and raising awareness** is an important task to ensure less primates living in poor and/or illegal situations will keep emerging.
- **Non-invasive Research**: Although studies regarding wild and captive primate populations are not scarce, few projects report on sanctuary primates who suffered adverse living conditions in their past. The Foundation made it an objective to provide and publish such content, while simultaneously supporting care and rehabilitation activities at the sanctuary.

2.2 Study sample

The study sample consisted of a total of 19 former pet and entertainment chimpanzees housed at the sanctuary. However, due to the fact that data collection extended over many years, some chimpanzees arrived during the observation period while others died or were relocated to another institution before the data collection ended. Thus, the study population consisted in total of seven females and twelve males, although not all individuals were present in all the years. Some individuals were infants or juveniles in the beginning of the data collection, but became all adults before the end of the observation period. Chimpanzees were living in two separate groups in adjacent but physically separate enclosures. The composition of each group was subject to several changes with new chimpanzees being integrated, individuals being permanently moved from one group to another and some passing away due to age or fatal health issues (see Table 1).

Information regarding each individual’s profile and background information was extracted from official paper work, such as relocation documents, statement reports, CITES documents and the daily caregiver reports. While reports and informs regarding their time at the sanctuary were very detailed, some information on the past living conditions could not be confirmed for all individuals to the same extent. Thus, some variables regarding the chimpanzees’ pasts, such as exact age at onset of maternal deprivation, information on the length and degree of human exposure or time spent on different entertainment related activities, could not be analyze analyzed as detailed as planned. However, enough information was available in order to label all individuals regarding their origin (wild- vs. captive-born) and their predominant housing condition during infancy, i.e., predominant social isolation from conspecifics during their first five years of life or predominant social housing.

Table 1

Characteristics and background information on the study population.

Name	ID	Sex	(Estimated) Year of Birth	Origin	Predominant Housing Condition During Infancy (With or Without Conspecifics)	Former Pet or Entertainment Chimpanzee*
Africa	AFR	F	2000	wild	without	Pet
Bea	BEA	F	1985	wild	with	Entertainment
Bongo	BON	M	2000	captive	with	Entertainment
Charly	CHA	M	1989	captive	with	Entertainment
Cheeta	CHE	F	1990	wild	without	Entertainment
Coco	COC	F	1994	wild	without	Pet/ Entertainment
Juanito	JUA	M	2003	captive	with	Pet/ Entertainment
Marco	MAR	M	1984	captive	with	Entertainment
Nico	NIC	M	2001	captive	without	Pet/ Entertainment
Pancho[1]	PAN	M	1990	captive	with	Entertainment
Romie[2]	ROM	F	1979	wild	with	Entertainment
Sara[3]	SAR	F	1998	captive	without	Pet/ Entertainment
Tico	TIC	M	1985	wild	without	Entertainment
Tom	TOM	M	1985	wild	with	Entertainment
Toni	TON	M	1983	wild	with	Entertainment
Toto[4]	TOT	M	1956	wild	with	Entertainment
Victor	VIC	M	1982	captive	without	Pet/ Entertainment
Waty	WAT	F	1996	captive	with	Entertainment

Note. Abbreviations: F = female, M = male.
[1]died in 2007, [2]died in 2011, [3]died in 2012, [4]died in 2013.
* Chimpanzees were often used for several purposes before arriving at the rescue center. The term "Entertainment" refers to any type of commercial use such as tourist attraction, street performing, media performing, circus performing and instances of zoo housing.

The housing facilities (see Figure 1) consist of two large and one small outdoor enclosure and five indoor night areas. The two big outdoor habitats are naturalistic enclosures (5 640 m^2 in total), equipped with a multitude of climbing structures, which give the chimpanzees the opportunity to exploit natural and artificial resources throughout the day. The two naturalistic enclosures measure 3 220 m^2 and 2 420 m^2, respectively, and are surrounded by a 191m long steel mesh and electrified fence capped with a semicircle metal overhang system. The small outdoor area is a closed top outdoor double cage measuring 50m^2 with a height of four meters. This area is connected to several indoor areas. It is located out of sight of the other naturalistic outdoor enclosures and is being used for newly rescued chimpanzees, their integration sessions and veterinary training/treatments.

Figure 1

Satellite image of Fundació MONA with marked chimpanzee living areas

Note. This satellite image of Fundació MONA was retrieved from Google maps (Google Maps, 2023). The two big naturalistic outdoor enclosures are marked in red, the five indoor night areas are marked in blue and the small closed top outdoor area is marked in purple.

The five indoor night areas, measuring a total of 113m^2 are connected to each other as well as to all outdoor enclosures. They are artificially-heated and naturally ventilated to provide species adequate living conditions following best practice guidelines. Both natural and artificial lights are used to illuminate these areas as required.

Each area contains one or two automatic drinkers to provide *ad libitum* access to water at all times. The chimpanzees are fed a minimum of four times per day, with the first and last portion of their diet being served in indoor areas. The second and third portion of their daily diet is scattered and hidden in the outdoor enclosures to stimulate natural foraging and activity levels as part of their daily enrichment program. Their nutrition plan was created in 2001, and although slightly updated over time, generally consists of a balanced diet based on fruits and vegetables, seeds and nuts, primate pellets and a limited quantity of other protein-rich foods.

For security and health reasons, chimpanzees are confined to indoor areas during nighttime and receive access to outdoor areas once the outdoor temperature is above 10ºC, which results in different schedules determined by the season. Depending on the group size and possible integration processes of new chimpanzees, habitat assignations might vary, but each social group is generally assigned to one naturalistic outdoor and two to three indoor areas. If the meteorological conditions are favorable (not producing a significant risk to their health), chimpanzees are typically limited to outdoor areas throughout the day, but may receive access to indoor areas after cleaning and maintenance activities are finished indoors.

Depending on the different profiles, people might be restricted to specific areas, with caregiver and veterinary staff members being the only staff members allowed access to all animal housing facilities at all times. Observers and researchers have access to all outdoor areas while remaining in designated observation areas, such as observation towers or specific viewpoint areas, but not indoor areas. Thus, all observational data analyze analyzed and presented in the following chapters have been collected from said designated areas only. Guides and visitors are the most restricted, being only allowed access during specific times, moving on a predesignated walkway around the two naturalistic outdoor enclosures. Furthermore, caregivers might temporarily restrict access or request observers and/or visitors to leave a certain area if the primates seem to be agitated or bothered by the human presence.

Observers, guides, and visitors are instructed not to attempt or respond to interactions with chimpanzees while performing their tasks. There generally is a strict non-contact policy, with only a few trained senior caregivers engaging in controlled physical contact in order to treat animals and perform care management training, such as veterinary training.

2.3 Data Collection

Data on the chimpanzees' behavior was collected without any invasive interventions and was conducted in accordance with all national and international guidelines for the care and management of primates as established by Fundació MONA. Any changes regarding the chimpanzees living conditions or environment that occurred during the observation time, such as alterations of group composition of the chimpanzees or visitors’ schedules were not influenced by any research activities or objectives related to this thesis.

All studies forming part of this compendium were conducted on the same study population housed at Fundació MONA and used the same data collection methodology and behavioral catalogue. Information on the chimpanzees’ behavior, proximity to each other as well as their potentially influencing surrounding was collected over 14 years from 2006 to 2019 by using instantaneous scan sampling (Altmann, 1974; Martin & Bateson, 1993) with two minute intervals for all individuals of one group in view during 20 minutes sessions. From 2006 until the end of 2017, observers used pen and paper, but changed to mobile devices with the ZooMonitor data scoring software (Ross et al., 2016) starting in 2018.

Data was recorded between approximately 1030 hours and 1830 hours, representing the typical time frame in which the chimpanzees had access or were restricted to the outdoor enclosure, i.e. the part of the chimpanzee enclosure visible to the observers. Behavior in indoor areas was never observed during this thesis. Observation sessions of 20 minutes were evenly distributed between mornings and afternoons on randomized days (Monday to Sunday). A total of 409,820 behavior scans (2006-2017: 303,123 scans; 2018-2019: 106,697 scans) were recorded, excluding training observations and when animals were not visible or the behavior was obscured. The author of this thesis took over the training and coordination of the observers in 2018 (in the beginning of this thesis), after ensuring the reliability with the former observation coordinator Miquel Llorente. However, data collected by the author of this thesis was not included in any of the published articles, as the observed chimpanzees were likely to react and to modify their behavior due to his presence. This was unavoidable as the chimpanzees were used to his presence and intervention during husbandry and veterinary activities. Every year, between 5–15 observers were trained and were only permitted to collect data after the completion of an observation training period and successfully passing an inter observer reliability test (agreement ≥ 85% with head of research). Due to a growing complexity of the recorded data, additional control measures consisting of a three-step inter observer reliability test were implemented over time to guarantee the quality of the collected data. The first step included data collection over a minimum of two weeks and ensuring that the observers were able to accurately identify all individuals at this point. This data was reviewed and checked by the research coordinator, used to explain and clarify certain doubts but was eventually deleted. In the second step, observers have to pass a methodology test focusing on the correct use of the behavioral catalogue and starting in 2018 also testing the correct use of the observation software. In the third step, the data collectors had to pass a video test that includes 20 different video clips with a percentage agreement of ≥ 85 percent to the head of research. All behaviors analyzed in the articles forming part of this compendium, were presented and tested in the second and third step of the inter observer reliability testing system to ensure the quality of the collected data.

The animal care department provided access to all reports and records regarding the chimpanzees' past, both before arriving at the sanctuary and while being housed at MONA. Although most of the information needed could be found in summarized reports, the author of this thesis, scanned through all daily informs and double-checked the data, using all documents available.

2.4 Statistical analysis in R environment

Studies on animal behaviors often violate the assumption of multiple predictors, refusing or ignoring the possibility that variations in the observed behaviors might be caused by multiple impacting factors, i.e., predictors, rather than just one. Although it might be impossible to account for all possible impacting factors, linear mixed models (LMM) allow us to at least consider and discuss several of the most likely, potentially most impacting predictors simultaneously.

The statistical analysis for all three studies was conducted in the R environment (R Core Team, 2018). Linear mixed models were run using the “lme4” package (Bates et al., 2015). Depending on the study, an additional “MuMln” package (Barton, 2018) was used for model averaging. The normal distribution of the residuals was checked by visually inspecting the QQ plots. At this point we refrain from adding details regarding the dependent variables, random and fixed factors, as these differed for each article and are already explained in detail within the corresponding chapters of each publication. Testing of the multicollinearity (high correlations among predictor variables, leading to unreliable and unstable results) between all fixed factors was done by calculating the variance inflation factor (VIF: factor measuring how much variance of an independent variable is influenced or inflated by its correlation/interaction with other independent variables) using the “car” package (Fox & Weisberg, 2011). Post hoc testing was performed via ANOVA Type III analysis of variance (ANOVA) using the Satterthwaite approximation for degrees of freedom and/or the “glht” function of multiple comparison of means with Turkey Contrast (p-values adjusted by the Holm-Bonferroni method) (Hothorn et al., 2008).

2.5 Social Network Analysis & Multiplex Networks

The use of social network analysis (SNA) during the last few decades has proven to be extremely useful for applied primatology as well as research related to topics such as social learning (Hobaiter et al., 2014), cooperation (Croft et al., 2009) or the spread of diseases (Carne et al., 2014; Rushmore et al., 2013). Furthermore, it enabled to efficiently model and predict patterns of hierarchies (Hobson, 2019), group cohesion and stability (Beisner et al., 2015; Lehmann & Boesch, 2004). Due to lacking analytical tools or purposely in order to maintain simple and easy to understand study designs, social networks were traditionally analyze analyzed by aggregating information or focusing only on one type of connection between individuals (e.g., one specific behavior as representative indicator). However, considering the complexity of chimpanzees' social life, their social capacities, limitations, flexibility and adaptability, simplified networks based on a single indicator, might result in misleading conclusions (Silk et al., 2018). In order to achieve in-depth knowledge regarding the social entanglement in captive chimpanzee populations, it is necessary to consider the multidimensional nature of the network components (Smith-Aguilar et al., 2018).

Because of the development and advances in algorithms and computational technologies, we are now able to visualize and analyze complex multilayer structures. We decided to work with the MuxViz software (De Domenico, Porter, et al., 2015) for several reasons: (1) MuxViz is an open source software, thus does not require a one-time purchase or monthly fee to be used. (2) It has been successfully used in a large variety of areas such as engineering, biological physical, social, and information sciences. (3) It has been developed to explore and analyze multilayer structures in depth as well as facilitate quick creation and modification of 2D and 3D network visualizations. Thus, it provides a strong coverage of both analysis and visualization. (4) Due to running within the R environment and not requiring a specific operating system, MuxViz can be used in Windows, Linux, Mac or any other operating system.

Visual representation of social networks were created using the "Igraph 0.5.5-3" package (Csardi & Nepusz, 2006) or the visualization tools provided in the Muxviz software (De Domenico, Porter, et al., 2015) within the R environment. While the social network indices, Vertex Strength Centrality (VSC) and Deviation from Edge Weight Disparity (DEWD) were calculated in Microsoft Excel (2007) as previously described by Kasper and Voelkl (Kasper & Voelkl, 2009), all calculations and analysis related to multiplex networks were performed using the Muxviz software (De Domenico, Porter, et al., 2015) within the R environment.

3. Empirical Studies

This thesis is presented as a compendium of three articles, successfully published in journals indexed in an international index system such as JCR and/or SJR. All three articles have been accepted and published in open access format between 2019 and 2020 in the journals PLOS One, Scientific Reports and Animals.

The order in which the papers are listed here, represents the suggested order in which to read the publications, although publication dates suggest a different order. Considering that all articles of this compendium have been published in open access format, we suggest to read the articles in the journal formatting style online (open access links are provided accordingly). However, the articles can also be read in this document in the formatting style of this thesis, presenting the exact same content as the published versions online.

Article A: Early life experience and alterations of group composition shape the social grooming networks of former pet and entertainment chimpanzees *(Pan troglodytes)*

This article was published in PLOS One in January 2020.

Crailsheim, D., Stüger, H. P., Kalcher-Sommersguter, E., & Llorente, M. (2020). **Early life experience and alterations of group composition shape the social grooming networks of former pet and entertainment chimpanzees (*Pan troglodytes*).** *PLoS ONE 15(1). e0226947.* doi: 10.1371/journal.pone.0226947

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Abstract: The long-term effects of early life adversities on social capacities have been documented in humans and wild-caught former laboratory chimpanzees *(Pan troglodytes)*. However, former pet and entertainment chimpanzees have received little attention to date. This study aimed to investigate the long-term effects of early life experience on 18 former pet and entertainment chimpanzees, based on social grooming data collected at a primate rescue center over a 12- year period. Moreover, we also focused on the possible short-term effects that alterations to group composition might have on grooming patterns. For this purpose, we compared stable and unstable periods (i.e., where alterations to group composition occurred). We used two individual social network measures to analyze the grooming activity and the distribution of grooming among group mates for each individual. We could show that wild-caught chimpanzees were significantly more selective regarding their grooming partners and spent less time grooming when compared to their captive born companions. We also found that individuals who were predominantly housed without conspecifics during infancy spent less time grooming compared to those who were predominantly housed with conspecifics during infancy. Furthermore, we found that alterations to the group composition had short-term effects on the distribution of social grooming from a more equal distribution during periods with a stable group composition towards a more unequal and selective distribution during unstable periods. Thus, we conclude that the social grooming networks of former pet and entertainment chimpanzees are shaped not only by long-term effects such as early life experience, but also by short-term effects such as alterations to group composition. Remarkably, we found not only captive born chimpanzees but also wild-caught individuals to adjust their grooming to socially challenging situations by modifying their grooming distribution in a similar way.

A1 Introduction

Adverse experiences in early infancy affect the behavior as well as the physical and mental health of human (Chugani et al., 2001; Kreppner et al., 2001; Pechtel & Pizzagalli, 2011) and non-human primates (Freeman & Ross, 2014; Gilmer & McKinney, 2003) in the long term (Clay et al., 2015; Conti et al., 2012; Kalcher et al., 2008; McEwen, 2003). This applies to individual as well as social behavior (Llorente et al., 2015). Wild infant chimpanzees spend their first two to five years of life either attached to or in close proximity to their mothers

(Bard, 1995; Goodall, 1986; Matsuzawa, 2006), and develop their social skills by interacting with their mother and other members of their group (Goodall, 1986; Plooij, 1984). The developmental trajectory of chimpanzees is similar to that of humans (Goodall, 1986), and their cognitive (Lonsdorf et al., 2010; Matsuzawa, 2009), emotional (Kano et al., 2012) and social skills (Goodall, 1986) are highly complex. This complexity is reflected in their social organization as well. Chimpanzees in the wild use a fission-fusion system, which implies regular transfers of individuals between small subgroups, increasing the individuals' survival chances and group functionality (Itani & Suzuki, 1967; Lehmann & Boesch, 2004; Wrangham, 1975). Between the 1950s and the 1980s, thousands of infant chimpanzees were taken from the wild (Kabasawa, 2011; Peterson & Goodall, 2000). These orphans experienced the separation from their mother and most likely witnessed the killing of their mother and other group members (Goodall, 1996; Hicks et al., 2010). Furthermore, they experienced a dramatic change in living conditions from wild to captivity and were transported to the United States of America, Asia and Europe under deplorable conditions (Kormos et al., 2003; Terry, 1970). Many of the imported orphans were used for biomedical research, but were also used for entertainment or kept as pets for decades. These orphans experienced early maternal loss (Kalcher-Sommersguter et al., 2015; Terry, 1970), and often additionally to this, prolonged solitary housing (Reimers et al., 2007) and the lack of diverse conspecific social partners (Aureli et al., 2008; Koski et al., 2012). Growing up as an orphan can have deleterious effects later in life in humans (Bos et al., 2011), chimpanzees (van Leeuwen et al., 2014) and other non-human primates (Kerr et al., 1969). Several studies suggest that early life stress induces long-term morphologic changes in primate brains expressing a delayed effect once the vulnerable brain system reaches maturation (Gluckman & Hanson, 2004; Spinelli et al., 2009).

While there are studies focusing on the lasting effects of laboratory housing on nonhuman primates (Bradshaw et al., 2009; Lopresti-Goodman et al., 2015), less is known in this regard about former pet (i.e. privately owned and kept for companionship or pleasure) and entertainment (i.e. were trained and used for commercial purpose) chimpanzees. Some studies report that extensive human exposure during the first years of life had an effect on the behavior of former pet and entertainment chimpanzees. For example, Freeman and Ross (2014) found that chimpanzees, living in accredited zoos and sanctuaries, who had more exposure to humans as infants exhibited less social grooming and sexual behaviors than chimpanzees with more conspecific exposure during infancy. Likewise, Llorente and colleagues (2015) found that chimpanzees living in a sanctuary who were younger at the onset of rehabilitation spent more time with social play and affiliative behaviors, less time inactive, and reached higher levels of behavioral and social competence than individuals who started their rehabilitation at an older age. Furthermore, former pet and entertainment chimpanzees, living in accredited zoos and sanctuaries, who were mainly exposed to humans in infancy showed lower levels of extraversion and exhibited deficiencies in social bonding (Freeman et al., 2016). Finally, Ortín et al. (2019) demonstrated that the personality development of chimpanzees who were rescued from bushmeat and pet trade was affected by these early life experiences, and resulted in higher ratings in the factors anxiety, restraint and dominance.

Social network analysis (SNA) allows us to statistically describe, quantify and compare the social relationships of individuals within a group (Farine & Whitehead, 2015; Jacobs & Petit, 2011; Koene & Ipema, 2014). Although it has been proven to be an extremely useful tool for describing complex social systems and investigating welfare of animals, few studies have focused on former pet and performer chimpanzees in zoos and rescue centers to date (Clark, 2011; Funkhouser et al., 2018). By detecting social patterns on a group level and analyzing asymmetries of certain individuals under specific conditions, we can go further and identify factors influencing social interactions and social group structures. As such, SNA can also be used as an animal welfare tool and can play a supporting role in animal management decisions (Dufour et al., 2011; Koene & Ipema, 2014). Investigating the social networks of former pet and entertainment chimpanzees has the potential to provide a better understanding of the long-term implications of early life adversities and to improve animal welfare (Beisner & McCowan, 2014; Koene & Ipema, 2014).

The recovery from early life adversities is a long lasting process, but can, at least in part, be achieved through social, psychological, emotional and environmental interventions in specialized institutions like primate rescue and rehabilitation centers (Llorente et al., 2015; McGoron et al., 2012). These centers strive to recreate living conditions similar to that of wild living conspecifics, i.e. permanent access to other conspecifics and occasional changes of group composition (Lehmann et al., 2007a). However, while chimpanzees living in the wild decide autonomously to move between subgroups, the social setting and any changes to the group composition are handled entirely by humans for chimpanzees living under human care. Accordingly, these centers typically apply a slow and stepwise approach towards a life within a social group, which remains one of the most effective ways of rehabilitation (Llorente et al., 2015; Rennie & Buchanan-Smith, 2006). Little is known about how captive held chimpanzees who suffered early life adversities recover in terms of stress sensibility, social competence and how well they respond to social challenges such as changes of group composition. Therefore, we aimed at investigating how the early life experience and changes of group composition would be reflected in the social grooming networks of 18 former pet and entertainment chimpanzees living in two groups.

Our study population consisted of chimpanzees who have been confiscated from circuses and private owners and/or relocated from zoos to the primate rescue center Fundació MONA. We focused on social grooming because it is one of the most relevant social interactions of chimpanzees (Goodall, 1986; Watts, 2000). Grooming, beside its hygienic function (Grueter et al., 2013), has important social functions such as to establish and maintain relationships, bonds and coalitions (Dunbar, 1991) as well. Additionally to promoting group cohesion and reducing tension (Schino et al., 1988; Terry, 1970), grooming others also provides individual benefits as it can be traded for support in agonistic interactions (Hemelrijk, 1994; Schino, 2006), for tolerance (Silk, 1982), for access to resources (Samuni et al., 2018) or for food itself (de Waal, 1997). Furthermore several studies based on social network analysis indicate that animals with more central positions (i.e. well connected) in a network attain greater fitness/benefits than peripheral ones (Gilby et al., 2013; Pasquaretta et al., 2014). On the contrary, in the wild a more central position might also come with the handicap of being more vulnerable to disease transmission (Carne et al., 2014; Rushmore et al., 2013). However, in a captive setting with controlled health and hygienic conditions this does not tend to be a major concern.

While high levels of self-grooming frequently have been associated with undesirable behaviors and seen as an indicator of lacking welfare (Birkett & Newton-Fisher, 2011; Lopresti-Goodman et al., 2013), to our knowledge high levels of social grooming have not been suggested to be a welfare issue yet. A successful integration of a new chimpanzee or the formation of a new group is, among others, often reflected in affiliative interactions with a variety of partners (Bashaw et al., 2010; Brent, 2001; Thunström et al., 2013), rather than simply the absence of aggression (Koski et al., 2012).

Studies conducted on wild populations of chimpanzees report on grooming activities ranging from 5.7 to 11.7 percent of their daily activity budget (Boesch & Boesch-Achermann, 2000; Matsumoto-Oda & Oda, 1998; Nishida, 1990; Tutin et al., 1983; White, 1992; White & Chapman, 1994; Wrangham, 1977; Yamakoshi, 1998). However, high variations were reported for example in a study done by Wrangham (1977), where grooming on average would rise up to 33 percent in artificial feeding areas.

In captivity, levels of social interaction are expected to be higher due to crowding produced by small enclosures and the absence of environmental constraints which may cause a more solitary life style in wild-living chimpanzees (Brent, 2001). In captive settings with a daily changing group composition (i.e. the individuals are split into two or three parties and the composition of these parties varies every day), social grooming can rise up to 25 percent of waking hours as reported by Levé et. al. (2016). Lehmann et al. (2007b) reported that primates, including chimpanzees, living in the wild, tend to increase and expand their grooming activity proportionally to group size, in order to service and maintain a multitude of relationships in groups containing up to 40 individuals, but when surpassing this group size grooming activity does not increase any further. However, time spend grooming may also vary between wild-living populations due to ecological pressures such as living in harsh habitats and/or seasonality (Lehmann et al., 2007b). Since our study population never exceeded the number of nine individuals per group and ecological time constraints were no odds, we argue that an increased grooming activity should be seen as beneficial to the group cohesion as well as on an individual level. Thus, chimpanzees never or only rarely grooming others or directing their grooming to only one or a few group member(s) would be positioned as peripheral individuals and would thus likely have reduced benefits. Establishing and maintaining advantageous relations through grooming seems especially important when taking limitations and restrictions of a captive environment into account, where avoiding group members might be difficult at times, and tension reduction is therefore of high importance (Caws & Aureli, 2003; de Waal, 1989). Furthermore, chimpanzees in captivity tend to be less stimulated and motivated to be active compared to wild populations, due to the lack of variation, a limited enclosure size and the absence of environmental constraints (Perkins, 1992; Pruetz & McGrew, 2001; Redshaw & Mallinson, 1991). Nevertheless, even without considering the social or hygienic functions/benefits, an increase in positive social interactions with a variety of individuals is a stimulation increment, which in captive care management tends to be a desired effect (Brando & Buchanan-Smith, 2017).

The fifth edition of the Diagnostic and Statistical Manual of Mental Disorders defines a traumatic event for children up to six years as direct or indirect exposure to the actual or threatened death, serious injury, or sexual violence or witnessing the event to a primary caregiver (American Psychiatric Association, 2013). According to this definition, our wild-caught chimpanzees most likely experienced a traumatic life event in early infancy. Similar approaches have already been applied to studies of chimpanzees who were housed under extreme conditions such as laboratories (Bradshaw et al., 2008; Schino, 2006). We predicted that such a traumatic experience would be reflected in the grooming networks of our wild-caught chimpanzees compared to the networks of captive born conspecifics. We are aware of the fact, that separation from the mother has detrimental effects not only on wild-caught but also on captive born infants. However, we think, that according to the descriptions found in "Visions of Caliban" (Peterson & Goodall, 2000) on how chimpanzee infants were captured from the wild, the experiences of these chimpanzees indisputably meet the criteria of a traumatic life event. Additionally, we predicted that the predominant housing condition (PHCinfant) of our study population during infancy, i.e. whether they were housed predominantly with conspecifics or without conspecifics during their first five years of life, would have an impact on their social grooming networks. We expected prolonged housing without access to conspecifics to have a negative impact on the grooming networks of the respective chimpanzees, as social grooming skills develop very slowly in infant chimpanzees (Nishida, 1988). Furthermore, we predicted that chimpanzees who arrived at the sanctuary at a younger age, i.e. as sub-adults, would spend more time grooming and be less choosy regarding their grooming partners compared to individuals who arrived as adults.

While early life adversities were predicted to have a long-lasting effect, still detectable after being introduced and living within a social group of conspecifics for years, we assumed care management activities, i.e. alteration to the group composition, to provoke only a short-term adaptation of the individuals' grooming interactions. To evaluate the effects of alterations of group composition on social grooming we compared the individual network measures of stable periods (i.e. periods without any changes in group composition) to those of unstable periods (i.e. periods following the introduction or separation of individuals) over a

12-year observation period. We supposed to find a difference between stable and unstable periods, as the addition of potential new allies or competitors as well as the loss of such might require a certain modification of the social strategy, though only for a short period, until already existing relationships have been reconfirmed and new ones established.

A2 Materials and methods

A2.1 Ethical Note

This study is based purely on observational data without any invasive interventions and was conducted in accordance with all national and institutional guidelines for the care and management of primates as established by Fundació MONA, Association for the Study of Animal Behavior/Animal Behavior Society and the Spanish Government (RD 53/2013). Any decision to alter the group composition of the chimpanzees was based on established care management protocols and at no time was influenced by research related staff members.

A2.2 Study Population

The study population consisted of a total of 19 former pet and entertainment chimpanzees (seven females and twelve males in the course of the total observation time from April 2006 to July 2018) housed at the primate rescue center Fundació MONA in Catalonia, Northern Spain. The center is a member of the European Alliance of Rescue Centers and Sanctuaries (EARS) and it is rehabilitating chimpanzees since 2001. Behavioral observations were conducted on all of the 19 chimpanzees at MONA, but one male was never observed within a group setting of more than two individuals before being transferred to Stichting AAP, another rescue center in Holland, and thus was excluded, resulting in a total of 18 chimpanzees included in the analysis of this study. Throughout the 12 years of observation, there were two social groups, but the number of chimpanzees housed at the center varied due to animals passing away and new arrivals. Biographic information on the 18 individuals is shown in Table A1. Nine chimpanzees were caught from the wild, i.e. all of these chimpanzees were orphans who most probably witnessed the killing of their mother and were imported to Europe. The other nine chimpanzees were born in captivity, i.e. in an European zoo or owned by a private person. We have no information on the age at onset of maternal deprivation, neither for the wild-caught nor for the captive born individuals. We only know whether the chimpanzees were housed predominantly with or without conspecifics during their infancy, i.e. during their first five years of life. Predominantly housed with conspecifics means that the chimpanzees were housed for more than 2.5 years of their first five years of life with other chimpanzees, while predominantly housing without conspecifics means they spent more than 2.5 years without access to other chimpanzees during these first five years. Information on the exact onset, duration and sequence of the previous housing condition was not available and as such we were unable to specify this variable in more detail. As former pet and entertainment chimpanzees, all of our individuals have been socialized with humans before arriving at the rescue center. However, we do not have detailed information on the degree or length of exposure to humans. As such, we only considered conspecifics when referring to the predominant housing condition.

Wild-caught chimpanzees typically arrived as adults (except for one adolescent individual) at Fundació MONA (mean age: 23.6 ± 10.4 years), whereas the captive born subjects were mostly sub-adults (except for two adults) upon arrival (mean age: 9.2 ± 7.5 years). Considering that our wild-caught chimpanzees have on average spent more time in the pet and entertainment business than captive born ones, we included the age at arrival at the sanctuary as another variable describing the chimpanzee’s past. Thus, we assigned all chimpanzees to the respective age category, i.e. adult or sub-adult, at their time of arrival at Fundació MONA.

The chimpanzees were living in one of the two different social groups (Mutamba group, Bilinga group). Over the 12-year observation period, several alterations to the group composition occurred in order to integrate new chimpanzees, transfer animals between groups for welfare reasons or due to the natural death of individuals. The alteration of a group composition is defined as the change of the minority of the individuals of a group by either adding or removing one or several individuals at a time. Within the 12 years of data collection, the group sizes could vary from a minimum of four to a maximum of nine individuals, but was most of the time between five to eight individuals per group (Table A2).

Observations were conducted only while the chimpanzees had access to a naturalistic outdoor enclosure (5 640 m^2), equipped with a multitude of climbing structures, which give them the opportunity to exploit natural and artificial resources. The enclosure is divided into two separate areas to accommodate both groups: the first of 3 220 m^2 and the second of 2 420 m^2, with a total perimeter of 191 m. A steel mesh and an electrified fence surround the enclosure. For more detailed information on the outdoor enclosure see (Cano, 2014; Llorente et al., 2012).

Table A1

Characteristics and background information on the study population

Name	ID	Sex	(Estimated) Year of Birth	Origin	Age Category at Arrival at MONA	Predominant Housing Condition During Infancy (With or Without Conspecifics)	Former Pet or Entertainment Chimpanzee*
Africa	AFR	F	2000	wild	Sub-adult	without	Pet
Bea	BEA	F	1985	wild	Adult	with	Entertainment
Bongo	BON	M	2000	captive	Sub-adult	with	Entertainment
Charly	CHA	M	1989	captive	Sub-adult	with	Entertainment
Cheeta	CHE	F	1990	wild	Adult	without	Entertainment
Coco	COC	F	1994	wild	Adult	without	Pet/ Entertainment
Juanito	JUA	M	2003	captive	Sub-adult	with	Pet/ Entertainment
Marco	MAR	M	1984	captive	Adult	with	Entertainment
Nico	NIC	M	2001	captive	Sub-adult	without	Pet/ Entertainment
Pancho[1]	PAN	M	1990	captive	Sub-adult	with	Entertainment
Romie[2]	ROM	F	1979	wild	Adult	with	Entertainment
Sara[3]	SAR	F	1998	captive	Sub-adult	without	Pet/ Entertainment
Tico	TIC	M	1985	wild	Adult	without	Entertainment
Tom	TOM	M	1985	wild	Adult	with	Entertainment
Toni	TON	M	1983	wild	Adult	with	Entertainment
Toto[4]	TOT	M	1956	wild	Adult	with	Entertainment
Victor	VIC	M	1982	captive	Adult	without	Pet/ Entertainment
Waty	WAT	F	1996	captive	Sub-adult	with	Entertainment

Note. Abbreviations: F = female, M = male.
[1]died in 2007, [2]died in 2011, [3]died in 2012, [4]died in 2013.
*Chimpanzees often were used for several purposes before arriving at the rescue center. The term "Entertainment" refers to any type of commercial use such as tourist attraction, street performing, media performing, circus performing and instances of zoo housing.

Table A2

Chronology of the different observation time periods for the two social groups, Mutamba (M1-M6) and Bilinga (B1-B12), included in this study

Observation time period	Observation phase	Group size	Individuals	Group composition	Explanatory note
M1	2006-2007	4	Mar, Cha, Ton, Pan	stable	
M2	2008	4	Mar, Cha, Ton, Bon	unstable	Bon just joined the group
M3	2008-2011	4	Mar, Cha, Ton, Bon	stable	
M4	2012-2017	5	Mar, Cha, Ton, Bon, Jua	stable	
M5	2017	7	Mar, Cha, Ton, Bon, Jua, Afr, Wat	unstable	Afr and Wat just joined the group
M6	2018	7	Mar, Cha, Ton, Bon, Jua, Afr, Wat	stable	
B1	2006-2007	7	Tot, Rom, Wat, Bon, Sar, Jua, Nic	stable	
B2	2010	9	Tot, Rom, Wat, Sar, Jua, Nic, Tic, Vic, Afr	unstable	Integration of Afr
B3	2010	9	Tot, Rom, Wat, Sar, Jua, Nic, Tic, Vic, Afr	unstable	Afr just joined the group
B4	2011	8	Tot, Wat, Sar, Jua, Nic, Tic, Vic, Afr	stable	
B5	2011	7	Tot, Wat, Sar, Nic, Tic, Vic, Afr	unstable	Jua just left the group
B6	2012	6	Tot, Wat, Nic, Tic, Vic, Afr	unstable	Integration of Tom
B7	2012	6	Tot, Wat, Nic, Tic, Vic, Afr	unstable	Integration of Tom, Coc, Bea
B8	2013	5	Wat, Nic, Tic, Vic, Afr	unstable	Right after passing of Tot
B9	2013-2015	8	Wat, Nic, Tic, Vic, Afr, Tom, Coc, Bea	unstable	Integration of Tom, Coc, Bea
B10	2017	9	Wat, Nic, Tic, Vic, Afr, Tom, Coc, Bea, Che	unstable	During fusion of Wat, Nic, Tic, Vic, Afr and Tom, Coc, Bea, Che
B11	2017	7	Nic, Tic, Vic, Tom, Coc, Bea, Che	unstable	After separation of Wat, Afr
B12	2018	7	Nic, Tic, Vic, Tom, Coc, Bea, Che	stable	

Note. Reasons for the gaps in between the observation phases are explained in the Data sampling section

The chimpanzees are fed four times per day with a balanced diet based on fruits, seeds and vegetables. They have limited quantities of other protein-rich foods (constant since 2001) and have access to water *ad libitum*. A big portion of their daily diet is scattered and hidden in the outdoor enclosures to stimulate natural foraging behavior and locomotion as part of their daily enrichment program.

A2.3 Data sampling

Data on the chimpanzees' behavior was recorded over 146 months from April 2006 to July 2018 by using instantaneous scan sampling (Martin & Bateson, 1993) every two minutes for all individuals of one group in view. Data was recorded between approximately 1030 hours and 1830 hours while the chimpanzees had access to the outdoor enclosure. Observation sessions of 20 minutes were evenly distributed between mornings and afternoons on randomized days (Monday to Sunday). Observers were only permitted to collect data after the completion of an observation training period and successfully passing the inter observer reliability test (agreement ≥85%) with the head of research at the center (M. Llorente).

Although a complete set of behaviors was recorded, for this study we only considered "social grooming given" to group members. For this purpose, we created a directed grooming matrix for each group composition within each observation time period (see Table A2). More precisely, we calculated the percent of scans where individual A groomed individual B within a certain group composition and observation time period. To this end, we divided the number of scans where individual A was grooming B by the number of scans both individuals spent together in the outdoor enclosure and had access to each other, and multiplied the quotient by 100. These calculations were done for every individual of the two social groups for every group composition and observation time period. A total of 303 123 scans have been filtered for "grooming given" and used for this study (Bilinga group 197 053; Mutamba group 106 070). Slight modifications to the behavioral catalogue have occurred between 2006 and 2018, however, none of them affecting the validity of the grooming records. Observers recorded social grooming including the sender and receiver of each grooming interaction, following previous research carried out at the sanctuary (Llorente et al., 2015).

Over the 12-year observation period we identified a total of 42 time periods where it was possible to define a clear 'stable' or 'unstable' condition produced by alteration of the group composition. A time period was labelled as 'stable' when group composition did not change for at least four months beforehand and did not experience any short- or long-term changes to its composition. A time period was labelled as ‘unstable’ when a permanent composition alteration (removal or addition of an individual) or frequent short-term changes of group composition due to active integration activities (process of adding a new individual) have occurred, for a minimum duration of four months. However, not all the data available could be included due to a lack of records or unevenly distributed observation sessions during certain time periods. Therefore, we selected 18 observation time periods (seven stable and 11 unstable) for this study. We excluded the rest due to an insufficient amount of observations (not reaching a minimum of 480 scans per individual and time period, which corresponds to 16 hours or two full days of observation) or an uneven distribution of the observation sessions within a time period.

For all of the 18 chimpanzees the percent of scans every single individual is grooming each of its group members in any of these 18 time periods are used for further analysis. The number of different time periods per chimpanzee varied from one to 12, varying among others due to the difference in the year of arrival.

The percent of scans an individual spent on grooming a group member per time period and group composition was used to calculate two individual social network measures to evaluate the standardized grooming activity of every chimpanzee and his choosiness in the distribution of grooming among group mates. This added up to 119 data points for the standardized grooming activity and 104 data points for the distribution of grooming as distribution of grooming could only be calculated for individuals who were grooming at least one group member in the respective observation time period.

A2.4 Social Network Analysis (SNA)

Most studies on chimpanzees define the social networks by scoring dyadic grooming interactions (Funkhouser et al., 2018; Koyama & Aureli, 2019; Levé et al., 2016), or by recording information of dyadic spatial association (Clark, 2011). Due to the database available for this study and based on the fact that grooming is an important social behavior in chimpanzees (Dunbar, 1991) we created matrices of directed dyadic grooming interactions obtained for each time period and group composition.

We created our networks in R environment (R Core Team, 2018) using Igraph 0.5.5-3 (Csardi & Nepusz, 2006) for visual representation of the graphs. R script was adapted according to McFarland et al. (2010). The weighted network graphs consist of nodes representing the individuals and directed edges representing the percent of scans an individual spent grooming its group members (Fig. SA1).

The grooming matrices were used to calculate the following two network measures which have been previously described by Kasper and Voelkl (2009) and used by Kalcher-Sommersguter et al. (2015):

VSC: The Vertex Strength Centrality

The vertex strength centrality $C_s(v_i) = \frac{s_i}{N-1}$ is a measure to describe the standardized strength of an individual's grooming activity. More precisely, it reflects the mean percent of scans an individual spent grooming another individual of his group, while taking the group size into account. It is being calculated by dividing the vertex strength s_i by the number of group members *-1 (N-1)*. The vertex strength *s* of vertex *i* is given by $s_i = \sum_{j=1}^{N} w_{ij}$, *w* being the corresponding weight of the edges connected to a vertex.

DEWD: Deviation from Edge Weight Disparity

The edge weight disparity $Y_2(v_i) = \sum_{j=1}^{N} (\frac{w_{ij}}{s_i})^2$ is a measure reflecting how evenly an individual is distributing his grooming among all group members. This value ranges from 1/(N-1) to 1, with 1/(N-1) representing a perfectly even distribution of grooming among all possible group members, higher values representing a more restricted distribution of grooming among group members and 1 means that all grooming is given towards one single group member. By calculating the deviation from this edge weight disparity *($Y_2(v_i)$)* we are able to compare the distribution of grooming between groups of different group size. This is being obtained by calculating the equal disparity Y_2 per group which is 1/(N-1) and computing the deviation from Y_2 for each individual by subtracting the group specific Y_2 from the individual $Y_2(v_i)$. Thus, the deviation from the edge weight disparity ranges from 0 to (N-2)/(N-1), where 0 represents a perfectly even distribution of grooming among all possible group members and (N-2)/(N-1) represents the total concentration of all grooming given towards one single group member. Note that the deviation from edge weight disparity could only be calculated for individuals who were grooming at all.

The summations in the formulas of vertex strength and edge weight disparity include the edges extending from vertex *i* to all vertexes other than *i* (i.e. with $j \neq i$).

A2.5 Statistical analysis

The effects of various factors on the two individual weighted network measures, vertex strength centrality (VSC) and deviation from edge weight disparity (DEWD) were assessed using linear mixed models (LMMs). Time-Period-Stability (i.e. stability of group composition: stable vs. unstable), Arrival-Age-Category (i.e. the age category at arrival at the sanctuary: sub-adult vs. adult, according to Goodall (1986)), Sex (female vs. male), Origin (wild-caught vs. captive born) and PHC-infant (i.e. predominant housing condition during infancy: predominantly housed with conspecifics vs. predominantly housed without conspecifics) were fixed factors in our full models. We examined the multicollinearity between fixed factors by calculating the variance inflation factor (VIF). Individual IDs and Observation-Time-Period (i.e. a code for the respective group composition in a certain time period; Table A2) were random factors. We included the Observation-Time-Period as a random factor as observations extended over a 12-year time period and could have been influenced by other unknown factors not recorded in our data.

We used multi-model interferences to compare and rank all 33 possible candidate models (including the Null-model) according to their respective *AICc* (Akaike Information Criterion after correction for small sample sizes) for DEWD and VSC models, respectively. Thus, all fixed factor combinations were taken into account and models were ranked according to the lowest/best *AICc*. We further calculated the Δ*AICc* and the *AICw* (normalized Akaike weights) for all candidate models.

Model interference and selection was performed using model averaging (Symonds & Moussalli, 2011). We based the selection of the subsets of best models on the Δ*AICc* and considered all models with a Δ*AICc* lower than 10 compared to the best model as equally possible candidates. We further indicate the *RVI* (relative variable importance) of all fixed factors of the averaged model, which is calculated as a sum of all *AICw* over all subset models that include the respective fixed factor. Model fit was assessed via graphical evaluation of the residuals (Figs. SA2-SA5).

In a next step, we created models based on the full models with now additionally including interactions of previously found significant fixed factors with high RVI scores. We analyzed the significance of said interactions via Type III analysis of variance (ANOVA) using the Satterthwaite approximation for degrees of freedom.

Post hoc Type III analysis of variance (ANOVA) was performed using the Satterthwaite approximation for degrees of freedom. We ran Linear Mixed Models (LMMs) using the "lme4" package (Bates et al., 2015) and all related analysis, such as the VIF calculations using the "car" package (Fox & Weisberg, 2011) and Model Averaging using the "MuMln" Package (Barton, 2018) in the R environment (R Core Team, 2018).

A3 Results

We calculated two different social network measures (i.e. the vertex strength centrality and the deviation from edge weight disparity) for each individual per time period and group composition, and ran LMMs to investigate the effects of an (un-)stable group composition, arrival age, sex, origin and predominant housing condition during infancy on social grooming networks. The vertex strength centrality (VSC) represents the standardized strength of an individual’s grooming activity. The deviation from edge weight disparity (DEWD) reflects an individual’s choosiness/restriction in his distribution of grooming among its group members. As the deviation from edge weight disparity is a value limited between 0 and (N-2)/(N-1) we applied a logit transformation. However, the transformation did not lead to any changes regarding the model selection and outcomes. Therefore, we decided to discuss the results of the original DEWD models without logit transformation.

For model selection, we chose the model averaging approach, which means that not only the best model (with the lowest *AICc*) is considered, but also models with a $\Delta AICc$ lower than 10 compared to the best model. These subsets including all model candidates with a $\Delta AICc$ lower than 10 are listed in the supplementary material (SA1 and SA2 Tables).

The variance inflation factor (VIFs) for the five fixed factors of our final full models ranged between 1.02-1.77 indicating that our fixed factors were not correlated.

All post hoc tests were conducted on the full models as all five fixed effects were retained within the averaged subsets.

A3.1 Effects on chimpanzees´ grooming activity

The standardized grooming activity of our chimpanzees, i.e. the VSC, was significantly influenced by Origin, Predominant housing condition during infancy (PHCinfant), and Sex (Table A3). With respect to Origin we found captive born chimpanzees (*N*=66 data points) to have a significantly higher grooming activity than wild-caught chimpanzees (*N*=53 data points; Fig. A1). The factor Origin had a strong influence on the grooming activity indicated by a high relevant variable importance of RVI_{VSC}=0.99 (Table A3) and ANOVA *post hoc* testing showed Origin to be a significant predictor influencing vertex strength centrality ($F_{1,11}$=15.52, *P*<0.01, SA3 Table). The factor Predominant housing condition during infancy had a relatively high relevant variable importance of RVI_{VSC}=0.86 (Table A3). We found that chimpanzees who were predominantly housed with conspecifics during infancy (N= 62 data points) groomed their group mates significantly more than chimpanzees who were predominantly housed without conspecifics during their first five years of life (N=57 data points; Fig. A1; ANOVA *post hoc* test: $F_{1,15}$=8.03, *P*<0.05; SA3 Table). With respect to Sex we found females (*N*=42 data points) to have a significantly higher grooming activity than males (*N*=77 data points; Fig. A1). The factor Sex had a high variable importance of RVI_{VSC}=0.92 (Table A3). An ANOVA *post hoc* test ($F_{1,15}$=11.98, *P*<0.01) showed that Sex was a significant predictor influencing the VSC (SA3 Table).

The factors Arrival age category (ArrivalAgeCat) and Stability of group composition (TPstability) were all retained variables in the best model selection but had a very low relative variable importance (RVI_{VSC}=0.26) and failed to show any significant effect on the grooming activity (Table A3).

Figure A1

Confidence Interval plots of VSC and all significant fixed factors (Origin, PHCinfant, Sex). Mean vertex strength centrality (±95% CI).

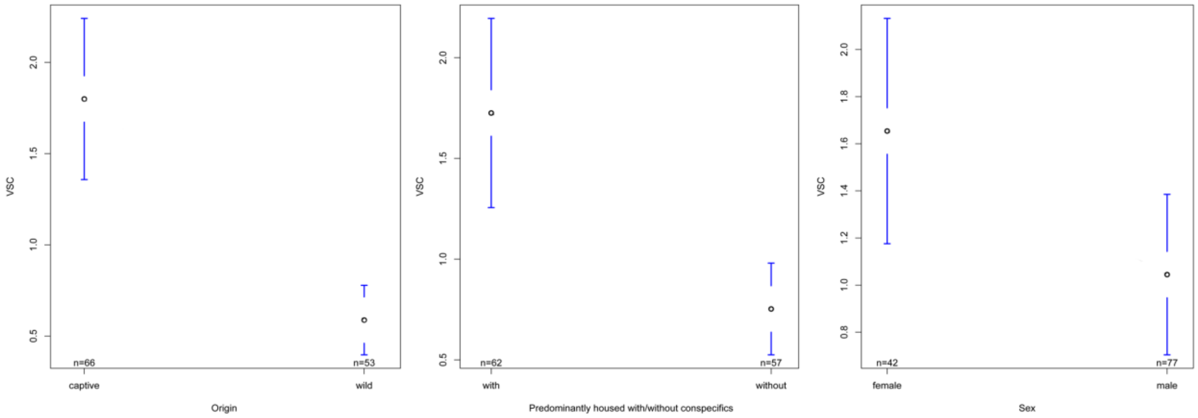


Table A3

Averaged best vertex strength centrality (VSC) model and relative importance of the fixed effects

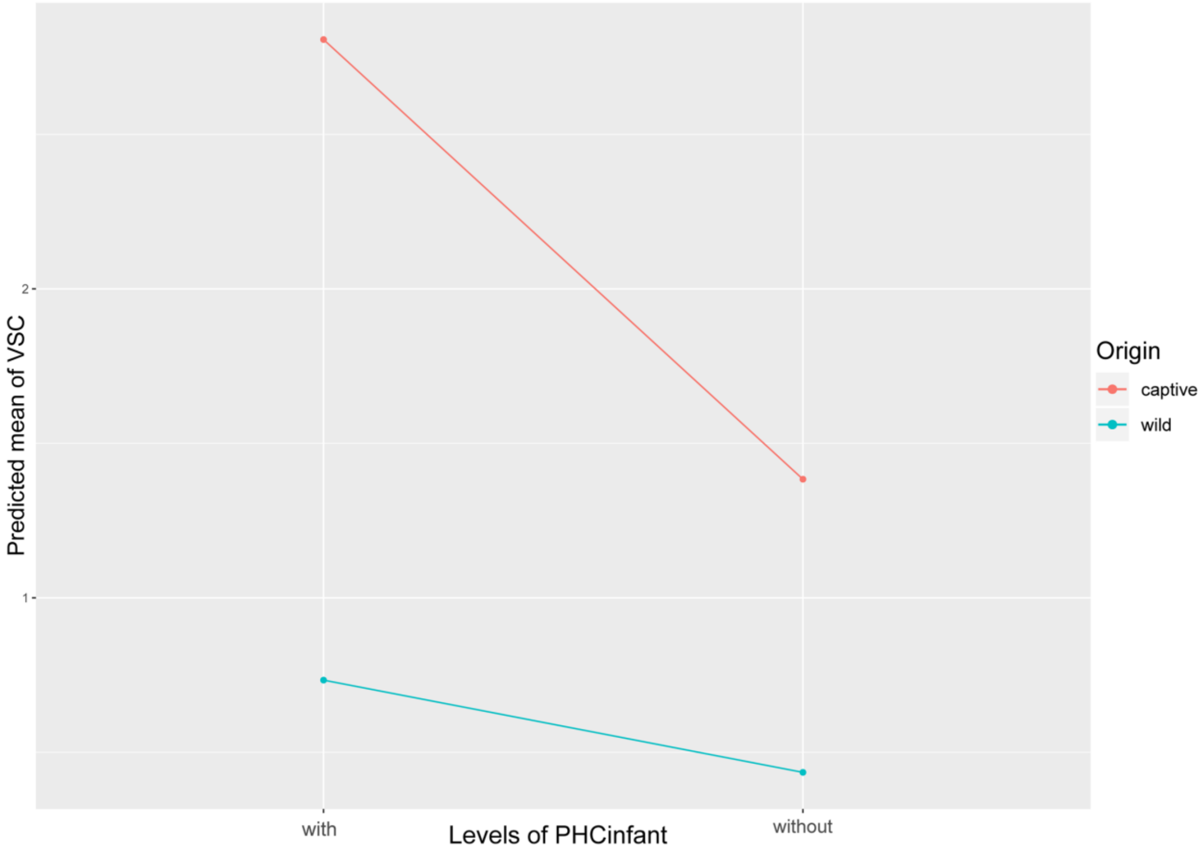
VSC Model: conditional average (ΔAIC<10)					
	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)
(Intercept)	2.198	0.514	0.518	4.243	<0.001 ***
Sex	-1.045	0.317	0.321	3.257	0.001 **
PHCinfant	0.840	0.301	0.304	2.762	0.006 **
Origin	-1.362	0.337	0.340	4.002	<0.001 ***
TPstability	-0.226	0.435	0.440	0.513	0.608
ArrivalAgeCat	-0.093	0.420	0.424	0.220	0.826
Relative variable importance:					
	Origin	Sex	PHCinfant	TPstability	ArrivalAgeCat
Importance:	0.99	0.92	0.86	0.26	0.26
N containing models:	14	8	8	6	8

Note. Output of the averaged best vertex strength centrality (VSC) model and relative importance of the fixed effects sex, predominant housing condition during infancy (PHCinfant), origin, arrival age category (ArrivalAgeCat) and stability of group composition (TPstability). All models included in this averaged results are presented in the supporting material (SA1 Table). Signif. codes: ‘***’ ≤0.001 ‘**’ ≤0.01 ‘*’ ≤0.05 ‘.’ ≤0.1 ‘ ’ ≤1

Considering that both, Origin and the Predominant housing condition during infancy, significantly affected the grooming strength (VSC) in our VSC model, both with high RVI scores, we ran a separate VSC model based on the full model but added the interaction of these two fixed factors. Due to slightly elevated VIFs (2.1-3.1) detected between the interaction and the separate components (Origin and PHCinfant) we ran this LMM apart from the averaged LMM. We found the interaction to have a significant impact on the grooming strength ($F_{1,13}$=4.90, $P<0.05$; SA4 Table). The plot (Fig. A2) shows, as already indicated in our averaged VSC model, that (a) captive born chimpanzees had a higher grooming activity than wild-caught chimpanzees, and (b) chimpanzees that were predominantly housed with conspecifics had a higher grooming activity than those predominantly housed without conspecifics during infancy. The interaction plot, however, also shows, that both, captive born chimpanzees predominantly housed with conspecifics and those predominantly housed without conspecifics during infancy, spent significantly more time on grooming given compared to wild-caught chimpanzees irrespective of their predominant housing condition during infancy.

Figure A2

Plot representing the effect of the interaction between Origin and PHCinfant on the grooming strength (VSC).



Note. Each point on the plot is a predicted mean VSC value and each connection of two points describes the effect, based on the data of the VSC LMM model with TPstability, Origin, Sex, Arrival Age Category, Predominant Housing Condition during Infancy and the interaction of Origin and PHCinfant as fixed factors.

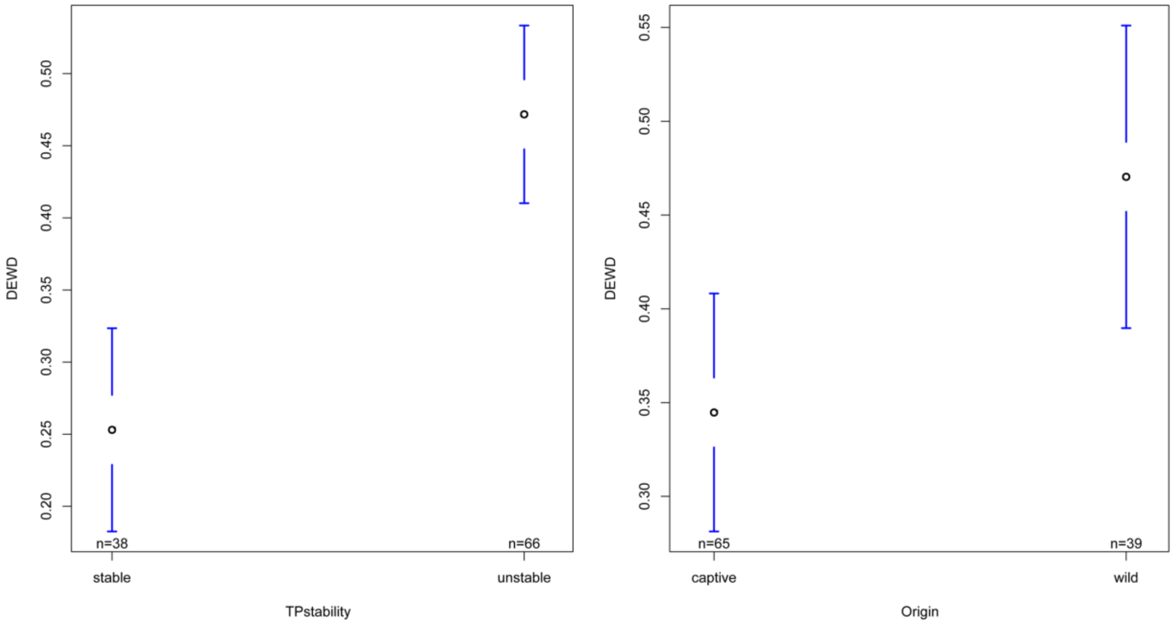
A3.2 Effects on chimpanzees´ grooming distribution

The individuals’ choosiness/restriction in their distribution of grooming, i.e. the DEWD, was significantly influenced by Origin and Stability of group composition (TPstability) (Table A4). With respect to Origin we found captive born chimpanzees (*N*=65 data points) to have a significantly lower deviation from edge weight disparity than wild-caught chimpanzees (*N*=39 data points; Fig. A3). That means that captive born chimpanzees distributed their grooming much more evenly among group mates than did wild-caught chimpanzees who were more restricted in whom they were grooming. Origin had a strong and significant influence with a relatively high relevant variable importance of $RVI_{DEWD}=0.83$ (Table A4). A ANOVA *post hoc* testing showed Origin to be a significant predictor influencing deviation from edge weight disparity ($F_{1,7}=9.60$, $P<0.05$; SA5 Table). Stability of the group composition (TPstability) proved to be a very important factor with a $RVI_{DEWD}=0.97$ (Table A4). The chimpanzees distributed grooming significantly more evenly among their group mates during stable periods, i.e. periods without any alteration to the composition of the group ($N=38$ data points), compared to unstable periods ($N=66$ data points; Fig. A3). A ANOVA *post hoc* test ($F_{1,15}=10.15$, $P<0.01$; SA5 Table) supported this finding.

The factors Predominant housing condition during infancy (PHCinfant), Arrival age category (ArrivalAgeCat) and Sex were retained variables in the best model selection, but scored low to medium in their relevant variable importance with $RVI_{DEWD}=0.30\text{-}0.55$ and did not demonstrate any significant influence on the grooming distribution among group mates (Table A4).

Figure A3

Confidence interval plots of DEWD and both significant fixed factors, Origin and TPstability.



Note. Mean deviation from edge weight disparity (±95% CI).

Table A4

Averaged best deviation from edge weight disparity (DEWD) model and relative importance of the fixed effects.

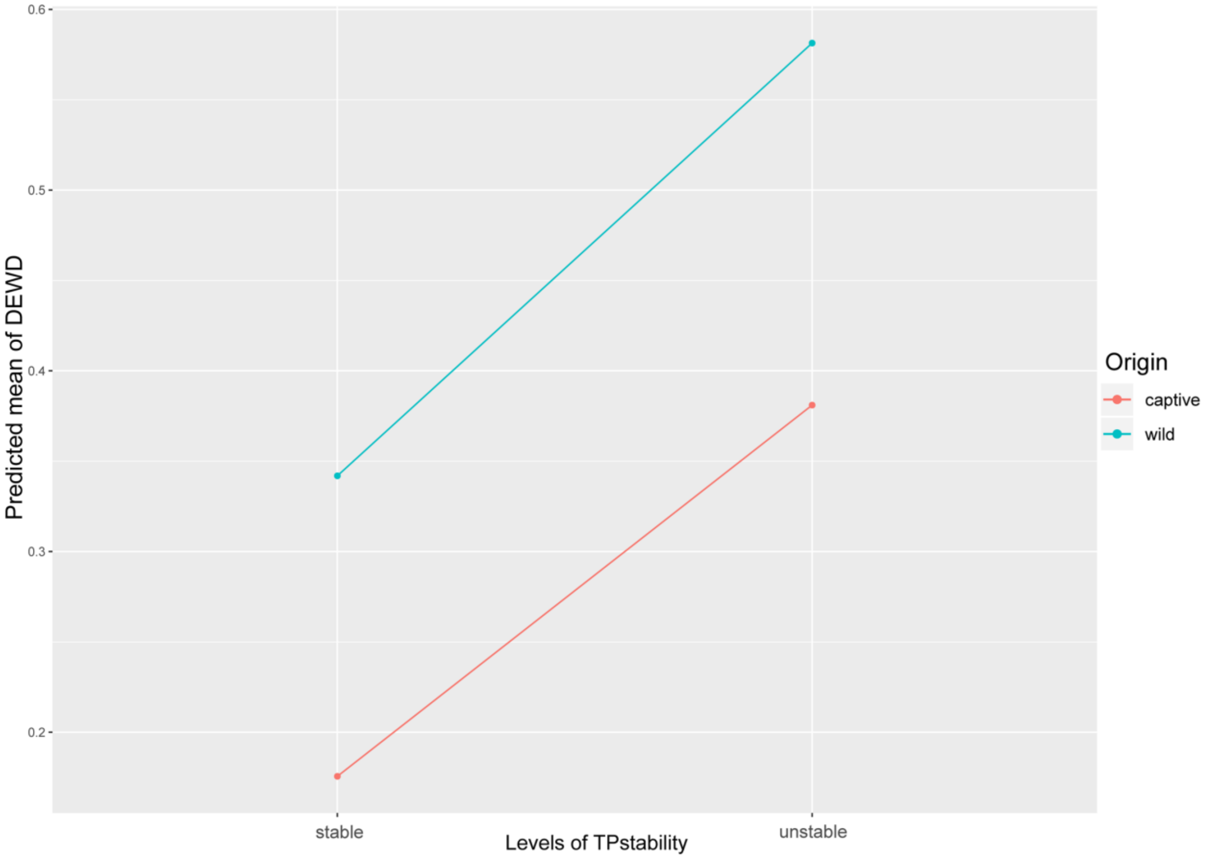
DEWD Model: conditional average (ΔAIC<10)					
	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)
(Intercept)	0.165	0.103	0.104	1.586	0.112
TPstability	0.214	0.066	0.067	3.199	0.001 **
Sex	0.113	0.061	0.061	1.831	0.067 .
Origin	0.153	0.062	0.063	2.433	0.015 *
PHCinfant	0.056	0.057	0.058	0.973	0.331
ArrivalAgeCat	0.022	0.077	0.077	0.287	0.774
Relative variable importance:					
	TPstability	Origin	Sex	PHCinfant	ArrivalAgeCat
Importance:	0.97	0.83	0.55	0.34	0.30
N containing models:	16	15	12	11	11

Note. Averaged best deviation from edge weight disparity (DEWD) model and relative importance of the fixed effects sex, predominant housing condition during infancy (PHCinfant), origin, arrival age category (ArrivalAgeCat) and stability of group composition (TPstability). All models included in this averaged results are presented in the supporting material (SA2 Table). Signif. codes: ‘***’ ≤0.001 ‘**’ ≤0.01 ‘*’ ≤0.05 ‘.’ ≤0.1 ‘ ’ ≤1

Considering that both, Origin and Stability of the group composition, significantly affected the distribution of grooming in our DEWD model, both with high RVI scores, we decided to run an additional DEWD model, based on the full model containing all five previously described fixed factors and added the interaction between TPstability and Origin. Due to slightly elevated VIFs (1.2-3.4) detected between the interaction and the separate components (TPstability and Origin) we ran this LMM apart from the averaged LMM. We found no significant result for the interaction (SA6 Table). Nevertheless, we show a figure, to be able to visualize and discuss the tendencies of the interaction between Origin and TPstability (Fig. A4). Here we can see, that (a) captive born chimpanzees distribute their grooming more evenly among their group mates than wild-caught chimpanzees, (b) unstable time periods are characterized by a more restricted grooming distribution compared to stable periods, and (c) both, captive born and wild-caught chimpanzees, distribute their grooming more evenly among group members during stable periods compared to unstable periods. Hence, captive born and wild-caught chimpanzees seem to react in a very similar way to alterations of the group composition, i.e. restricting the grooming distribution during unstable periods and grooming more evenly distributed during stable periods.

Figure A4

Plot representing the effect of the interaction between Origin and TPstability on the grooming distribution



Note. Each point on the plot is a predicted mean DEWD value and each connection of two points describes the effect, based on the data of the DEWD LMM model with TPstability, Origin, Sex, Arrival Age Category, Predominant Housing Condition during Infancy and the interaction of TPstability and Origin as fixed factors.

Graphical representations of the weighted social grooming networks of all 18 Observation Time Periods/Group compositions for both chimpanzee groups are presented in chronological order in the supporting information (Fig. SA1). These networks also show that there is one male, Tico (TIC), who was observed grooming only in one out of a total of eleven time periods. Tico is a wild-caught male who was predominantly housed without conspecifics during his infancy.

A4 Discussion

For this study, we chose two individual social network measures in order to describe the social grooming networks and the individuals’ social capacities: the standardized strength of grooming given and the distribution of grooming given among group mates. The findings of our study show that early life adversity is reflected in the social grooming networks of former pet and entertainment chimpanzees. Two out of the three factors referring to past experiences/conditions, i.e. Origin and Predominant housing conditions during infancy, significantly affected one or both social network measures. With respect to Origin, we found that the wild-caught chimpanzees of our study groups spent less time on "grooming given" and were much more restricted in the selection of grooming partners compared to captive born ones. Regarding Predominant housing conditions during infancy, we could show that chimpanzees who were housed predominantly with conspecifics spent more time grooming their group members compared to individuals that were housed predominantly without conspecifics during infancy. Relating to the third factor, Age at arrival at the rescue center, we did not find any differences between chimpanzees who arrived as sub-adults and those arriving as adults.

Beyond that, alterations to the composition of the group had an impact on social grooming, as the distribution of grooming among group mates was significantly more restricted during the unstable periods where alterations occurred, compared to stable periods without any alterations to the group composition.

A4.1 Long lasting influence of early life adversities on social capacities

It is known that chimpanzees are highly social animals who create and live in complex social networks (Shimada & Sueur, 2014). In order to develop normally in these complex social systems, chimpanzees learn from their mother and group mates from an early age (Goodall, 1986). An early environment satisfying the needs for security and exploration as provided by the mother and access to social partners are essential to develop the necessary social skills and become socially competent. This environment is especially important during the first two to three years of life, when infant chimpanzees tend to be inseparable from their mother (Bard, 1995).

By comparison, none of the chimpanzees of our study population did grow up under species-appropriate conditions. While most of the former pet chimpanzees grew up with humans only, the majority of the former entertainment chimpanzees were at least partially socially reared but were dressed and trained to perform for instance in a circus. Bloomsmith et al. (2006) showed that social isolation and sensory deprivation during the first years of an infant's life has a negative impact on the ability to live in social groups. Some studies even suggest that traumatic early life events could lead to mood and anxiety disorders in chimpanzees which, among others, become obvious in no or little interest in social interactions with conspecifics (Ferdowsian et al., 2011).

In order to gain a central position within a social group it is necessary to invest energy and time in social bonding activities, in chimpanzees this is often achieved through grooming interactions. Thus, lacking social experience and skills might reduce the capacity and/or the desire to engage in social grooming interactions and result in the inability to manage multiple relations at any one time. As such, this reduced social activity was found to have a negative impact on the individual's social position and possibly welfare in early maternally and socially deprived former laboratory chimpanzees who were all caught from the wild (Kalcher-Sommersguter et al., 2011).

While we know that all of the chimpanzees of our study sample had harmful experiences in the past and most were separated from their mothers at an early age, we nevertheless believe that the chimpanzees who were caught in the wild had an additional traumatic experience. This traumatic experience consisted of witnessing the killing of their mother and other group members, capture and transportation under extreme and often harmful conditions, as well as a dramatic change in their living conditions from wild to captivity. Although all this occurred in a relatively short amount of time, the extreme conditions, potential injuries and stress experienced by these infants during the most vulnerable period of early infancy often led to death during capture and transportation (Beck, 2010; Stiles et al., 2013). As for those who survived, we expected said traumatic experiences to be reflected in their social grooming activity, even after living in a social group for years. Indeed, we found our wild-caught chimpanzees to engage less in social grooming and to be more selective in whom they groomed compared to our captive born chimpanzees. Furthermore, individuals who were completely isolated from the grooming network in some of the observation periods, i.e. individuals who did not groom other chimpanzees at all, were mainly wild-caught ones. Interestingly, a recent study (van Leeuwen et al., 2018) did not find an effect of origin on social grooming. This might be explained by the fact that only frequency, but not duration of grooming was taken into account and no differentiation was made between grooming given and received.

The majority of our wild-caught chimpanzees arrived as adults (mean age: 23.6 ± 10.4 years) and most of the captive born individuals were sub-adults (mean age: 9.2 ± 7.5 years) upon arrival at the sanctuary. We were aware of the fact that this difference in age might be a confounding variable affecting origin. Therefore, we also tested for a possible effect of age at arrival at the rehabilitation center. In view of this, it was surprising, that we did not find any effect of age at arrival at the rehabilitation center, neither in the chimpanzees' grooming activity nor in their distribution of grooming among group members. This finding suggests that the significant difference in grooming between wild-caught chimpanzees, who by majority arrived as adults, and captive born chimpanzees, who by majority arrived as sub-adults, seems not to be due to the age at arrival at the rescue center but due to the origin of the chimpanzees. However, we do believe that an older age at arrival at the rescue center might result in more difficulties during the initial integration process compared to a younger one. Furthermore, the arrival age category, as the name indicates, only refers to the time the chimpanzees arrived at the sanctuary and started their rehabilitation and social integration into one of the two existing groups. However, several of the individuals were not transferred directly to the sanctuary after their time as pets or entertainment animals, but instead spent some time (in some cases years) without being forced to train or perform or were temporarily relocated to zoological gardens, before arriving at the sanctuary. These in between housing situations were at times marked by improved living conditions, as in some cases the chimpanzees were housed with conspecifics and/or received species-appropriate care.

Since Kalcher-Sommersguter et al. (2011) could show that early socially deprived wild-caught former laboratory chimpanzees spent significantly less time on "grooming given" compared to later deprived ones, we tested for predominant housing conditions during infancy and expected chimpanzees predominantly housed without conspecifics during infancy to be more restricted and less active groomers compared to those housed predominantly with conspecifics. We did not find any significant differences regarding the distribution of grooming, but our results indicate that chimpanzees predominantly housed with conspecifics during infancy spent more time grooming others than those predominantly housed without conspecifics.

One possible explanation for this finding might be related to the amount of human exposure. Although we do not have detailed information on our study subjects with respect to the amount of human exposure, it seems very likely that chimpanzees predominantly housed without conspecifics during infancy had more interactions with humans compared to those predominantly housed with conspecifics. The social interaction with one or several humans might have helped to develop certain social skills. However, as humans usually do not use grooming to interact with chimpanzees, the slowly developing grooming behavior (Nishida, 1988) might not have received a sufficient amount of practice opportunities and reinforcement during infancy in the chimpanzees living without conspecifics. Freeman & Ross (2014) reported that chimpanzees who experienced more exposure to conspecifics and less exposure to humans during their first four years of life showed the most grooming. Furthermore, Jacobson et al. (2017) found that chimpanzees with more exposure to humans during their early life had higher levels of cortisol, indicating elevated stress levels. In this line, a study looking into the relationship between social behaviors and hair cortisol concentrations, reported that rhesus macaques who spent more time socially active with conspecifics had significantly lower levels of cortisol (Wooddell et al., 2017). Regarding our results and these findings, we argue that the lower grooming activity of our wild-caught chimpanzees and those predominantly housed without conspecifics during infancy has to be seen as a social limitation, which is potentially resulting in higher levels of stress and a reduced wellbeing.

The interaction between Origin and the Predominant housing condition during infancy on the grooming strength revealed that while captive born chimpanzees generally exhibited a far higher grooming activity than wild-caught chimpanzees the former also seemed to be affected more strongly by the Predominant housing condition. This became visible through a steeper decline in the grooming activity between captive born chimpanzees predominantly housed with conspecifics and those housed predominantly without conspecifics compared to the much smaller decline between wild-caught chimpanzees housed predominantly with conspecifics and those housed predominantly without conspecifics.

In a study conducted by Kalcher-Sommersguter et al. (2015), the same social network measures were applied to compare the social grooming networks of ex-laboratory and zoo chimpanzees. Mother-reared zoo chimpanzees were found to distribute their grooming evenly among group mates, whereas wild-caught zoo chimpanzees who were maternally deprived but socially reared in their first two years of life were restricted in their distribution of grooming among group members similar to what we found in our wild-caught former pet and entertainment chimpanzees.

According to our findings, we suggest considering information on the animals´ life history, such as the origin and the predominant housing condition during infancy, when introducing new individuals into already existing groups and during the formation of new groups.

A4.2 The influence of sex on individual social network measures

Even though the focus of our study was on social conditions, we found sex to have an impact on the social grooming networks as well. Lehmann and Boesch (2008) suggest that even though previous studies on wild chimpanzees indicated males to be more socially active than females, this might depend greatly on the dispersal pattern and habitat quality. Moreover, it has been shown that the social potential of females becomes apparent in captive settings where competition for resources is less of an issue (de Waal, 1996). This is in line with our findings as the grooming activity was even higher in females compared to males and females did not differ from males regarding their distribution of grooming among group mates.

A4.3 Short-term reactions to alterations of group composition

Living in a social group cannot be compared directly between wild ranging populations and groups living in captivity (Hemelrijk, 1994) due to significant differences in living conditions such as food availability, medical care, etc.. However, it has to be expected that the significance of being able to establish and maintain social relationships with other group members and to perform complex social interactions holds not only for individuals living in the wild (Langergraber et al., 2007; Ziegler & Crockford, 2017) but also for those in captivity. Nevertheless, social activity might also cause a certain amount of stress and becomes even more demanding when changes to the group composition occur or new unfamiliar individuals join a group (Lehmann et al., 2007a). We were able to study the adaptation of individuals to group alterations, i.e. during social challenging time periods, by comparing observation periods with alterations in group composition (unstable periods) to periods without alterations (stable periods). As such, we were able to demonstrate, that chimpanzees changed their social strategy during unstable periods compared to stable periods, by modifying their distribution of grooming among group members, i.e. by abandoning or weakening certain bonds while strengthening others or forming new ones without changing the amount of "grooming given".

Our findings show that unstable periods were characterized by a more selective choice of grooming partners. It is important to note, that we refrain from labelling this mentioned adaption, i.e. the change in the distribution pattern, as either positive or negative, but argue that this indicates a certain capacity to react to a social alteration. More importantly, this adaptation seems to be shown by all of our chimpanzees, regardless of their level of choosiness/restriction. Interestingly, the individuals did not differ in the time they spent on "grooming given" between stable and unstable periods, but seemed to be choosier during unstable periods compared to stable periods.

One possible explanation for this might be that the amount of grooming needed to maintain a position during stable periods is similar to the amount of the, then more unevenly distributed, grooming needed to form new relationships beside the maintenance of already formed bonds during unstable periods. Another possible explanation might be that the individual’s grooming activity in stable periods already represents the maximum amount an individual is willing to engage. We can exclude the possibility that adding new individuals produced the more uneven distribution of grooming during unstable periods, as unstable time periods include not only the addition of group members, but also reductions in group size and changes to the routine (temporarily splitting and shuffling of a group).

One important finding of our study is that the changes in the distribution of grooming among group mates during unstable periods did not last permanently. This became apparent by the fact that unstable periods alternated with stable periods during the 12-years of observations (see Table A2) and the distribution pattern differed clearly between stable and unstable periods.

Due to the interaction plot between Origin and Time period stability we could further see, that regardless of the differences in origin, the chimpanzees modified their grooming distribution similarly. This means that, at least under attentive caring conditions, provided for example by a sanctuary such as Fundació MONA, even individuals with adverse early life experiences detect and react to socially challenging situations such as group alterations, by adjusting and after a few months slowly readjusting their grooming distribution pattern.

We do know that the socio-emotional development is a complex process and retrospective studies focusing on early life history include several risks, which can easily lead to misinterpretations. The relatively small sample size of 18 individuals and the vague information on the early life history and pre-sanctuary experience might have caused that we overlooked other potentially important factors. However, the observation period of 12 years and detailed information on the group management allowed us to analyses the effects of alterations to the group composition in detail. By no means do we suggest that the factors, considered here, are the only factors influencing the social grooming of these study population, but rather wish to emphasize that diverse factors and possibly their combinations could have a potentiating or moderating effect.

The wild-caught chimpanzees of our study population are on average older than the captive born chimpanzees and as such, most of the wild-caught individuals arrived at an older age at the sanctuary compared to the captive born ones. We considered this in our analysis and found origin but not age at arrival to influence the chimpanzees' grooming activity. A study conducted on former laboratory chimpanzees has shown that the age at onset of deprivation but not the age at observation time and the years spent in deprivation accounted for differences found in social behavior (Kalcher et al., 2008), supporting our finding. However, to be able to clearly disentangle the effects of origin and age at arrival at the sanctuary would require a study population consisting of wild-caught and captive born individuals in the same age ranges and with detailed information on every individual's life history.

In conclusion, we could show that early traumatic life events and adverse living conditions during infancy, affect the social grooming of former pet and entertainment chimpanzees in the long term. Wild-caught individuals spent less time on grooming given and were more restricted in whom they groomed compared to captive born ones, and chimpanzees who have been predominantly housed without conspecifics during infancy engaged less in grooming others than those predominantly housed with conspecifics during infancy. Astonishingly, all of these former pet and entertainment chimpanzees reacted in a similar way to alterations of group composition as grooming among group members reverted to a more even distribution in stable periods, after a more restricted distribution during unstable periods, throughout the whole 12 years of observation.

We believe that these results might be a valuable addition to the already existing knowledge, especially with respect to care management decisions regarding integration and group formations. For future studies, we suggest using multi-level networks including diverse social behaviors and social proximity as this might give an even better understanding, ideally with a larger sample size and more detailed information on the chimpanzees' past history.

A5 Acknowledgments

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Article B: Assessing the sociability of former pet and entertainment chimpanzees by using multiplex networks

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Abstract: Advances in the field of social network analysis facilitate the creation of multiplex networks where several interaction types can be analyze analyzed simultaneously. In order to test the potential benefits of this approach, we investigated the sociability of atypically raised chimpanzees by constructing and analyzing 4-layered multiplex networks of two groups of former pet and entertainment chimpanzees (*Pan troglodytes*). These networks are based on four social interaction types (stationary vicinity, affiliative behavior, allogrooming, passive close proximity) representing low- to high-level interaction types in terms of sociability. Using the tools provided by the MuxViz software, we could assess and compare the similarity and information gain of each these social interaction types. We found some social interaction types to be more similar than other ones. However, each social interaction type imparted different information. We also tested for a possible impact of the chimpanzees' biographical background on the social interaction types and found affiliative behavior as well as allogrooming to be affected by adverse early life experiences. We conclude that this multiplex approach provides a more realistic framework giving detailed insight into the sociability of these chimpanzees and can function as a tool to support captive care management decisions.

B1 Introduction

Network approaches based on social behaviors of nonhuman animals facilitated the successful evaluation of how sociality is shaped by evolutionary and ecological conditions and reflected in behavioral processes, such as social learning (Hobaiter et al., 2014) and cooperation (Croft et al., 2009), and also in the spread of diseases (Carne et al., 2014; Rushmore et al., 2013). Furthermore, it enabled researchers to investigate, simulate and predict patterns of hierarchies (Hobson, 2019), information transmission efficiency (Pasquaretta et al., 2015), group cohesion and stability (Beisner et al., 2015; Lehmann & Boesch, 2004). Traditionally social networks were analyzed by aggregating information and/or investigating only one type (e.g. a certain behavior or distance) of connection between individuals. While this approach might seem narrow, it did allow the explanation of trends and patterns, which had been misinterpreted or underrated previously (Kivela et al., 2014). However, as research on social networks advanced over time and databases became bigger and more varied, the necessity arose to get insights in social networks that are even more realistic. Considering the multi-dimensional nature of the network components in space and time (Barrett et al., 2012; Pinter-Wollman et al., 2014), it became obvious that in order to fully grasp social structures and dynamics, it was essential to construct multiple social networks based on a variety of edges (i.e. connections between nodes) between the same set of nodes (i.e. individuals) (Wasserman & Faust, 1994).

A great many studies on a variety of species, ranging from insects to nonhuman primates demonstrated the complexity of social structures in the animal kingdom (Hobson et al., 2019; Whitehead, 1997). Particularly for nonhuman primates, who are living in complex social societies, using a variety of strategies and behaviors to interact and connect with each other (Smuts et al., 1987), it seems a promising approach to implement a more realistic framework in order to explore their social structures. Especially during the last two decades, algorithms and computational technologies have been developed, providing the means to analyses and visualize complex multilayer relationships (De Domenico, Porter, et al., 2015). Hence, the use of these multilayer networks is now also recommended (Finn et al., 2019) and it has already been used in the studies of primate behavior (Pereira et al., 2020; Smith-Aguilar et al., 2018).

While it is recommendable to create a multilayer network based on several edges, the question of how many edges should be taken into account remains. Keeping in mind that an increase of data collected comes with a certain price, the right equilibrium between information gain, efficiency and redundancy has to be found (De Domenico et al., 2014; De Domenico, Nicosia, et al., 2015).

One of the most relevant social behaviors of chimpanzees is allogrooming (Goodall, 1986; Watts, 2000), which beside its hygienic function (Grueter et al., 2013) is used to establish and maintain relationships, bonds and coalitions (Dunbar, 1991). As such, many studies investigating the social networks of chimpanzees focus on social grooming as their edge variable (Crailsheim et al., 2020; Kalcher-Sommersguter et al., 2015; Kanngiesser et al., 2011; Levé et al., 2016; Rodrigues & Boeving, 2019). In cases where allogrooming is rare or difficult to observe, information might be limited to spatial or temporal co-occurrences of two individuals (Clark, 2011).

Our latest long-term study on grooming networks in former pet and entertainment chimpanzees demonstrated variations in the grooming activity on an individual level based on the chimpanzees' biographical background (Crailsheim et al., 2020). More precisely, we found wild-caught chimpanzees as well as chimpanzees who were predominantly housed without conspecifics during infancy to be more affected in their grooming activity and their distribution of grooming compared to those who were captive born as well as those who were predominantly housed with conspecifics during infancy. This could be explained by the fact, that similar to humans, the infancy in chimpanzees is a sensitive and crucial time period with respect to the social and emotional development (Suomi, 1997; Wiedenmayer, 2010).

Chimpanzee infants are heavily dependent on their mother and are nursed for their first five years of life. The loss of the mother causes behavioral disturbances and in case of unweaned infants may cause even the death of the infant (Boesch & Boesch-Achermann, 2000; Boesch et al., 2010; Davenport & Rogers, 1970; Goodall, 1986). With respect to the behavioral development of free-living chimpanzees, it is known that social play already occurs during the first month of an infant's life (Goodall, 1968), whereas grooming starts to develop steadily at about the age of two years but is infrequent until the age of four years (Nishida, 1988).

Only recently, a study on wild living chimpanzees revealed the significance of maternal care on the survival of infant chimpanzees even beyond nutritional dependence (Stanton et al., 2020). Several studies demonstrated that atypical rearing conditions and traumatic experiences during this time period produce long-lasting negative effects in chimpanzees (Bradshaw et al., 2009; Ferdowsian & Merskin, 2012; Parker & Maestripieri, 2011), affecting among others, their social skills (Bloomsmith et al., 2006), their personality profile (Ortín et al., 2019) and their cortisol levels at an adult age (Jacobson et al., 2017). Bradshaw et al. (2008) and Ferdowsian et al. (2011) supposed that traumatic early life experiences in chimpanzees cause symptoms which they defined as Complex Post-Traumatic Stress Disorder (PTSD), and these symptoms are comparable to those of human trauma survivors who suffered highly distressing events at an early age. Some studies even documented atypical rearing conditions to lead to structural covariations of the gray matter in the brains of adult chimpanzees (Bard & Hopkins, 2018).

Based on these findings we might expect not only allogrooming but also other social behaviors to be affected by the early life history of our study population. We were interested in how these former pet and entertainment chimpanzees with their atypical life histories would tolerate and deal with different types of social interaction. It has to be expected, that the experience of being caught in the wild and/or being housed without conspecifics during infancy, i.e. during their first five years of life, would affect the occurrence of certain interaction types, in particular those that require the toleration of permanent body contact and close proximity. However, these social interaction types might not be affected in the same way and/or to the same degree by the atypical life history, which would support the idea that analyzing various potentially important social interaction types simultaneously might provide more precise and realistic results.

In previous studies (Crailsheim et al., 2020; Kalcher-Sommersguter et al., 2015) we assessed chimpanzees sociability by looking into how their atypical life history affected their grooming activities based on their individual centrality scores. In this study, however, we chose a relational approach by taking the atypical life history not only of the individual but also of his/her partner into account when investigating their directed dyadic interactions.

To investigate this assumption, we chose four different social interaction types. Stationary vicinity (i.e. staying out of an arm's reach but within 5 meters without further interacting) represents a low-level interaction type in terms of sociability due to the distance between the individuals and as no bodily contact occurs. Affiliative behavior (including behaviors such as social play and socio-sexual behaviors except for allogrooming) represents a medium-level interaction type due to a decrease in the distance of the interacting individuals and as bodily contact may occur. Allogrooming and passive close proximity represent high-level interaction types in terms of sociability as allogrooming requires the toleration of permanent body contact and passive close proximity (i.e. staying within an arm's reach without further interacting) requires a certain amount of trust in the individual close by as the intention of that individual is, contrary to allogrooming, not immediately apparent. We used these different interaction types as they have already been tested and approved in severely deprived former laboratory chimpanzees (Kalcher-Sommersguter et al., 2011).

In the current study, we attempt to implement the use of a multiplex network analysis because it allows us to consider the four interaction types simultaneously. We want to find out if (1) the multiplex approach indeed increases the information gain compared to traditional single-layer and aggregate network analyses (even in small sized groups of 7 individuals), (2) (dis-)similarities might be found between the four interaction types, and (3) if there are individual differences in the occurrence of certain social interaction types. Furthermore, we were interested to see if potential differences detected between individuals and/or groups could be partially explained not only by the individual chimpanzee's early life history but also that of his/her group members.

For this end, we created multiplex networks of the two groups of former pet and entertainment chimpanzees housed at Fundació Mona, consisting of seven individuals per group. The four layers of our multilayer networks are based on the four different social interaction types (explained in detail above): stationary vicinity, affiliative behavior (except for allogrooming), allogrooming, and passive close proximity. We will evaluate each layer separately, its aggregated and multiplex components, and compare the obtained insights by using the open-source MuxViz software (De Domenico, Porter, et al., 2015). We predict that each layer will provide different information, and by taking all of the four layers into account, we expect to achieve a more detailed and realistic representation of the sociability of these two groups. More specifically, based on earlier findings in ex-laboratory chimpanzees, we expect to find an interlayer correlation between allogrooming and passive close proximity as both are representing high-level interaction types in terms of sociability. We expect to find an interlayer correlation between affiliative behavior and allogrooming, as both interaction types require the toleration of body contact. We do not expect to find an interlayer correlation between stationary vicinity, representing a low-level interaction type, and either allogrooming or passive close proximity, representing high-level interaction types. Based on findings of long-term observations on this study population over a period of 12 years (Crailsheim et al., 2020) and on ex-laboratory chimpanzees (Kalcher-Sommersguter et al., 2013; Kalcher-Sommersguter et al., 2011), we also expected the chimpanzees' biographical background to have an effect on the four different social interaction types. Here, we predict allogrooming as well as passive close proximity to be affected by early life history, as the toleration of permanent body contact and the ability to perceive the group members as trust-worthy may be impaired in adversely reared chimpanzees. This should be reflected in a reduced (or even lacking) grooming activity as well as a reduced toleration of passive close proximity in individuals who were caught in the wild and/or predominantly housed without conspecifics during infancy compared to those individuals who were born in captivity and/or predominantly housed with conspecifics during infancy. We also expect affiliative behavior to be affected by early life history, as it might be at least partly socially learned during infancy similar to allogrooming and thus might be reduced in individuals who are predominantly housed without conspecifics during infancy. We did not expect to find the toleration of stationary vicinity to be affected by the chimpanzees' biography because in terms of sociability this is a low-level interaction type as the individuals are out of reach of each other. Beyond these four interaction types, we also tested the impact of the chimpanzees' biographical background on the aggregated variable of these four interaction types, in order to check whether this aggregated variable produces an information loss as expected.

B2 Materials and methods

B2.1 Ethical Note

This study is based purely on behavioral observations and was conducted in accordance with all national and institutional guidelines for the care and management of primates as established by Fundació MONA, the Association for the Study of Animal Behavior/Animal Behavior Society and the Spanish Government (RD 53/2013).

B2.2 Study Sample

The study sample consisted of a total of 14 former pet and entertainment chimpanzees (9 males and 5 females) living in two different social groups and housed at the primate rescue center Fundació MONA in Catalonia, Northern Spain. The center is a member of the European Alliance of Rescue Centers and Sanctuaries (EARS) and it is rehabilitating chimpanzees since 2001. Biographic information of the study subjects is presented in Table B1.

Both groups consisted of adult chimpanzees (Mutamba group: 5 males and 2 females, Bilinga group: 4 males and 3 females) and no changes to the group composition occurred during data collection for this study.

Observations were conducted only while the chimpanzees had access to one of the two enriched and naturalistic outdoor enclosures (size of 2 420m^2 and 3 220m^2, respectively) which gave them the opportunity to exploit natural and artificial resources. Group members of a social group could see but not physically interact with group members of the other social group. For more detailed information on the housing facilities see (Cano, 2014; Llorente et al., 2012).

Table B1

Characteristics and background information on the study population

Name	ID	Sex	Origin	Predominant housing condition during infancy (with or without conspecifics)	(Est.) Year of Birth	Year of arrival at MONA	Group
Bea	**BEA**	F	wild-caught	with	1985	2012	Bilinga
Cheeta	**CHE**	F	wild-caught	without	1990	2015	
Coco	**COC**	F	wild-caught	without	1994	2012	
Nico	**NIC**	M	captive born	without	2001	2004	
Tico	**TIC**	M	wild-caught	without	1985	2005	
Tom	**TOM**	M	wild-caught	with	1985	2011	
Victor	**VIC**	M	captive born	without	1982	2006	
Africa	**AFR**	F	wild-caught	without	2000	2009	Mutamba
Bongo	**BON**	M	captive born	with	2000	2002	
Charly	**CHA**	M	captive born	with	1989	2001	
Juanito	**JUA**	M	captive born	with	2003	2005	
Marco	**MAR**	M	captive born	with	1984	2001	
Toni	**TON**	M	wild-caught	with	1983	2001	
Waty	**WAT**	F	captive born	with	1996	2002	

Note. Abbreviations: F = female, M = male.

The chimpanzees were fed four times per day with a balanced diet based on fruits, seeds and vegetables. They have limited quantities of other protein-rich foods (constant since 2001) and have access to water *ad libitum*. A big portion of their daily diet is scattered and hidden in the outdoor enclosures to stimulate natural foraging behavior and locomotion as part of their daily enrichment program.

B2.3 Data sampling

Data on the chimpanzees' behavior and proximity were recorded between May 2018 and January 2019 by conducting two-minutes scan sampling (Altmann, 1974; Martin & Bateson, 1993). One observation session lasted for 20 minutes where the behavior, the proximity (passive close proximity), position and height within the enclosure of all the individuals of one group were recorded every two minutes simultaneously. Data was recorded between approximately 10.30 a.m. and 6.30 p.m., i.e. while the chimpanzees had access to the outdoor enclosure. The observation sessions were evenly distributed between mornings and afternoons on randomized days (Monday to Sunday). Observers were located in one of the two observation towers while conducting their observations, allowing them to oversee the respective enclosure. Observers (n=9) were only allowed to collect data if they successfully passed a three-step inter observer reliability test. The first step included data collection over about two weeks; this data was checked and then deleted. In the second step observers have to pass a methodology test and in the third step they had to pass a video test that includes 20 different video clips with an agreement of ≥85 percent to the head of research.

Although a complete set of behaviors was recorded, for this study we only considered social interactions that occurred among group members and recorded if two individuals stayed within close proximity (i.e. within an arm's reach). Furthermore, data on the chimpanzees' position within the enclosure was recorded digitally on a GPS scaled enclosure map. Additionally, the observers recorded the height level of the chimpanzees (ground and four levels of the climbing structures, respectively). We calculated linear distance values between each pair of individuals of a group every two minutes, using the matrix distance plugin available in QGis 2.18 (QGIS Development Team, 2016) and counted the pairs that were within 5 m (i.e. for the calculation of stationary vicinity) per scan. We corrected these values by subtracting the occurrences where the respective pairs were within an arm's reach, and also if the height level difference was more than one. Observers used tablets with the ZooMonitor data scoring software (Ross et al., 2016) programmed with the sanctuary's monitoring ethogram and facility map data. A total of 67 997 scans have been collected for this study (Bilinga group 32 320; Mutamba group 35 677).

B2.4 Data Preparations

The edges represent the four social interaction types. Scan data was used to calculate index values of stationary vicinity (i.e. staying out of an arm's reach but within 5 meters without further interacting), affiliative behavior (except for allogrooming), allogrooming and passive close proximity (i.e. staying within an arm's reach without further interacting). The four indices are mutually exclusive (see Table B2 for edge definitions), i.e. if individual A is grooming individual B, these two individuals cannot be in close proximity simultaneously. Note, however, that individual A and B can be in close proximity or stationary vicinity to their other group members simultaneously.

Table B2

Definition of edge variables (i.e. indices)

	Edge	Definition	Calculation of index values
Social interaction types	Stationary vicinity	Being out of an arm's reach but within a 5 m distance without further interacting	Number of scans where individual A and individual B where out of an arm's reach but within a 5 m distance divided by the number of scans where individual A and individual B had access to each other.
	Affiliative behavior	Including social play, socio-sexual and other affiliative behaviors such as follow*, embrace, feed together, touch, mouth-to-mouth, short body contact, extend arm (except for allogrooming)	Sum of the number of scans where individual A exhibits affiliative behavior towards individual B divided by the number of scans where individual A and individual B had access to each other.
	Allogrooming	Cleaning and/or manipulating the hair/body of a group member (unidirectional or mutual)	Sum of the number of scans where individual A is grooming individual B divided by the number of scans where individual A and individual B had access to each other.
	Passive close proximity	Being within an arm's reach without further interacting	Number of scans where individual A and individual B were within an arm's reach divided by the number of scans where individual A and individual B had access to each other.

Note. All indices are mutually exclusive, i.e. allogrooming was not counted as affiliative behavior, and passive close proximity and stationary vicinity were only recorded in the absence of other social interactions between two individuals.
* Follow is defined as following another individual by moving beside or behind with occasional physical contact.

The index values per individual are expressed as proportions for all four indices. With respect to affiliative behavior and allogrooming, we considered the direction of the behavior by calculating the percent of scans an individual spent with exhibiting affiliative behavior towards an individual group member and grooming of a group mate, respectively. Since stationary vicinity and passive close proximity are symmetric, the index values are the same for the two interacting individuals in that case. Calculations are based on the number of scans the two interacting individuals had access to each other. Access to each other means that both individuals had access to the outdoor enclosure, which includes the scans where both individuals were in the outdoor enclosure, but also scans where one of the two individuals was indoors and thus not visible to the observer (access to indoor area depended on care decisions typically related to the weather conditions). We did consider total observation time per dyad because it could vary between the different dyads of a group as some individuals could have been separated for veterinary or care-management purposes or voluntarily stayed inside without access to the outdoor enclosure for periods of time.

For the multiplex analysis, in order to avoid an influence of layers on multiplex measures due to scaling effects, we normalized the index values of all four indices by dividing the individual values by the maximum value recorded for the respective layer (i.e. the highest value that occurred in one of the two groups). These values (=weighted index values) ranged from 0 (for a none existing edge) to 1 (representing the maximum index value layer) for all four indices then. In the multilayer analysis, within the MuxViz environment, the two social groups were analyzed separately.

For statistical analysis in R (linear mixed models), we used the index values per individual for each social interaction type. The index definitions are the same as for the multilayer analysis. Here, all 14 individuals were analyzed together when testing for effects of the biographic background on the indices. We considered the fact that the chimpanzees are living in two social groups by adding group as random effect and the ID of the sender as nested within group.

B2.5 Network construction

We used the MuxViz software (De Domenico, Porter, et al., 2015), in the R environment (R Core Team, 2018), an open-source multilayer network visualization and analysis software, for all network construction and exploration procedures presented in this study. We created a 4-layered multiplex network for each of the two groups of chimpanzees separately. All layers of the multiplex network were created as directed weighted networks, based on values ranging between 0 and 1, and all layers are interconnected by the nodes (representing the individuals) they have in common. Each layer contained only information of one of the four edge variables, as described in Table B2. As such, edges between two nodes reflect the existence and weight of a specific type of social interaction between them (De Domenico et al., 2013).

B2.6 Social Network Analysis (SNA)

We applied several tools of network analysis offered by MuxViz:

Graphical visualization

The MuxViz software offers a wide range of possibilities to graphically explore and represent social networks (De Domenico, Porter, et al., 2015). As visual representations help to detect trends or tendencies, we produced social networks for all layers and for the two social groups separately. We will also present annular visualizations of the node properties and layer rankings.

Interlayer correlation and reducibility

We examined the structural similarities between the four layers by inspecting the interlayer correlations in terms of edge-overlap. For testing structural similarities the sum of the weights of all edges connected to a node are considered by taking into account the fractions of edges shared between all four layers (Battiston et al., 2013; De Domenico, Porter, et al., 2015).

In the next step, we applied the MuxViz reducibility analysis, based on the Von Neumann entropy, where the semi-aggregated states of multilayer networks are compared with the completely aggregated form. At each step of the algorithm, a multilayer network with one layer less is generated by aggregating the two most similar layers, i.e. the two layers with the smallest value of the quantum Jensen-Shannon divergence (Ward method for hierarchical clustering). Layers in which nodes are connected more similarly have a shorter Jensen-Shannon distance with a value closer to 0, whereas layers with very different connection patterns of nodes have values close to 1 (De Domenico et al., 2014; De Domenico, Nicosia, et al., 2015). Since our multiplex networks are based on four layers, we reached the fully aggregated state of our networks after three steps of this merging procedure.

The fact that the reducibility analysis is based not only on the amount of connections but also the weights of each layer enabled us to apply this methodology even for small and densely connected networks where differences are more likely to occur due to the weights.

Node Centrality/Versatility

MuxViz offers a range of node measures for monolayer (centralities) as well as multilayer (versatilities) analysis (Farine & Whitehead, 2015; Rodrigues, 2019; Segarra & Ribeiro, 2014). We chose to calculate the eigenvector centrality and versatility to measure the importance of group members within a layer and between the layers within each of the two groups (De Domenico, Solé-Ribalta, et al., 2015; Solá et al., 2013). Eigenvector centrality is particularly suited for densely connected and small networks, as often found in primates (Kasper & Voelkl, 2009), as it accounts for edge weights, where more differences between individuals can be found compared to degree based centralities. This centrality measure considers the degree and strength of direct connections, but also takes indirect connections into account (Bonacich, 2007; Newman, 2004; Segarra & Ribeiro, 2014). Each individual obtains a value between 0 (disconnected) to 1 (most densely connected) in each layer, the aggregate and multiplex state, which are than ranked accordingly. This allows us to compare the ranking position of the chimpanzees in a certain layer to their ranking positions in the other layers, the aggregate and multiplex states.

B2.7 Linear mixed models

For this part of the analysis, we included all 14 chimpanzees, but considered that they are living in two social groups. To investigate possible effects of the early life experience of our chimpanzees on the social interaction types (edges), we ran four linear mixed models

(LMMs) with each of the edge variables (i.e. the index values) as dependent variable (Table SB5). We ran a fifth linear mixed model with the aggregated values, calculated as the sum of the four edge variables, as dependent variable. All models were run by using the "lme4" package (Bates et al., 2015) in R 3.5.0 (R Core Team, 2018).

In our recently published long-term study (Crailsheim et al., 2020), covering data from April 2006 to July 2018, we found allogrooming to be affected by predominant housing conditions during infancy (with or without conspecifics), origin (wild-caught vs. captive born) and sex (male vs. female), but not age (although wild-caught individuals were on average older than captive-born ones). We used the same fixed effects in this study to test for their effects on the four different social interaction types. Predominant housing condition during infancy (PHCinfant) considers if the chimpanzees were housed for more than 2.5 years of their first five years of life with or without conspecifics. With respect to predominant housing conditions during infancy and origin, we differentiated whether the individual directed the behavior to a group member with the same experience or to a group member with a different experience. This resulted in four categories for predominant housing conditions during infancy (with->with, without->without, with->without, without->with) and origin (wild->wild, captive->captive, wild->captive, captive->wild). The same differentiation was done for sex (M->M, F->F, M->F, F->M). As the 14 chimpanzees live in two social groups, we included group as random factor and the ID of the sender of the behavior as nested within group. We visually checked QQ plots for a normal distribution of the residuals (Fig. SB1&SB2). Fixed factors were the same in all LMMs, only the dependent variable differed for each model (i.e. the four edge variables and the aggregated value).

First, we tested whether full models (containing all three fixed factors) were significant improvements over the null models (without fixed factors). In case a full model differed significantly from the corresponding null model, we applied the ANOVA function (Type III Analysis of Variance with Satterthwaite´s method) and a post hoc test based on the p-value obtained with the “glht” function (multiple comparison of means with Tukey Contrast, p-values adjusted by the Holm-Bonferroni method). We tested for multicollinearity between all fixed factors by calculating the variance inflation factor (VIF) using the "car" package in R (Fox & Weisberg, 2011). All VIFs (variance inflation factor), calculated for our three fixed factors were below 1.2, indicating that our fixed factors were not correlated.

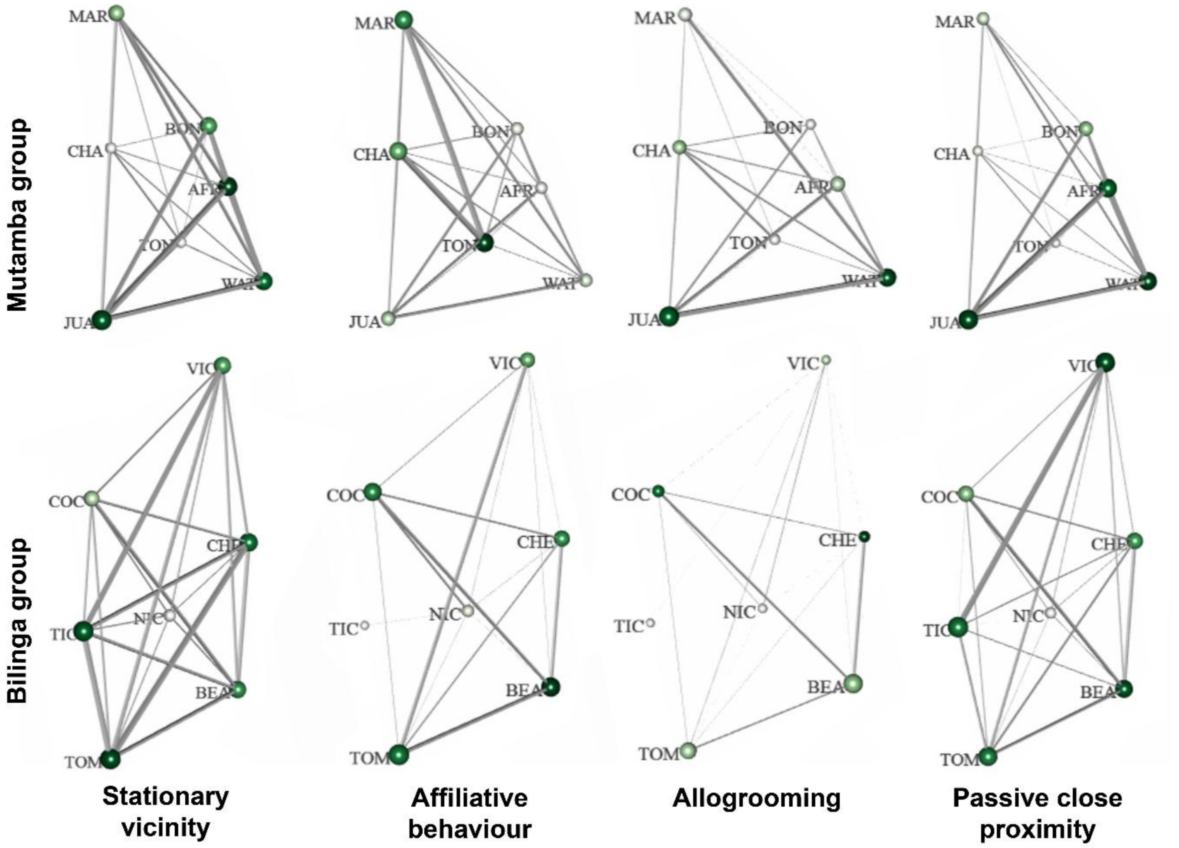
B3 Results

B3.1 Graphical visualization of the 4-layered multiplex networks

The visual representation of each layer of the 4-layered multiplex networks for two groups of chimpanzees is shown in Fig. B1. The edges of the respective layers represent the particular social interaction types (stationary vicinity, affiliative behavior, allogrooming, passive close proximity). The nodes represent the individuals of the respective group. The size of the nodes is based on the eigenvector centralities of the individual chimpanzees, i.e. the bigger a node the more *densely* is the respective individual connected to its group mates. The color of the nodes refers to the strength centralities of the individual chimpanzees, i.e. the darker green a node the more *strongly* is the respective individual on average connected to its group members. The distribution of the nodes is based on the Kamada-Kawai algorithm. To give an example, female Cheeta (CHE) of the Bilinga group is strongly connected in all four interaction types as indicated by the darker green shaded node color. However, she is not densely connected in the allogrooming layer, representing her eigenvector centrality, indicated by her small node size. For each of the two groups, each network of every single layer consists of seven nodes, representing the seven individuals (who are all in both groups present in all four layers). Thus, the 4-layered multiplex network has 168 possible edges for each of the two groups, of which 139 edges (i.e. 83%) are expressed in the Bilinga group and 166 edges (i.e. 99%) in the Mutamba group.

Figure B1

Multiplex networks of the two social groups (Mutamba and Bilinga)



Note. Each layer represents one of the four different social interaction types (stationary vicinity, affiliative behavior, allogrooming and passive close proximity). Edge width is proportional to the directed weighted index value of node pairs. Node size is proportional to the eigenvector centrality. Node colors depend on the individual's strength centrality. Node labels correspond to the individuals listed in Table B1. The node layout is based on the force-directed algorithm Kamada-Kawai to the aggregated network of all four layers, nodes have the same position on all layers.

The present edges of the 4-layered multiplex network result in a network density of 0.83 for Bilinga and 0.99 for Mutamba, indicating densely connected networks for both groups. The network densities of the individual layers, however, are ranging from 0.57 to 1 (Table SB1). The stationary vicinity layer had a network density of 1 in both social groups, i.e. all individuals spent some time out of an arm's reach but within 5 m distance to all their group members. While affiliative behavior was exchanged within all dyads of the Mutamba group, this was not the case in the Bilinga group where more than 25% of the possible edges were missing in this layer. The allogrooming layer had a network density of 0.57 in Bilinga group and 0.95 in Mutamba group, which means that allogrooming has been exchanged only in about half of the possible combinations in Bilinga group but in almost all combinations in Mutamba group. The passive close proximity layer had a network density of 1, again in both groups, i.e. all individuals spent some time within an arm's reach to all their group members.

Network density (Table SB1) also revealed that Mutamba group is more densely connected in three out of the four layers compared to Bilinga group. Stationary vicinity, representing a low-level social interaction type in terms of sociability, occurred much more often than the three other social interaction types, which are representing medium- to high-level social interaction types. Mean index values and mean weighted index values of the stationary vicinity layer were similar in both social groups, though the Mutamba group scored higher in all four interaction types. Affiliative behavior, representing a medium-level social interaction type, occurred least frequently. Mean index values and mean weighted index values of the affiliative behavior layer were again similar in both social groups. While the mean index values of the two social groups were similar for the close proximity layer, the two groups did differ in the allogrooming layer where we found a two times higher mean index value in the Mutamba group compared to the Bilinga group. Moreover, the comparison of the edges revealed that the individuals of the Bilinga group were much more selective with respect to allogrooming and affiliative behavior than were the individuals of the Mutamba group.

B3.2 Interlayer correlation & Layer reducibility

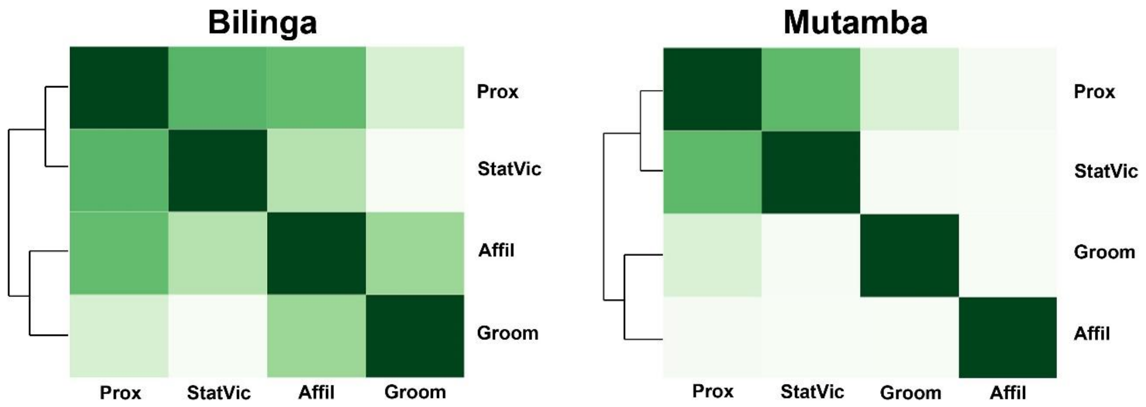
In order to evaluate differences and similarities between layers, we looked (1) into the overlapping of edges and (2) conducted a reducibility analysis. The overlapping of edges (reflecting the social interaction types) is presented in Fig. B2. The interlayer similarity is indicated by a dendrogram and the tone of the squares, i.e. the darker a tone the more similar are the respective layers.

The mean global edge-overlap (i.e. representing the fraction of edges, which are found in all four layers) is 10 percent for Bilinga group and 19 percent for Mutamba group (Table SB2).

Fig. B2 shows that the stationary vicinity layer and the close proximity layer are most similar to each other in both social groups (edge-overlap of 65% for Bilinga and 79% for Mutamba). In Bilinga group, the affiliative behavior and the close proximity layer ranked second with an edge-overlap of 62%, followed by the layers allogrooming and affiliative behavior with an overlap of 49%. The lowest edge-overlap was found between the layers allogrooming and stationary vicinity with 17%. In Mutamba group, the allogrooming and the close proximity layer ranked second with an edge-overlap of 61%, while all the other layer combinations had an overlap of 54%. In sum, it became apparent that individuals who were frequently in stationary vicinity to their group members were also often in close proximity to them in both social groups. There are, however, differences with respect to close proximity and allogrooming where we found a high edge-overlap in the Mutamba group but a low edge-overlap in Bilinga group indicating that individuals in Bilinga group who spent more time in close proximity to their group mates did not also spent more time grooming these group mates.

Figure B2

Interlayer differences evaluated via the edge-overlap between layers by detecting the fraction of edge values shared between all two-layer combinations, separately for the two social groups



Note. Darker tones indicate a higher edge-overlap.

For the reducibility analysis, the interlayer similarity is calculated by the quantum Jensen-Shannon divergence, which estimates the similarity between two networks based on their Von Neumann entropy. Then a hierarchical clustering is performed by using the Ward method (Fig. B3a and B3b; Table SB3). The dendrogram and the tone of the squares indicate the similarity of layers. Note that here a lighter tone indicates a higher similarity between layers. This is another measure to evaluate (dis-)similarities between layers where gradually the two layers with the shortest Jensen-Shannon distance (i.e. the most similar) are aggregated to one layer.

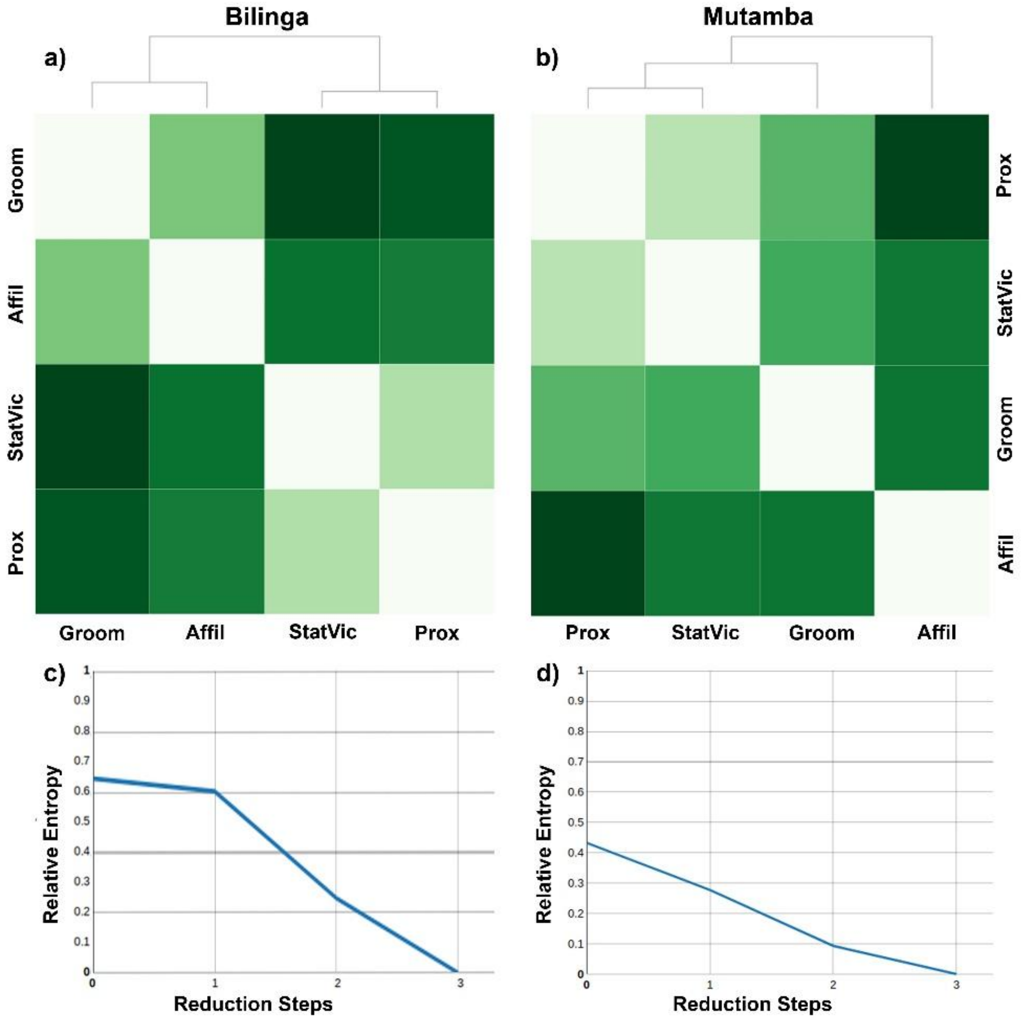
The reducibility analysis revealed – as seen before in overlapping of edges – that the stationary vicinity layer and the close proximity layer shared most similarities in both groups (Jensen-Shannon distances for Bilinga is 0.117 and for Mutamba is 0.102). In the Bilinga group, the allogrooming and the affiliative behavior layer were next similar (0.172), followed by the affiliative behavior and the close proximity layer (0.291). The highest dissimilarity was found for the allogrooming and the stationary vicinity layer (0.358). This ranking (Table SB3) is almost the same as the one found when comparing the overlapping of edges.

In the Mutamba group the allogrooming layer and the close proximity layer ranked second with respect to their similarity (0.197) consistent to the finding in the overlapping of edges. Compared to the edge-overlap where all the other layer combinations ranked the same, these layer combinations ranked different here. The greatest dissimilarity was found between the affiliative behavior and the close proximity layer (0.344; Table SB3).

Additionally, to the visual presentation, the relative entropy is calculated for every reduction step (Fig. B3c and 3d). For both social groups the reducibility analysis clearly revealed that each layer aggregation step leads to a loss of information indicated by a decreasing relative entropy. This shows that the 4-layered multiplex networks are the most optimal representation in both social groups.

Figure B3

Visual representation of the reducibility analysis



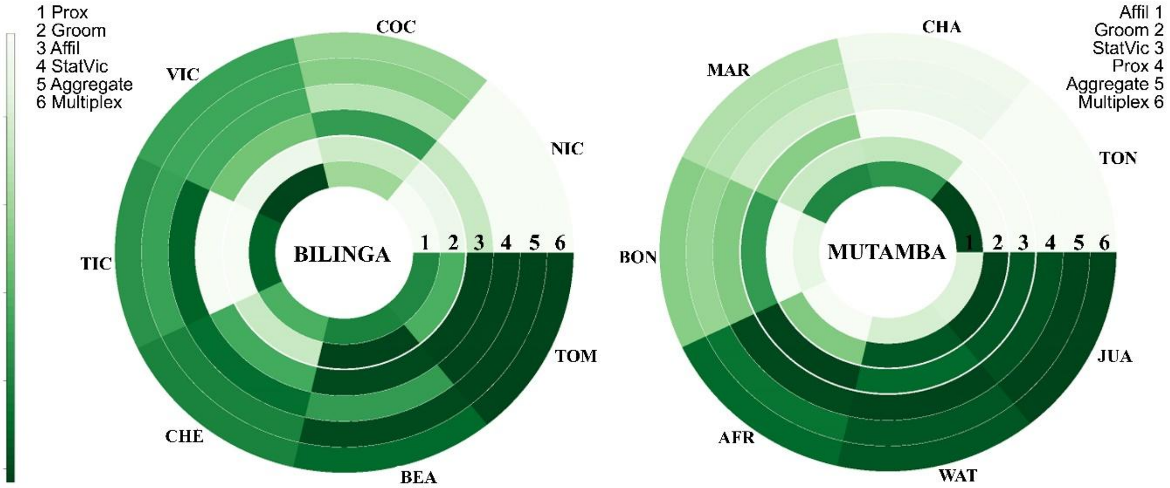
Note. Reducibility distance table for (a) Bilinga group and (b) Mutamba group. Layer-aggregation and network reducibility for (c) Bilinga group and (d) Mutamba group. In Fig. B3a and B3b layers have been sorted through a hierarchical clustering process using the Ward method with the dendrograms depicting the order of similarities. Darker tones indicate a greater distance (dissimilarity) between layers. Fig. B3c and B3d present the relative entropy at each reduction step when comparing the 4-layered multiplex network with its respective semi- and fully aggregated network versions. At each step, the pair of layers with the shortest Jensen-Shannon distance (see Fig. B3a and B3b) is aggregated, reducing the number of layers by one. For both social groups the highest value of the relative entropy is reached in 4-layered multiplex network.

B3.3 Node Centralities & Versatilities

For the annular visualization we calculated the eigenvector centrality (for each layer and for the fully aggregated network where all four layers are aggregated to a single layer) and the eigenvector versatility for each node (individual). In this visualization (Fig. B4), each ring represents the eigenvector centralities of a single layer and the aggregated layer as well the eigenvector versatility of the multiplex network. For differences between the aggregated layer and the multiplex network, see Solé-Ribalta et al. (2014). The order of the rings is based on the similarity ascertained by a Spearman correlation. Each triangle shaped segment represents the eigenvector values of one individual where darker tones indicate higher values. The order of the individuals is based on the individuals' versatility rank (see Table SB4).

Figure B4

Annular visualization of the eigenvector centralities and versatility for both chimpanzee groups (Bilinga, Mutamba)



Note. Eigenvector values are color-scaled with darker tones representing higher values according to the scale on the left side. Each ring represents either a single layer, an aggregated layer or the multiplex network. Note that the ring order is different for the two groups (numbering of the rings refers to the respective legend). Each triangle shaped segment, cutting across all six rings, represents the eigenvector values of one particular chimpanzee. The order of the segments is based on the versatility rank of the individuals (clockwise order of the eigenvector versatility from highest to lowest), i.e. ordering of Bilinga group is based on ring 1 (inner ring), ordering of Mutamba group is based on ring 6 (outer ring).

The annular visualizations of the eigenvector centralities and versatilities of the two social groups provide an insight not only on the layer level but also on the individual level.

Higher eigenvector centralities, indicated by a darker tone, refer to the relative importance of the respective individual. It becomes apparent that some individuals such as Juanito, Waty and Africa in the Mutamba group, and Tom and Bea in the Bilinga group are more sociable than other ones as they scored high in almost all layers. Whereas individuals such as Nico in Bilinga group, and Charly and Toni in Mutamba group seem less sociable than their group members as they scored low in almost all layers. On closer inspection, however, it becomes obvious, that the supposedly less sociable individuals Charly and Toni scored very high in the affiliative behavior layer. This explains also our findings from edge overlapping and the reducibility analysis. There we found in the Mutamba group the affiliative behavior layer to be most dissimilar from the stationary vicinity and the close proximity layer. Similarly, the finding of the greatest dissimilarity between the allogrooming layer and the close proximity layer can be explained by Victor and Tico who scored very low in the allogrooming layer but very high in the close proximity layer. This shows that sociability can only be reliably estimated by taking several different interaction types into account.

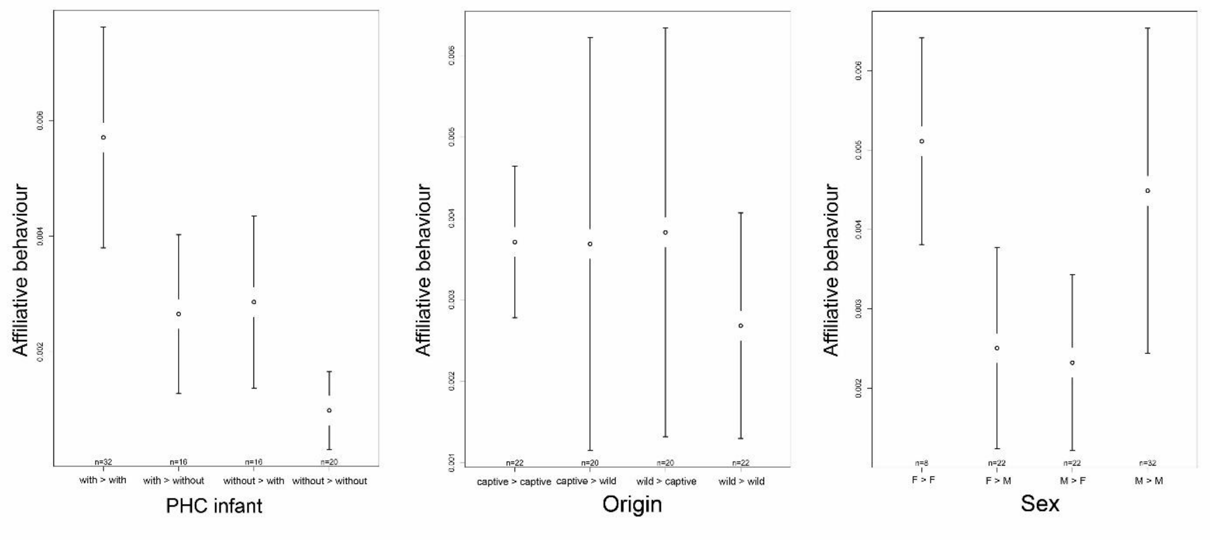
B3.4 Linear mixed models

Since the annular visualization provided an indication of individual differences, we ran linear mixed models where we considered the biographical background of our individuals. We found three out of the five full models to show significant improvements compared to their respective null models. The full models with stationary vicinity and the aggregated variable as dependent variables showed no improvement compared to the null model. All outcomes of the three LMMs and the respective post hoc analyses are presented in the supplementary tables SB5-SB6.

The full model with affiliative behavior as dependent variable revealed a significant effect of origin (F=4.272, p=0.007), predominant housing condition during infancy (PHCinfant; F=12.447, p<0.001) and sex (F=2.892, p=0.040) on the occurrence of affiliative behavior (see Table SB5). With respect to origin, we found wild-caught individuals to exhibit significantly more affiliative behavior toward captive born individuals and captive born individuals to exhibit significantly more affiliative behavior toward wild-caught individuals compared to the affiliative behavior exhibited between two captive born individuals (captive->wild vs. captive->captive: z=3.120, p=0.009; wild->captive vs. captive->captive: z=3.184, p=0.009; Fig. B5 and Table SB6). With respect to predominant housing condition during infancy, affiliative behavior was shown significantly more often between individuals who were both predominantly housed with conspecifics compared to the other combinations (with->without vs. with->with: z=-4.328, p<0.001; without->with vs. with->with: z=-4.193, p<0.001; without->without vs. with->with: z=-5.967, p<0.001; Fig. B5 and Table SB6). Regarding sex, we found females to direct significantly more affiliative behavior toward females than toward males (F->M vs. F->F: z=-2.590, p=0.048), and males to direct significantly less affiliative behavior toward females than females toward females (M->F vs. F->F: z=-2.673, p=0.045; Fig. B5 and Table SB6).

Figure B5

Confidence interval plots of affiliative behavior and the three fixed effects predominant housing condition during infancy (PHC infant), origin and sex

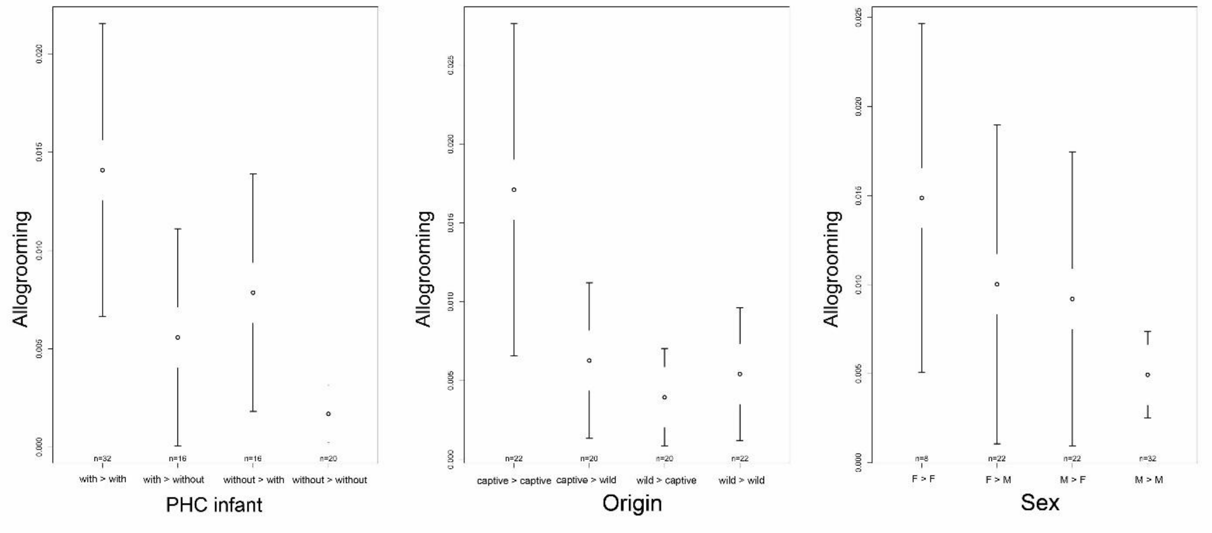


Note. Mean index value over all directed dyads (±95% CI).

In our full model with allogrooming as dependent variable we found a significant effect of origin (F=3.085, p=0.032) and sex (F=6.032, p<0.001) on the time spent allogrooming (see Table SB5). Predominant housing condition during infancy did not significantly affect time spent on allogrooming. However, there was a trend showing that grooming was exchanged less frequently among individuals who were housed predominantly without conspecifics compared to the exchange of grooming among individuals who were housed predominantly with conspecifics during infancy (without->without vs. with->with: z=-2.485, p=0.078, Fig. B6 and Table SB6). With respect to origin, we found wild-caught individuals to spent significantly less time grooming their wild-caught group mates compared to the time captive born individuals spent grooming their captive born group members (wild->wild vs. captive-<captive: z=-2.904, p=0.022; Fig. B6 and Table SB6). A trend became apparent when comparing the time wild-caught individuals spent grooming their captive born group members and the time captive born individuals spent grooming their captive born group mates (wild->captive vs. captive->captive: z=-2.501, p=0.062). Regarding sex, we found males to spend significantly less time grooming other males than females (M->M vs. M->F: z=-2.630, p=0.034). Males groomed each other also significantly less often than females groomed each other but also males (M->M vs. F->F: z=-3.783, p<0.001; M->M vs. F->M: z:-3.092, p=0.010; Fig. B6 and Table SB6).

Figure B6

Confidence interval plots of allogrooming and the three fixed effects predominant housing condition during infancy (PHC infant), origin and sex

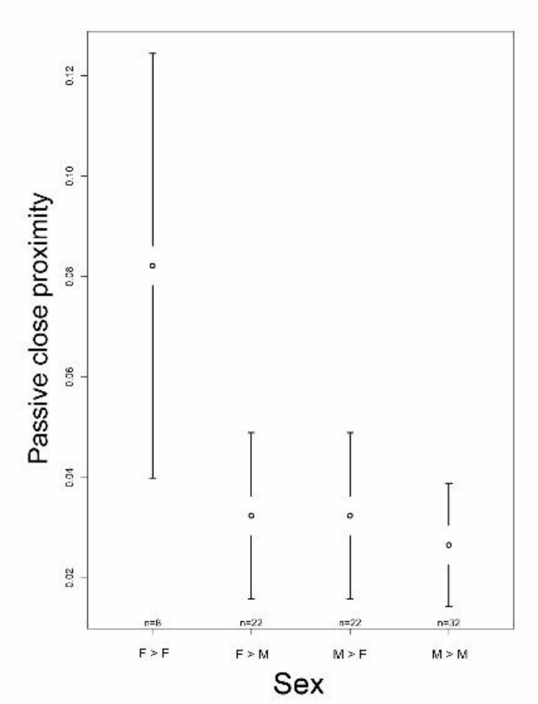


Note. Mean index value over all directed dyads (±95% CI).

The full model with passive close proximity as dependent variable revealed a significant effect of sex (F=6.527, p<0.001) on the time spent in passive close proximity (see Table SB5). Predominant housing condition during infancy and origin did not significantly affect passive close proximity. With respect to sex, we found females to spend significantly more time in close proximity to females than to males (F->M vs. F->F: z=-4.003, p<0.001). Males spent significantly less time in close proximity to males but also to females than females spent in close proximity to females (M->M vs. F->F: z=-4.142, p<0.001; M->F vs. F->F: z=-3.656, p=0.001; Fig. B7 and Table SB6).

Figure B7

Confidence interval plots of passive close proximity and the two fixed effects origin and sex



Note. Mean index value over all dyads (±95% CI).

In sum, we found sociability, reflected in affiliative behavior and allogrooming, to be affected by predominant housing conditions during infancy and/or origin as well as sex. Affiliative behavior as well as allogrooming were most frequently exchanged among individuals who were both predominantly housed with conspecifics during infancy. In addition, allogrooming was exchanged most frequently among captive born individuals and least frequently among wild-caught individuals. Sex was the only fixed factor that was consistently affecting the depended variables in all three models, where females had the highest values in their exchange of affiliative behavior as well as allogrooming among each other and spent most time in close proximity to each other compared to the other combinations.

B4 Discussion

The multiplex approach revealed that it is possible to consider different social interaction types simultaneously even in small social groups of chimpanzees, i.e. with a group size of seven individuals. We did find similarities but also differences between the four social interaction types stationary vicinity, affiliative behavior, allogrooming and passive close proximity, which in turn increased the information gain by giving insights into the sociability of these two groups of former pet and entertainment chimpanzees. By taking into account the early life history of interaction partners and doing so in two social groups with different group composition regarding said early life experiences, we could detect certain differences in the occurrence of social interaction types.

Although admittedly the data collection and preparation has been more complex and extensive, by applying the multiplex approach, we were able to conduct a far more realistic social network representation and analysis. Looking at the (dis-)similarities between layers and eigenvector rankings across the interaction types, none of the four individual layers on their own provides insights representing the information from the remaining layers. While the aggregate layer would have at least assured that chimpanzees scoring low in one particular layer would not have been marked automatically as an outsider or individual with a low sociability, it still failed in our secondary objective related to the early life experiences of the interaction partners. According to our results, at least for small networks such as ours, the aggregate layer might be a better option than a single layer network, but is prone to lose much information content as demonstrated in the reducibility analysis and LMM analysis regarding the atypical life history.

A general overview on the (dis-)similarities of the four social interaction types was provided by investigating the overlapping of edges. There it became apparent that individuals who spent more time in stationary vicinity, i.e. out of an arm's reach but within 5 m of their group mates, also spent more time in passive close proximity, i.e. within an arm's reach of their group members. This pattern was found in both social groups. A more detailed view on the similarity of the layers, i.e. the four social interaction types, and the information value of each layer is given by the reducibility analysis. The outcome of this analysis confirmed the edge-overlap finding on the similarity of the stationary vicinity and the passive close proximity layer. However, in addition, it also showed that in the Bilinga group there is high dissimilarity between stationary vicinity and allogrooming. Generally speaking, this means that individuals who spent more time in stationary vicinity to their group mates spent less time grooming their group mates and vice versa. In the Mutamba group, the highest dissimilarity was found between affiliative behavior and passive close proximity, which means that there was a tendency that individuals who performed more affiliative behavior toward their conspecifics spent less time in close proximity to them and vice versa. Since Bilinga group consists of a majority of wild-caught individual and Mutamba group of a majority of captive born individuals this already provides a first indication that the biographical background of the individuals may be important for these differences found in the two social groups. We will come back to this when discussing the outcome of the linear mixed models where we considered the individuals' early life experience.

The reducibility analysis is, furthermore, beneficial in that it shows whether layers can be reduced without losing information. In our case, the analysis revealed that each layer provides information that would be lost by a reduction of layers. The most detailed view is given by the annular visualizations of the eigenvector centralities and versatilities, which measure the importance of group members within a layer and between the layers, and the graphical visualization of the multiplex networks. The annular visualization allows a direct comparison of the eigenvector values of the social interaction types per individual as these values are ordered in rings. In our case, this visualization revealed that some individuals scored high in almost all social interaction types and some individuals scored low in most of the social interaction types. That means that some individuals are much more sociable than other ones. However, this annular visualization also indicates that sociability can only be reliably accessed by looking at different social interaction types simultaneously as some individuals scored low in some social interaction types but high in other ones. A different way of representation is the visualization of the multiplex network where information on not only the strength, but also the density (eigenvector centrality) of the connection of every individual of a group is shown. Here it became obvious as well, that some individuals are more strongly and densely connected to their group mates in most of the social interaction types than are other ones.

This is why we conducted linear mixed models in addition to find out whether the biographic background of our chimpanzees might at least partly explain these differences found and thus emphasize the benefit of taking several interaction types into account. We considered the origin of the interaction partners, i.e. whether they were caught from the wild or born in captivity, the predominant housing condition during their infancy, i.e. whether they were housed more than 2.5 of their first five years of life with or without conspecifics, and the sex. Thus, we differentiated if the sender directed the behavior to a conspecific with the same experience or to a group mate with a different experience as we expected some flexibility in the behavior of captive born and/or predominantly socially housed individuals. Whereas we expected wild-caught and predominantly singly housed individuals to be more impaired by their adverse early life experience and accordingly to be more rigid in their behavior, especially with respect to medium- to high-level social interactions types such as affiliative behavior, allogrooming and passive close proximity.

Indeed, we found the effects of early life experience to be detectable in certain social interaction types. Affiliative behavior was significantly more often exchanged within dyads where both individuals were predominantly housed with conspecifics during their infancy compared to the other dyadic combinations. It occurred least often within dyads consisting of two individuals who were both predominantly housed without conspecifics during infancy.

The same trend was found for allogrooming, though it did not reach significance. This findings stress the importance of social learning, especially during infancy, which requires an appropriate social environment including the mother and peers among other group members (Bard, 1995; Bard et al., 2014; Goodall, 1986; Plooij et al., 1984). Atypically reared chimpanzees lacking tactile stimulation during infancy may not experience the tension-reducing and relaxing effects of allogrooming (Crockford et al., 2014; Schino et al., 1988) but may find physical contact rather stressful, which would be reflected in an avoidance of grooming activities.

Affiliative behavior and allogrooming were both significantly affected by origin as well. Interestingly, affiliative behavior occurred most frequently in captive born individuals towards wild-caught group mates and vice versa, whereas allogrooming was exchanged most often within dyads consisting of two captive born subjects and least often within dyads composed of two wild-caught individuals. This pattern implies that captive born individuals adjust their behavior to their vis-á-vis. While they exchange allogrooming, a high-level social interaction type with each other, they switch to the exchange of a medium-level social interaction type – affiliative behavior including social play and follow – when interacting with wild-caught group mates. This is in line with findings in ex-laboratory chimpanzees where later deprived individuals compensated the lack of social grooming of early deprived conspecifics by time spent on gentle social play with them (Kalcher-Sommersguter et al., 2013). We believe that these results provide an indication of the significance of considering the sociability of the individuals when composing groups, which among other factors is influenced by the individuals' early life history. Socially functioning groups are one key factor to ensure the wellbeing of individuals who are cared for in captivity.

Unexpectedly, we did not find any effect of origin and/or predominant housing conditions during infancy on the toleration of passive close proximity, which we rated as high-level social interaction type. This outcome is in contrast to the results found in early deprived ex-laboratory chimpanzees who were living in solitary confinements for decades before being re-socialized compared to their later deprived conspecifics (Kalcher-Sommersguter et al., 2013) but in line with findings on wild-caught zoo chimpanzees who had been socially reared in comparison to maternally and socially reared captive born individuals (Kalcher-Sommersguter et al., 2015).

With respect to our wild-caught individuals, it is known that there are long-lasting outcomes of childhood trauma reflected in an impaired social adjustment not only in chimpanzees (Bradshaw et al., 2008) but also in humans (Cloitre et al., 2005). However, we did not find our wild-caught chimpanzees to be unable to perceive their social environment as safe and their conspecifics close by as not thrust-worthy (Porges, 2003) as this would have been reflected in an avoidance of close proximity. The impairment of our adult wild-caught chimpanzees and those who grew up without conspecifics with respect to allogrooming may also be based on the lacking stimulation and arousal modulation experienced during early infancy (Field, 1985). Bründl et al. (2020) mapped the development of social interaction and communication traits in a longitudinal sample of wild chimpanzees and found the emergence of social interactions at a mean age of 14 months, with mutual grooming not occurring before around 38 months of age. These findings reaffirm that the first years of life are a crucial period in a chimpanzee's development.

Returning to our hypotheses concerning the multiplex network analysis, where we expected to find correlations between 1) medium- to high-level social interactions types that require the toleration of body contact, i.e. between affiliative behavior and allogrooming, and 2) high-level social interaction types in terms of sociability, i.e. allogrooming and passive close proximity, the following can be said. We could confirm our first hypothesis as we found a high similarity between affiliative behavior and allogrooming, social interaction types that both require at least some physical contact, but not our second hypothesis as we found a high dissimilarity between allogrooming and passive close proximity. Contrary to our expectation, we found the highest similarity between stationary vicinity and passive close proximity. With respect to the effects of the biographical background of our chimpanzees on the different interaction types, we found origin and/or predominant housing conditions during infancy to affect affiliative behavior and allogrooming but not passive close proximity. Beyond that, the sex of the chimpanzees had an effect on affiliative behavior, allogrooming and passive close proximity. Although studies on wild-living chimpanzees found social interactions to be more frequent among males than females, Lehman and Boesch (2008) suggested that this is mainly caused by the habitat conditions including food availability and dispersal patterns. With these factors controlled for by captive management decisions and competition for resources being less of an issue in captivity, the social potential of female chimpanzees becomes apparent (de Waal, 1996). Thus, we were not surprised that our results indicated that social interactions were most frequent within female-female dyads and occurred less frequently within male-male as well as within mixed-sex dyads.

The fact that we found early life experience to have an effect on medium- to high-level social interaction types in term of sociability does not rule out that other factors such as personality (Massen et al., 2013; Úbeda & Llorente, 2015) may play a role as well. Moreover, we do expect an at least partial recovery in a nurturing environment as provided by a rescue center (Llorente et al., 2015).

We think that the full potential of the multiplex analyses can be utilized when used for the investigation of larger social groups of primates as has been done with a group of free-living Geoffroy’s spider monkeys (Pereira et al., 2020; Smith-Aguilar et al., 2018). In case of captive managed groups of primates, the multiplex analyses would for example allow to investigate the exchange of affiliative and agonistic behavior simultaneously and, thus, to detect problematic relationships among certain group. It could also be used to realistically identify outsiders, where the assessment is based on more than one specific social interaction type, which as demonstrated might be an imperfect indicator for sociability on its own. In such a manner, the multiplex approach could be used as a kind of diagnostic tool, supporting care management decisions including decisions on alterations of groups. Furthermore, these multilayer network analyses would also allow to visualize and test complex exchanges of interactions such as whom helps social grooming to gain agonistic support (Hemelrijk, 1994; Schino, 2006) and in whom is allogrooming reducing tension (Schino et al., 1988; Terry, 1970).

In larger social groups, it would also be possible to take the biography of the individuals into account, e.g. whether the sender was maternally or hand-reared, and by creating separate layers for maternally reared senders and hand-reared senders the distribution of a certain behavior could be directly compared. We therefore believe that the multiplex approach may be a helpful tool in the management of larger groups of primates in captivity.

In conclusion, it can be said, that the multiplex analyses are a useful tool for investigating the sociability of, as in our case, former pet and entertainment chimpanzees because different social interaction types can be considered simultaneously. Furthermore, the reducibility analysis allows testing for redundancy, i.e. whether different social interaction types provide an information gain or not. We believe that it is worthwhile to apply this multiplex approach even to small groups of primates, although small sized populations produce certain limitations as, for example, several tools, such as community structure analysis or triadic relationships, provided by the MuxViz software cannot be used when investigating small social groups. Furthermore, the algorithms that differentiate the simple aggregation layer from the multiplex state become relevant and useful in large scale networks with more scattered connections between nodes and layers (see Solé-Ribalta et al. (2014) for differences between the aggregated and multiplex state). The full potential of this multiplex approach could be utilized by applying it to large groups of primates where, e.g. individual characteristics such as the biographic background could be considered when comparing the different social interaction types. Unfortunately, this was not possible in our small groups consisting of seven chimpanzees. With long-term data collected over several years, it would also be possible to expand the number of layers by adding behaviors that occur less often as, for example, agonistic behavior. By considering the direction of these behaviors, the exchange of affiliative and agonistic behavior could be investigated simultaneously. Hence, the multiplex approach can be seen as a promising tool for the management of (larger) groups of primates housed in captivity as it allows to detect problematic relationships among certain group members and individuals who are not involved in any social interactions as all.

B5 Acknowledgements

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Article C: Looking for Visitor's Effect in Sanctuaries: Implications of Guided Visitor Groups on the Behavior of the Chimpanzees at Fundació Mona

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Abstract: The question of 'if and how captive primates are affected by visitors' has gained increasing attention over the last decades. Although the majority reported undesirable effects on behavior and wellbeing, many studies reported contradicting results. Most of these studies were conducted at zoos, typically with little or no control over visitors' actions. Yet little is known about the impact under very controlled visitor conditions. In order to fill this gap, we conducted this study at a primate sanctuary which allows public access only via a guided visit under strict supervision. We observed 14 chimpanzees, recording their behavior during, after and in the absence of guided visits over a 10-month period. Furthermore, we categorized the visitors regarding group size and composition to see if certain group types would produce a stronger impact on the chimpanzees' behavior. As expected, we found visitors at the sanctuary to produce only a neutral impact on the chimpanzees' behavior, detecting a slight increase of locomotion and decrease of inactivity during visitor activities with chimpanzees demonstrating more interest towards larger sized groups. We argue that the impact has been greatly mitigated by the strict visitor restrictions and care strategies allowing chimpanzees a certain control regarding their visibility.

C1 Introduction

The fascination towards wildlife as well as its exhibition can be traced throughout history right up to the present day (Baratay & Hardouin-Fugier, 2004). Animals, especially exotic species, were and are a matter of great interest. Humans want to be able to see as well as learn about animals (Patrick et al., 2007) with records of the existence of zoological collections dating back to the fifteenth century (Kisling, 2000). Primates, particularly great apes, have been one of the most exhibited and popular animals in zoos (Moss & Esson, 2010). Several survey studies demonstrated that the attraction towards monkeys and great apes often surpasses that of other species (Cantin & Prescott, 1980; Morris, 1962; Surinova, 1971). Over the last few decades, an increasing number of zoos changed from being purely entertainment-orientated to a more modern approach with education, conservation and research as primary goals (Conde et al., 2011). These new responsibilities might be achieved via educational activities, captive breeding programs and management of wildlife within the zoo installations, (Tribe & Booth, 2003) or in some cases in-situ conservation efforts consisting of reintroduction programs or financial support of field conservation projects (Ancrenaz et al., 2018; Breuer et al., 2018).

Zoos have the capacity to reach an enormous number of people and influence their perception of animals as well as inform about their needs and the dangers they face in their natural habitat, mostly caused by human activities. Regardless of the mission statement or general objective of an animal housing organization, their success depends greatly on the wellbeing and health state of their animal collection. Thus, while educating the public about the influence of human activities on wild populations, it seems logical to also have in mind the possible effects humans have on captive populations.

The conservation status of nonhuman primates, especially great apes, is critical. Almost 60% of primate species are classified as endangered, with all great apes species being listed as either vulnerable, endangered or critically endangered (Estrada et al., 2017). The latest reports from the Convention on International Trade in Endangered Species (CITES) state a global primate trade of 450,000 live animals during 2005–2014 (Estrada et al., 2017). Some reports estimate that 22,000 wild great apes were lost between 2005 and 2011 (Stiles et al., 2013). Furthermore, the number of primates confiscated from the pet and entertainment industry, laboratories and illegal trafficking continues to grow (Baker et al., 2013). Due to health conditions, financial limitations, habitat destruction, land-cover changes and industry-driven deforestation, many of these confiscated animals are being transferred to zoological parks or animal rescue centers as their only option (Stokes et al., 2018). Others, often even legally obtained and housed, end up at zoos or sanctuaries after becoming a ‘surplus’, no longer useful for their original commercial purpose (Grimm, 2017).

European and North American primate sanctuaries mostly take in primates used formerly in the biomedical research, entertainment and pet industries. One currently accepted definition of an animal sanctuary in the United States comes from the Captive Wildlife Safety Act (CWSA) of 2007 (‘Captive Wildlife’), which is specific to big cats. According to this document, a sanctuary is an accredited, non-profit institution that does not propagate, commercially trade, allow direct contact or breed with the animals in their care (Kagan, 2017). These requirements also form a part of the North American Primate Sanctuary Alliance (NAPSA) definition of a true sanctuary. NAPSA goes even further and adds: “animals are not removed from the sanctuary for exhibition, education, research, or commercial purposes; public visitation is limited; animals are not trained to perform; the organization is fiscally responsible with a goal of providing lifetime care for sanctuary residents; and the sanctuary advocates for the species they care for” (Fultz, 2017). The European Alliance of Rescue Centers and Sanctuaries (EARS) uses a similar definition, uniting NGOs dedicated to the rescue and rehabilitation of a variety of species, not only limited to primates.

Nowadays, wildlife sanctuaries not only house and care for rescued animals, but also strive to advocate for improved captive animal welfare conditions, law enforcement, raising awareness and in-situ conservation (EARS, 2019). Some sanctuaries, such as the Fundació Mona, additionally conduct non-invasive research focused on animal welfare (Llorente et al., 2015) and education programs in the form of guided visits and academic programs (Llorente et al., 2014). These efforts to share information with the public and professionals are orientated towards reducing harm and threats to captive and wild primate populations. Yet some entities argue against displaying rescued animals to the public, due to a concern about the potential negative impact on the welfare of these animals. These concerns are addressed in the more common sanctuary definitions mentioned above, with remarks such as "not to use animals for commercial purposes" or "only limited public visitation".

Behavioral studies related to human–animal interactions have become more popular since the 1970s, typically as attempts to quantify the welfare impacts of humans on zoo animals (Hosey, 2000; Smith, 2016). Many such studies focused on primates housed in a zoo setting, and reported contradicting results (Davey, 2007). Whereas some studies concluded that visitor presence increases the animals' stress levels (Rajagopal et al., 2011) and leads to behavioral changes such as increased agonistic or stereotypical behaviors and decreased intra-group affiliations and exploration (Cooke & Schillaci, 2007; Davis et al., 2005; Mitchell et al., 1991; Sekar et al., 2008), others suggest human–animal interactions to have a positive effect functioning as environmental enrichment (Cook & Hosey, 1995). Some of these contradictions might be explained by studies suggesting that the response to human presence may vary among individuals (Collins & Marples, 2016; Pérez-Galicia et al., 2017) and can be mediated by personality (Polgár et al., 2017) and thus can be difficult to detect.

Considering the high amount of attention this topic received in zoo settings, the lack of information on sanctuary housed animals is surprising and regretful. Primate sanctuaries aim to rehabilitate, and socially integrate rescued primates, by offering an environment suitable to express species-typical behaviors, allowing for a slow recovery and introduction in an adequate social network. As such, it seems extremely important to assess whether non-familiar human–animal interactions can delay, disrupt or distort subject's rehabilitation and their state of wellbeing. In zoos as well as some primate rescue centers, animals are confronted with both familiar (caregivers, volunteers and researchers) and unfamiliar humans (visitors).

However, differences in the enclosure designs and visitor access strategies are expected to influence the impact of visitors on animals greatly. Enclosures can be designed to maximize the possibility of spotting animals to increase the visitor's satisfaction or to allow animals to easily retreat to off-display areas avoiding a forced on human presence. Visitors might be allowed to roam freely without any supervision or can be restricted to a guided visit under strict supervision (Davey, 2006; Sherwen et al., 2015). Visitors might be encouraged to feed or interact with animals while other organizations might follow a strict no human–animal interaction protocol (Kreger & Mench, 1995). We expect that such factors influence the effects non-familiar human presence might have on the animals and believe this could be a possible explanation for the controversial results from previous studies.

With much information already available from zoos, with little to unrestricted visitor access towards the animals, the aim of this study is to gain insights on the human impact in a sanctuary setting, being typically much more concerned about human interferences.

At Fundació Mona, visitors have a very restricted access to the animals, favoring the animal's privacy over the visitor's freedom of movement and action. Animals are exposed for only a limited number of hours a day with all visitor groups being guided and following strict behavioral protocols to minimize non-familiar human influence.

The general objective of this study is to test if and how the visitor presence has an impact on the chimpanzees housed at Fundació Mona, considering its very controlled visitor activity. For that purpose, we split our observation data depending on the visitor presence as "absence of visits", "during a visit" and "after a visit", expecting to find only mild alterations in their behaviors. Furthermore, we want to assess if certain aspects of visitor groups increase a possible impact on the chimpanzee's behavior, by taking group size and composition into account.

C2 Materials and Methods

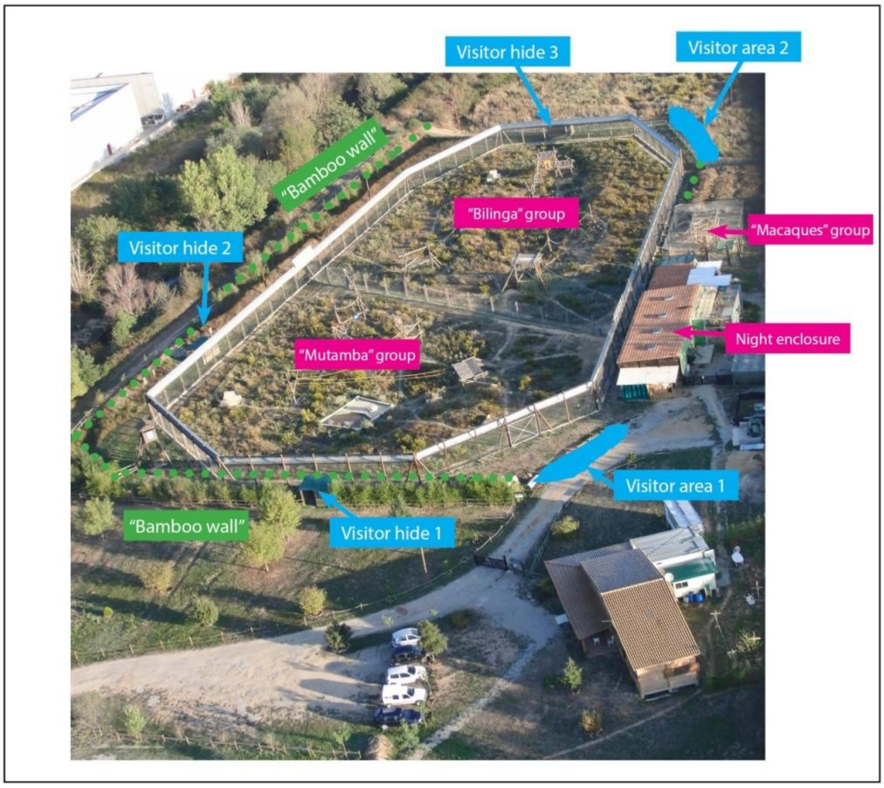
C2.1 Study Site and Animals

This study has been conducted at Fundació Mona a primate rescue center located in Riudellots de la Selva (Girona, Catalonia, Spain). Fundació Mona is member of the European Alliance Rescue Centers dedicated to the rescue and rehabilitation of chimpanzees (*Pan troglodytes*) and Barbary macaques (*Macaca sylvanus*) since 2001. At the time of this study, a total of 14 chimpanzees were housed in two social groups at the center. Each group had a habitat consisting of an outdoor and two to three indoor areas. At night time, chimpanzees were confined to the indoor areas while during day time had either access to all areas or were confined to the outdoor areas, depending on the weather conditions and maintenance activities.

The chimpanzee outdoor area consists of two separate but adjunct enclosures, measuring 2420 m^2 and 3220 m^2 respectively, with a total perimeter of 191 m. The enclosures are surrounded by a steel fence and electrified wires for security reasons. Both enclosures were equipped with climbing structures, such as wooden platforms, towers and other structures as well as climbing ropes, enrichment devices, hammocks and ad libitum water dispensers. The outdoor area was a naturalistic environment maintaining the original ground substrate and Mediterranean vegetation. In order to provide certain privacy for the chimpanzees, a thick wall of vegetation mostly consisting of bamboo (*Phyllosta chysaurea*) has been planted around the enclosures limiting the visitor visibility to two open space and three “hidden” viewpoints (Fig. C1). All visitor areas are separated by at least a two-meter distance from the animal fencing, making physical interactions impossible.

Figure C1

View of the animal facilities and visitor areas at Fundació Mona



Note. Animal habitats labeled in pink; Visitor viewpoints labeled in blue; Bamboo visibility block labeled in green.

All 14 chimpanzees (*Pan troglodytes*) housed at the sanctuary, split in two mixed-sex groups (Bilinga group 4M3F, Mutamba group 5M2F), have been observed for this study (Table C1). Most of the primates housed at the center were previously held as pets or used in the entertainment industry before being confiscated and handed over to Fundació Mona. New rescues are being housed separately from conspecifics for several weeks before starting their integration into social groups. The time needed for the adaptation to their new home, the physical rehabilitation and social integration differs for each individual. Initial treatment and care protocols are specifically developed for each individual. A strict hands-off policy is being maintained at the center, with physical contact only allowed for a few qualified staff members for rehabilitation and veterinary purposes.

The chimpanzees were fed at least four times per day and water was provided ad libitum in the outdoor and indoor enclosures. The diet consisted mainly of seasonal vegetables and fruits, boiled rice, a variety of dried fruits, seeds and some protein-rich food items. A big portion of their diet was scattered and hidden in the outdoor areas in order to encourage foraging behaviors. Animals were routinely environmentally stimulated through feeding (Llorente & Campi, 2014), social (Ortin et al., 2014), sensorial (Sauquet et al., 2014) and cognitive (Rodriguez Escalada et al., 2014) enrichment. Interactions with familiar humans (staff members) were maintained at a minimum, with care givers approaching the animals only during feeding times or care management activities in order to not interrupt but encourage intra-group interactions.

Table C1

List of biographical information on all chimpanzees housed at Fundació Mona

Name	Gender	Birth Year	Arrival at Mona	Group
Bongo	Male	2000	July 2002	Mutamba
Waty	Female	1997	June 2002	Mutamba
Marco	Male	1984	March 2001	Mutamba
Charly	Male	1989	March 2001	Mutamba
Africa	Female	1999	May 2009	Mutamba
Toni	Male	1983	August 2001	Mutamba
Juanito	Male	2003	January 2005	Mutamba
Bea	Female	1985	May 2012	Bilinga
Coco	Female	1994	May 2012	Bilinga
Victor	Male	1982	May 2006	Bilinga
Nico	Male	2001	March 2004	Bilinga
Tico	Male	1987	July 2005	Bilinga
Cheeta	Female	1990	November 2015	Bilinga
Tom	Male	1985	June 2011	Bilinga

C2.2. Visitor Strategies Applied at the Study Site

At the sanctuary only guided visits were conducted to give the public the possibility to see the chimpanzees while keeping possible disturbance for the primates to a minimum. Free roaming or unsupervised visitors were strictly forbidden. During the duration of this study organized scholar groups would visit the center only on week days while family and adults could participate in joined guided visits throughout the weekend. All visitor activities were limited to the morning hours and finished before 14:30. Although a visit could last between two to four hours, visitors would only spend about 1–1.5 h in areas close to the animals, potentially influencing the chimpanzees. All other parts of the visit, such as presentations or workshops were conducted either indoors or far off the animal areas. Trained visitor guides would inform participants before entering areas close to the animals about behavioral rules, including (1) restriction to cross any barrier in order to approach the animal installations; (2) not to try to interact, call the attention, talk to or disturb the animals in any way; (3) restriction of not eating, drinking or smoking in sight of the animals; and (4) trying to feed any animals during the tour. The main tasks of a visitor guide were to educate visitors about the needs, threads and dangers wild and captive primates are currently facing as well as to assure that visitors would abide to the visitor protocol.

C2.3. Data Collection

Data on their behavior were collected only in the outdoor areas once access was granted to the chimpanzees, between 10:00 AM and 15:00 PM (slight variation due to weather conditions). We excluded observations between 15:00 PM and 19:00 PM as more than 90% of this data were labelled as “in absence of visit” and chimpanzees might act differently in the afternoon compared to the morning hours independently from visitor activities. Data were recorded from observation towers located between the outdoor enclosures and the visitor walk-around. Chimpanzees were already habituated to the presence of observers due to ongoing monitoring projects. Data on the chimpanzees' behavior and visitor presence were recorded from March 2018 until January 2019, resulting in 38,700 recorded behaviors, excluding when animals were not visible or the behavior was obscured (average of 2766 ± 710 behaviors per individual). Observations were equally distributed throughout the week and across the morning hours. Only data from trained observers were used for this study after successfully passing the inter-observer reliability test (agreement ≥ 85%) with the head of research at the center (M. Llorente).

Data were coded using the instantaneous scan sampling method (Martin & Bateson, 1993) every two minutes on all chimpanzees present of one group for 20 min. Observers used tablets with the ZooMonitor data scoring software (Ross et al., 2016) programmed with the sanctuaries monitoring ethogram, consisting of 18 behavior-related (Table C3) and three visitor-related (Table C2) categories.

Table C2

List of parameters recorded for visitor group categorization

	Visit Group Type [1]	**Families, Scholars**
Visitor Related Variables	Visit group size [2]	Small (<15)
		Medium (15–30)
		Big (30–52)
	Visit condition [3]	No Visit
		During a visit
		After a visit

Note. [1] Group type differentiates between organized "Scholars" groups consisting of pupils with a small number of adult patrons and "Families" consisting of Families and adults that are unfamiliar to each other. [2] Group size intervals are based on the tendency of the sanctuary of organizing visits, typically having one guide for up to 30 participants and trying to avoid visitor groups of more than 30 people. [3] Condition is based on the presence of visitors at the viewpoints located around the enclosures and "after a visit" was defined as the time period up to 20 min (full observation session) after the visit group left the observed groups enclosure surrounding.

Table C3

List of behaviors recorded using two minutes instantaneous scan sampling

Behavior Variables	**Individual**	Inactivity, Feeding, Locomotion, Manipulation, Self-Directed, Solitary Play, Abnormal, Human Interaction, Other Individual
	Social	Grooming, Social Play, Other Affiliative, Agonistic Dominance, Agonistic Submission, Other Agonistic, Socio Sexual
	Other	Not visible

Based on the behavioral records we calculated two welfare indices previously used by Llorente et al. (2015). We calculated the Behavioral Competence Index (BCI), which contrasts individual desirable behaviors (positive) against individual not desirable behaviors (negative in excess), using the following formula:

$$\text{BCI} = \frac{\text{Positive individual behaviors} - \text{Negative individual behaviors}}{\text{Positive individual behaviors} + \text{Negative individual behaviors}}$$

We considered feeding, locomotion, manipulation and individual play as positive individual behaviors; and abnormal, inactivity and self-directed as negative individual behaviors. Although inactivity and self-directed behaviors belong to the normal chimpanzee ethogram, we considered a high frequency of these behaviors as not desirable.

We calculated the Social Preference Index (SPI) which contrasts the sum of all individual behaviors against all social behaviors, using the following formula:

$$\text{SPI} = \frac{\text{Social behaviors} - \text{Individual behaviors}}{\text{Social behaviors} + \text{Individual behaviors}}$$

Values of both indices range between −1 and +1. Similar indices have proved to be useful in other behavioral studies (Hopkins et al., 2007).

The definition for the behavior “human interaction”, having a somehow misleading name, does not refer to humans interacting with the chimpanzees, but rather the chimpanzees exhibiting one of the following reactions: (1) agonistic display directed towards location of visitor group; (2) following the visitors and their approximate trajectory (while out of sight); (3) approaching the fence closest to the visitors directing attention towards location of visitor group; or (4) calling visitors attention.

C2.4. Statistical Analysis

We converted the absolute frequencies of behaviors into ratios, whilst excluding the "not visible" entries from the total frequency of observed behaviors. We than calculated the data points for the statistical analysis based on the observed behaviors for each chimpanzee per contrasted visitor parameter. For the first set of analysis we obtained three values for each behavior per chimpanzee and visitor condition (none, visit, after). For the second set of analysis we further included the visitor group aspects (size, type). However, in order to maintain a high quality, we excluded all data points from this study that were calculated with less than 40 recognizable behaviors.

To demonstrate the general impact visitors have on the animals we used SPSS to compare chimpanzees' behaviors (inactivity, locomotion, intra-group affiliative and intra-group agonistic interactions, abnormal & self-directed behaviors) and welfare indices (SPI and BCI) during, after and in the absence of visitors. Friedman ANOVA and Wilcoxon signed rank test have been applied with an alpha level of <0.05 to evaluate these effects.

Furthermore, we ran generalized linear mixed models (GLMMs) using the "lme4" package (Bates et al., 2015) in R, using only records of the chimpanzees behavior during and after visitor presence in order to gain a better understanding on which specific aspects of the visitor groups cause alteration of the chimpanzee's behavior. We ran normal GLMMs with an identity link function after visually inspecting the residuals normal distribution in the QQ plots (Figures SC1 and SC2). GLMMs were created with the same model composition (random and fixed factors), only changing the depended variable for each model. We used the individuals "ID" and "Group" as random factors (Table C1) and "Visit condition", "Visit group type" and "Visit group size" as fixed factors (Table C2). We included "Group" as a random factor, suspecting that the location and/or design of the chimpanzee group's respective installations might influence the visitor impact. Model 3 with human interaction as a dependent variable was the only exception, which excluded "Visitor condition" as a human interaction towards visitors could not occur “after a visit” and would result in a false significance.

We chose to use SPI, BCI, human interaction, intra-group affiliative and agonistic interactions, locomotion, inactivity and abnormal & self-directed behaviors as dependent variables. In all models we tested that the full models, containing all fixed factors, were significant improvements over the null models, without fixed factors, by applying the likelihood ratio test. When full models differed significantly from the null models, we applied likelihood tests on the full model to obtain a p-value for each fixed factor by using the R function ANOVA (Satterthwaite’s method) (Dobson, 2001). For the fixed factor “Visit group size” with three categories (small, medium, big) we applied a multiple comparison of means post hoc test with Tukey Contrast and Holm–Bonferroni p-value adjustment to verify the significance between the categories.

We tested for multicollinearity between all fixed factors by calculating the variance inflation factor (VIF) using the “car” package in R (Fox & Weisberg, 2011). All VIFs calculated for our three fixed factors were below 1.1, indicating that our fixed factors were not correlated.

C2.5. Ethical Note

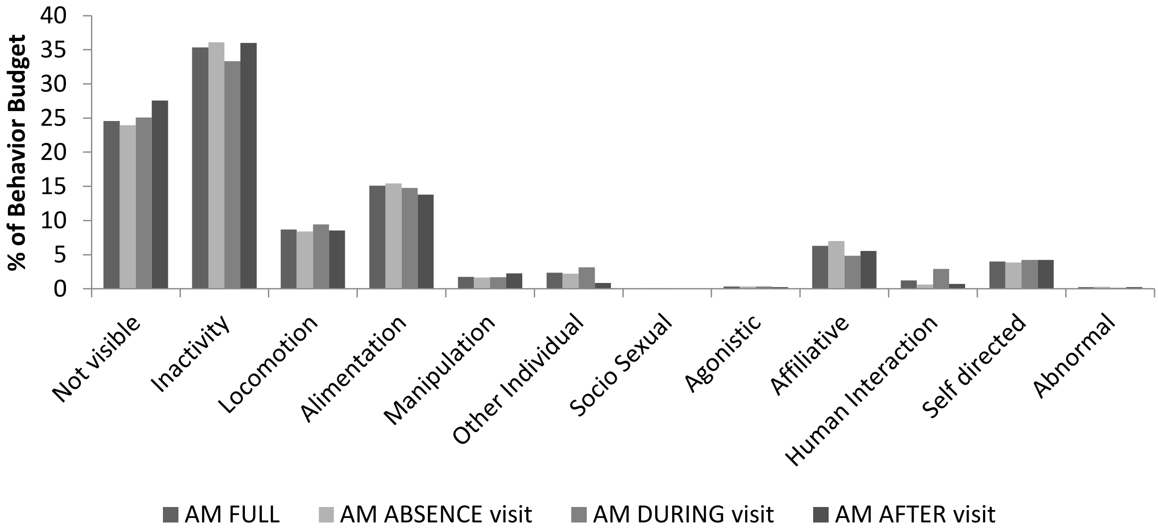
This research was conducted in accordance with all national and intuitional guidelines for the care and management of primates established by Fundació Mona, Association for the Study of Animal Behavior Society and the Spanish Government (RD 53/2013).

C3 Results

As can be observed by looking at the differences between the behavioral budgets calculated, first globally then for each visitor condition (none, visit, after), no drastic alterations were detected. We included “not visible” (described as either “behavior obscured” or “individual not visible”) in the graphic representation (Fig. C2) in order to demonstrate the capacity of the chimpanzees to choose not to be seen by humans (familiar and non-familiar alike). However, we did not include “not visible” in any of the statistical analysis, as we were often unable to discern if chimpanzees chose to spend time in areas not visible to visitors alone or visitors and observers at the same time (due to differences in standpoint from which observers and visitors watched the chimpanzees).

Figure C2

Chimpanzee behavior budget, based on the observation records (AM: from 10:00–15:00) used in this study



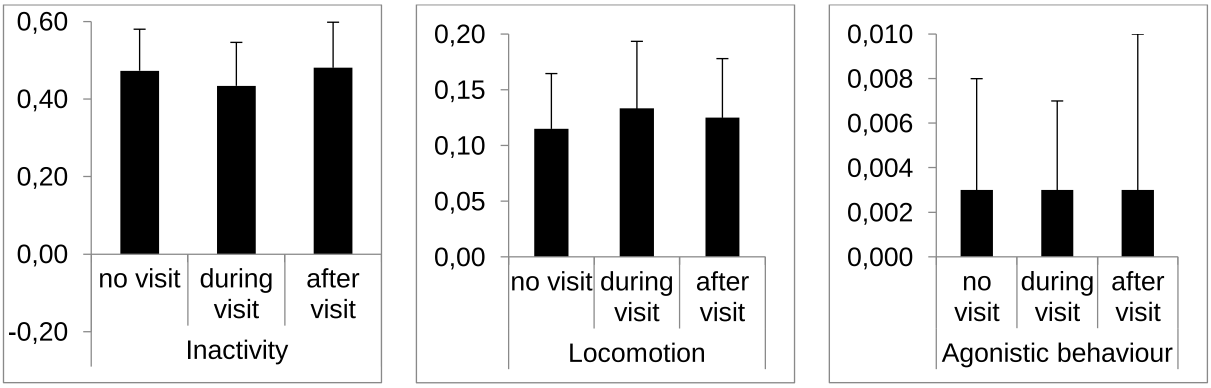
Note. Behavior budget were calculated independently first using all available data (AM FULL), but also calculated for each Visitor condition (none, visit, after), to allow a visual quick overview.

C3.1. Impact of Visitor Presence on Chimpanzee Behavior

For this analysis, we compared the dependent variables between the three possible conditions of visitor presence ((Table C4) none, visit, after). We obtained significant differences in inactivity (χ^2 = 11.286, p < 0.01), locomotion (χ^2 = 9.571, p < 0.01) and agonistic intra-group interactions (χ^2 = 6.167, p < 0.05). Chimpanzees were significantly less active after a visit, compared to during a visit and spend more time on locomotion during a visit than in the absence of visitor groups. Although agonistic intra-group interaction scored a significant result, we could not detect any clear differences between the three categories, which might be due to the relatively infrequent occurrence and high individual variations between individuals (Fig. C3).

Figure C3

Averages of inactivity, locomotion and intra-group agonistic behavior according to visitor presence (none, visit, after)



The BCI and abnormal and self-directed behaviors did not seem to be affected by the visitor condition, while the SPI and affiliative intra-group interactions, although not producing any significant results, exhibited certain tendencies of decreased social activities during visits compared to after as well as during the absence of a visit.

Table C4

Dependent variables affected by the visitor presence condition, comparing the three sub categories (none, visit, after)

			Wilcoxon Test					
	Friedman Test		**None-Visit**		**Visit-After**		**None-After**	
Dependent Variables	**Chi-Square**	***p***	**Z**	***p***	**z**	***p***	**z**	***p***
BCI	2.714	0.257	–	–	–	–	–	–
SPI	5.571	*0.062*	2.794	0.005 **	1.287	0.198	2.291	0.022 *
Inactivity	11.286	**0.004** **	1.915	*0.056*	2.731	**0.006** **	0.910	0.363
Locomotion	9.571	**0.008** **	2.919	**0.004** **	1.726	*0.084*	1.224	0.221
Affiliative	5.538	0.063	2.830	0.005 **	1.572	0.116	1.992	0.046 *
Agonistic	6.167	**0.046** *	0.245	0.807	0.652	0.515	1.503	0.133
Abnormal & Self-Directed	1.714	0.424	–	–	–	–	–	–

Note. * $p \leq 0.05$, ** $p \leq 0.01$.

C3.2. Influence of Visitor Group Aspects on the Chimpanzees Behavior

Here we intended to demonstrate that specific aspects like the size and the type of visitor groups might alter the magnitude of the impact during and after visits. We decided to use GLMMs in order to control for repeated observations of the same individual under different visitor conditions and aspects, as well as the possibilities that the groups could receive more or less visitor attention depending on the enclosure locations. We created a total of eight models (Table C5), but only two models (3 and 5) proved to be significantly better fits in order to help explain the possible alterations of the depend variables.

Table C5

List of all generalized linear mixed models (GLMMs) and the results from the likelihood ratio test between the respective null and full models

GLMM Model	Dependent Variable	Chi-Square	Df	*p*
MODEL 1	SPI	6.336	4	0.176
MODEL 2	BCI	5.447	4	0.244
MODEL 3	Human interaction	29.623	3	**0.000 *****
MODEL 4	Inactivity	6.684	4	0.154
MODEL 5	Locomotion	14.044	4	**0.007 ****
MODEL 6	Affiliative	7.654	4	0.105
MODEL 7	Agonistic	8.035	4	0.090
MODEL 8	Abnormal & Self-Directed	8.022	4	0.091

Note. All models included the individuals ID and group as random factors and visitor condition (visit, after), visitor group size (small, medium, big) and visitor group type (families, scholars), with the exception of Model 3 (Human Interaction) which was excluding the fixed factor visitor condition. ** $p \leq 0.01$, *** $p \leq 0.001$.

After discarding all models that failed to show a significant improvement to explain de dependent variables (Table C5), we continued further statistics only with models 3 and 5. We found significant differences in locomotion for size and type (Table C6) with chimpanzees engaging significantly more in locomotion with smaller than bigger visits (Table C7) as well as increased locomotion with family compared to scholar visits (Fig. C4).

Figure C4

Behaviors (locomotion and human interaction) of the chimpanzees significantly affected by aspects of the visitor groups with a confidence interval of 95%

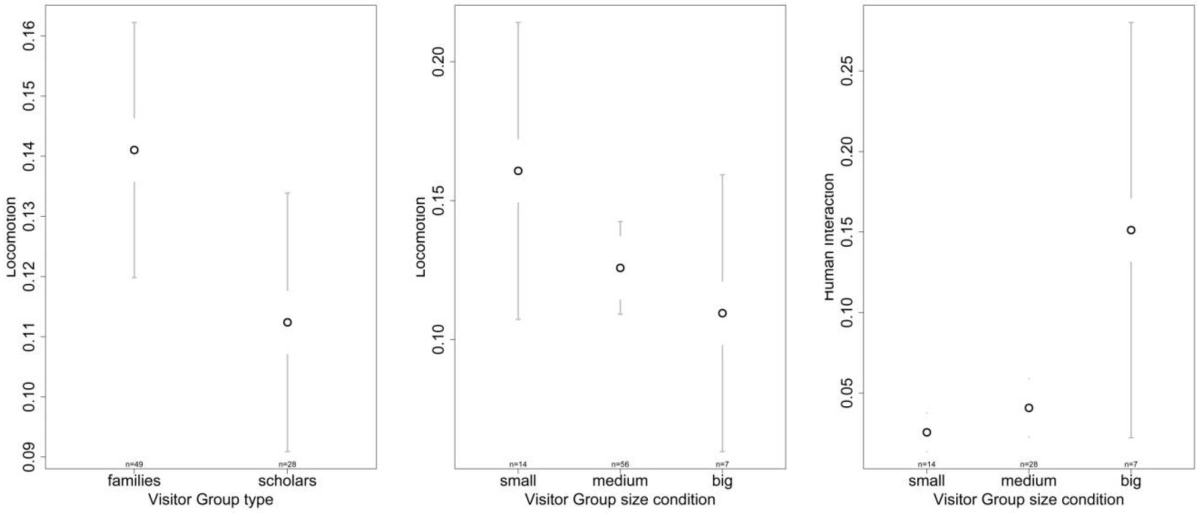


Table C6

Behavior of the chimpanzees significantly affected by aspects of the visitor groups

				Fixed Factors (Visitor)		
GLMM	**Random Factor**	**Dependent Variable**		**Condition**	**Size**	**Type**
MODEL 3	ID, Group	Human interaction	F	−	15.101	2.658
			df	−	2	1
			p	−	0.000 **	0.108
MODEL 5	ID, Group	Locomotion	F	0.359	3.295	5.730
			df	1	2	1
			p	0.551	0.044 *	0.020 *

Note. * $p \leq 0.05$, ** $p \leq 0.001$.

Table C7

Post hoc test for comparison between sub categories of the visitor group size (small, medium, big)

			Predictors		
GLMM Model	Dependent Variable		Medium—Big	Small—Big	Small—Medium
MODEL 3	Human Interaction	z	−5.085	−5.175	−0.741
		p	0.000 **	0.000 **	0.459
MODEL 5	Locomotion	z	1.712	2.562	1.237
		p	0.174	0.031 *	0.216

Note. * $p \leq 0.05$, ** $p \leq 0.001$.

C4. Discussion

Humans in the past and today have a great desire to see animals up close. Zoos and sanctuaries facilitate a quick and easy way to do so, without the need for lengthy and costly travels in order to see them in their natural habitat. This attraction might originate from personal curiosity, the simple wish to be entertained or the desire to learn about animals and possibly support causes to help specific individuals or species (Altman, 1998; Carr & Cohen, 2011). Regardless of the reason for visiting, modern zoos and sanctuaries have the potential and responsibility to educate visitors and actively raise awareness about the needs and threats many species currently face, converting visitors into part of the solution rather than being part of the problem. For the great majority of endangered species, like chimpanzees, this includes explaining that human actions pose the biggest threat (Cowlishaw, 1999). However, allowing public access to animal collections and converting these animals into ambassadors for animal welfare and conservation causes, does not mean that their own wellbeing can be ignored. On the contrary, it should be compensated for by an additional effort to provide the best care possible and shield them from potentially negative stimulations.

Many aspects of a captive environment need to be controlled, designed and well organized to provide a high level of welfare (Brando & Buchanan-Smith, 2017; Mellor, 2016). The more actively used or present an element or aspect in the chimpanzee's day to day life, the more important it seems to monitor and, if necessary, control its effects on the animals. Thus, we argue that the effects of non-familiar human presence (visitors) should be monitored and regulated.

If we summarize the results of this study in simple terms of "how visitors affected the chimpanzees housed at the sanctuary", we would report the impact as neutral or ambivalent, with no clear indications of any positive or negative orientated alterations in their behavior budget and in extension wellbeing. This study has been conducted on purpose at a sanctuary with very strict care and welfare strategies as well as a very controlled and restricted visitor access, favoring the animal's privacy and mediation of visitor effects. Thus, we expected to find little to no significant alterations in their behavior, which has been confirmed by our data.

Although the visitor activity at our study has to be considered a very controlled condition, we wish to emphasize the possibility of individual differences regarding the animals' perceptions and in continuation reaction to stimulations such as visitor presence. These differences, detectable as variations in intensity of interest in visitors and stronger/weaker changes to their behavior budget might be explained by the individuals´ personality (Gartner & Weiss, 2018; Polgár et al., 2017) or past traumatic experiences (Freeman & Ross, 2014; Kalcher et al., 2008; Vandeleest et al., 2011). While in this study we did not wish to investigate individual differences, we were aware of this possibility and thus controlled these through the use of random factors (ID, group) in our GLMMs, to assure that our results would not be affected. This seemed especially important due to our relatively small sample size of only 14 chimpanzees in two groups.

In our first set of analysis, comparing the chimpanzee’s behavior budget between the absence of visitors, while being exposed to visitors and shortly after visits, only three behaviors were affected. Locomotion increased during visits compared to absence of visitors and inactivity decreased during visits compared to after a visit. Activity levels are frequently reported to change in visitor impact studies, especially in primates (Queiroz & Young, 2018). Hosey reported locomotion and inactivity to increase drastically in several studies of different primate species (Hosey, 2008). Others argue that an increase in locomotion should be taken seriously as it could be a first step towards developing stereotypical behaviors such as pacing (Poirier & Bateson, 2017). However, we found only an average increase of 1.8% in locomotion and average decrease of 4.8% in inactivity. Still, even a small increase in locomotion could be argued to be a sign of agitation. Nevertheless, as locomotion in our ethogram only represents the change of location, not including pacing (which was recorded as abnormal behavior in this study) or human interaction (animals moving or positioning themselves close to or following the trajectory of visitor groups), we would not identify this as an agitation-triggered response. We argue that neither of those behavioral alterations would be considered an extreme reaction or would suggest a clear negative or positive impact on the animal’s wellbeing. Intra-group agonistic interaction was the third behavior initially detected as significantly affected. However, the following Wilcoxon signed rank test failed to confirm any significant difference between during, after or in absence of visits. This false positive was most likely caused by the extremely low occurrence of agonistic behaviors with only 0.3% ± 0.5% of their behavior budget and the fact that several animals were never observed to engage in agonistic behaviors during and after visits.

Regarding the analysis of visit specific factors “visit group size” and “visit group type” during and after visits, only two out of eight models were significant improvements over the respective null models. This implies that none of our recorded visitor parameters were suited to explain any changes in the SPI and BCI, inactivity, affiliative and agonistic behaviors or abnormal and self-directed behaviors. Hence, we have to assume that the effects of the visitor group attributes were either too mild to be detected in our sample or that other variables, not taken into account in this study, might have stronger influences. Only the full models of locomotion and human interaction were significantly better fits than their corresponding null models. Locomotion increased significantly during family visits compared to scholar visits and decreased significantly while being exposed to big sized visits (more than 30 people) compared to small sized visits (less than 15 people). As mentioned before, the increase of locomotion to the small extent found in our sample does not indicate any welfare related problems. However, we were surprised to find that this increase occurred due to small sized visitors groups, considering how most studies typically reported bigger crowd sizes provoked increased wounding (Hosey et al., 2016), elevated stress levels (Scott et al., 2017) or undesirable alterations of behaviors (Fernandez et al., 2009).

The human interaction model, only containing "visitor group size" and "type" as fixed effects, showed a significant increase during big visitor groups. This indicates a stronger attraction or interest in humans when group size exceeded a total of 30 people. This could be considered an interruption of their normal routine. However, considering that human interaction behaviors only made up 3.5% of the chimpanzees' activity budget during visits, this should be regarded a minor alteration of their activity budget. Furthermore, out of all observed interactions from chimpanzees towards visitors, only 8.1% were categorized as negative, mostly consisting of agonistic displays directed at visitors, while all others were labelled as neutral/positive, consisting of approaching and following the visitors or closely observing visitor groups. Nevertheless, the fact that human interaction behaviors augmented with increasing group size coincides with observations on gorillas (Wells, 2005) and orangutans (*Pongo borneo*) (Birke, 2002) who exhibited stronger reactions towards bigger compared to smaller crowds at zoos.

We believe to have evidenced that a sanctuary can be open to the public, with rescued chimpanzees as ambassadors to promote animal welfare and conservation without necessarily affecting the chimpanzee's wellbeing if certain conditions, such as adequately restricted visitor strategies carefully designed enclosures and appropriate care management strategies, are met.

C5 Conclusions

Davey pointed out in a review about visitor effects how contradictory the results of past studies were. Although the majority of studies conclude visitor effects to be either stressful or at least ambivalent, it seems clear that more aspects have to be taken into account (Davey, 2007). While it seems obvious to expect differences between species (Chamove et al., 1988) or even individuals, we want to emphasize the importance of parameters that are being controlled by the organizations. This includes restricting visitor's freedom of movement and actions, and providing the animals with means to avoid visitor presence. We believe that, in many cases, contradicting study results could be explained by looking at how the visitor activities were organized and which strategies were used to buffer and reduce potential visitor effects. Thus, we deduce that the visitor impact turned out to be very mild at Fundació Mona due to the following strategies applied by the sanctuary:

Allowing the animals, a certain amount of choice towards de-visibility, by creating off-display areas and maintaining an adequate buffer distance between enclosures and visitor areas. Blaney and Wells described a reduction of aggressive and abnormal behaviors after installing a camouflaged netting around a gorilla (*Gorilla gorilla*) enclosure (Blaney & Wells, 2004). Several studies reported favorable improvements after remodeling enclosures with the goal to provide animals with retreat possibilities (Anderson, Benne, et al., 2002). A study on cotton-top tamarins (*Saguinus oedipus*) reported significant improvements in social behaviors for groups being housed off-display compared to groups being visible to zoo visitors (Glatston et al., 1984). At our study site, a dense wall of vegetation was installed on long stretches around the enclosure to reduce visibility (both ways). Furthermore, enclosures were designed in a way to allow chimpanzees to retreat without being seen and to keep their distance from visitors if desired.

Restricting and supervising visitor's movements and actions, making active intents to interact or react to animals impossible. To our knowledge most studies have been conducted in zoos with visitors roaming freely and unsupervised. To us, it seems that this might be the biggest difference between our study site compared to most studies that have reported negative reactions. This would suggest that the quality might be more important than the quantity (Fernandez et al., 2009). With quality we refer to the visitor's attitude towards the animals, in terms of acting respectful, abiding visitor regulations, attempting not to disturb or startle animals. In addition to the strict visitor protocol put in place at Fundació Mona, the visitor guides have the important task of passively and actively preventing visitors from disturbing or attempting to interact with the chimpanzees. Parker et al. tested (Parker et al., 2018) the efficiency of "do not feed" signs at zoos and reported that while animal feeding decreased, other behaviors such as attempts to touch the animals increased at the same time. This study showed that visitors, although possibly being informed not to disturb or interact with the animals, when allowed to move freely and unsupervised close to the habitats will most likely cause disturbances for the animals. That being said, it might have been interesting to also collect information on the age of visitors, the ratio between adults and children in each group and especially taking the presence of toddlers and infants into account. While the majority of children in scholar groups ranged between the age of four and 12, with groups consisting nearly entirely of children, the adult to children ratio in family groups could vary greatly and children of all ages could be present (including <4 years of age). Assuming that younger visitors and toddlers are less likely to understand and follow strict behavioral rules and are more likely to produce sporadic loud noises or unpredictable movements which could potentially startle animals, they might affect animals more strongly. As such information was not recorded in our observation phase, we have no clear results confirming this suspicion, but wish to state this as one possible explanation to why locomotion increased more strongly during family groups than scholar groups. Accordingly, we suggest controlling for visitor age and likelihood to comprehend and follow visitor guidelines in future study designs.

We argue that zoos and sanctuaries have a great potential to influence people, raise awareness and promote conservation programs, but strongly advise strict monitoring and regulation of visitor activities to ensure the wellbeing of the displayed animals.

The visitor impact on exhibited animals depends greatly on both the actions of the visitors as well as the capacity and possibilities of the animals to control their environment and cope with the situations. That being said, it is the sheltering organization that has the power to restrict and guide visitors' actions and it has to offer the animals a certain amount of choice and control.

Although this study was conducted only on chimpanzees, we are convinced that our conclusions would be valid for a variety of other species as well. Thus, we hope and strongly suggest a reproduction of this study with other species in the future.

C6 Acknowledgments

The authors thank all the students and researchers who participated in the behavioral observations. The authors also wish to extend their gratitude to the caregivers and the volunteer staff involved in the care of the chimpanzees at Fundació MONA, as well as the Communication & Education Team, especially all visitor guides for supporting this study and doing a wonderful job at the sanctuary.

4. General Discussion & Conclusion

4.1 Discussion

We do feel confident in declaring that by investing our resources purposefully, we managed to produce results which expand our understanding and potentially improves our capacities to evaluate, manage and care for chimpanzees in captivity, particularly chimpanzees with an adverse life history. Hence the obtained results bring us one step closer to improve and update the definition of welfare promoting environments. We were able to meet most of our objectives, yet are aware that much more work is required. A such, this thesis only represents the initial steps needed to advance and promote research activities in captivity focused on understanding the chimpanzees needs and capacities in order to provide them with a welfare promoting environment.

As such we were able to provide further evidence that (1) traumatic live experiences and adverse living conditions during infancy produce a lasting effect on the social abilities of former pet and entertainment chimpanzees; (2) affiliative behaviors other than allogrooming as well as social proximity measures need to be considered when evaluating the social networks and social abilities of chimpanzees, as they may provide important and very different information in comparison to traditional analysis based only on allogrooming data; (3) human exposure to unfamiliar people, i.e., visitors, needs to be monitored, yet entertaining controlled and regulated education activities at a primate housing institution is possible without negatively effecting the primate´s welfare, even in a sanctuary housing former pet and entertainment chimpanzees.

Over time the efforts of many professionals, such as caregivers, researchers and veterinarians, allowed us to advance our knowledge regarding chimpanzees tremendously. Aspects such as recognizing chimpanzees to have emotions (de Waal, 2011; Kret et al., 2018), personality (Massen et al., 2013; Massen & Koski, 2014; Padrell et al., 2020), their social complexity (Aureli et al., 2008; Aureli & Schino, 2019; Pasquaretta et al., 2014) as well as their susceptibility to traumas physical deficiencies (Laurence et al., 2017; Lowenstine et al., 2016; Ross et al., 2022), mental disorders and psychological problems (Bradshaw et al., 2008; Bradshaw et al., 2009; Lopresti-Goodman et al., 2015; Úbeda et al., 2020), are important milestones, yet also imply complex challenges when working with these animals in captivity. By better understanding what makes a chimpanzee a chimpanzee and how they are impacted by their past and present living conditions and environment, we have to continuously re-evaluate the many components of their captive lives. Thus, the more we learn about these animals, the more challenging it becomes, to provide them with a welfare promoting environment that actually encompasses all aspects of our growing understanding. Improving captive care management strategies and enclosures, often requires considerable financial one-time and/or ongoing expenses and as such need to be well planned in order to use availably resources as efficient as possible. Realistically, due to limited resources, even knowledgeable housing institutions might struggle to achieve to provide the ideal environment for chimpanzees in captivity. That being said, it is necessary to advance our understanding, specifically aiming to discern which factors might have the biggest impact on the animal's welfare, in order use available resources adequately.

The same can be said for captive chimpanzee's welfare assessment. Welfare still remains a relative concept, and questions such as, what information needs to be included and how extensive such an assessment needs to be, are still being discussed (Robinson & Weiss, 2023a). Theoretically, the more information we include, the more detailed and precise the evaluation. Yet evaluation tools, that depend upon excessive amount of information and/or require a considerable amount of time for data collection and analysis, will eventually lose efficiency and in continuation its purpose. The growing body of information suggests a great many aspects of the chimpanzees lives to influence their welfare, yet we might need to limit the information to the most essential aspects.

This being said, the information gained within this thesis is meant to help to advance the selection of aspects that need to be taken into account when managing and evaluating captive housed chimpanzees. Having this in mind, we managed to evidence the potential strong impact of human decisions (short- and long-term). Yet at the same time, under the right conditions, it may be possible to have captive chimpanzees exposed to humans (visitors) without creating a detectable negative impact. Moreover, our results highlight the importance of including information regarding past adverse living conditions (here, origin and predominant social housing during infancy) in their behavioral profile (Sachser et al., 2011; Sachser et al., 2013). Hence, we should not assume that all chimpanzees require the same treatment or are capable to handle or strive in the same environment. We managed to show that their social complexity by far exceeds what we might expect by simply analyzing their social grooming networks. Although grooming remains definitely as the most prominent and important means to socialize, they use a variety of other social behaviors as well as proximity-based interactions to navigate their social networks.

Long-term impact of past adverse living conditions

Humans are an influential and essential part of chimpanzees' lives in captivity (Baker, 2004; Jensvold, 2008). Even in the wild, most populations are inescapably affected by humans in their vicinity (Arcus Foundation, 2014, 2015, 2018). Along these lines, we strive to highlight aspects of this inescapable and far-reaching relationship between humans and chimpanzees in captivity. There exist a great many relationships between humans and chimpanzees. Thus, it is essential to distinguish between the many types of humans who are somehow involved with chimpanzees at some point of their lives, taking into consideration their potential impact. With humans being the exclusive suppliers, they can also be regarded an essential necessity. At the same time, the supply quality and quantity are entirely determined by said humans. Habitat size and complexity, in the wild depends on territoriality, availability of food resources and manageability of travel distances (Chapman & Wrangham, 1993; Green et al., 2020), yet in captivity depends on humans entirely. Lastly, all aspects of access to conspecifics are decided by humans as well. This includes aspects such as maternal care, access to peers during infancy, group composition as well as access to the other sex and the possibility to mate and reproduce. In conclusion, humans' intention, including their knowledgeability and willingness to invest resources in the animal's care and environmental setting, is the most critical factor for the animal´s welfare. The combinations between knowledgeability, resource availability and resource assignation create an infinite number of captive scenarios, ranging from very poor species-inadequate to welfare promoting living conditions (Hevesi, 2023). Yet how the provided care and environment is being perceived and taken advantage of by the chimpanzees, depends greatly on the animal's earlier acquisition of skills and experiences, i.e., the animal's perception and their coping possibilities (Veissier et al., 2012; Veissier & Boissy, 2007). Regarding the impact of past experiences, several studies conducted on farm and laboratory animals suggest that the repetition of negative emotional experiences and/or prolonged exposure to harmful living conditions, affect the way animals appraise their environment, reducing their awareness of positive and making them more susceptible to negative cues (Doyle et al., 2011; Harding et al., 2004; Willner, 2005). Becker et al. (2001) proposes that individual variations in animal susceptibility to stressors is strongly influenced by the appraisal process, as animals that tend to assess events as threatening are more likely to develop chronic stress as well as might assess future events even more negatively. Veenema et al. (2003) on the other hand provides data suggesting that the variations in animal susceptibility to stressors may strongly depend on the coping style (proactive vs. reactive coping style). The acquisition of skills, including the behavioral repertoire to function/survive in a given environment, the social skill set as well as coping behaviors, depends strongly on the chimpanzees social environment during infancy, i.e., conspecifics to learn from and practice with (Bloomsmith et al., 2006; Bloomsmith et al., 1994). Thus, it seems essential to take the animals' life history into account in order to predict the impact of present environments and care strategies.

In our case, taking into account the information available regarding the past of the former pet and entertainment chimpanzees housed at Fundació MONA, we looked into the factors of origin and predominant social housing during infancy. Previous studies already focused on other factors such as onset of maternal deprivation (Kalcher et al., 2008), peer-housing condition (Bard & Nadler, 1983; van Hooff et al., 1996), maternal vs. hand rearing (King & Mellen, 1994; Maki et al., 1993; Martin, 2005), levels of human exposure (Freeman & Ross, 2014) or commercial use (King & Mellen, 1994). They successfully demonstrated, those factors to have a clear impact on the chimpanzee's individual, social and even sexual behavior, thus producing a long-term impact.

Origin (wild-caught vs. captive born), is a factor representing the likelihood of having experienced extreme traumatic situations, additionally to what can be expected for captive adverse living conditions. Specifically, we expect wild-caught chimpanzees to be behaviorally more impaired for the following reasons. We are aware of the fact that maternal deprivation may occur in both settings, yet wild-caught infants were not only separated, but most likely also witnessed the killing of their mother and other group members. According to the definition of the fifth edition of the Diagnostic and Statistical Manual of Mental Disorders, direct or indirect exposure to the actual or threatened death, serious injury, or sexual violence or witnessing the event to a primary caregiver, is considered a traumatic event for children under 6 years of age (American Psychiatric Association, 2013). Additionally, the chimpanzee orphans were then captured and transported under deplorable, typically harmful or even life-threatening conditions. Eventually they experienced in continuation a dramatic change in their living conditions from a wild to a captive setting (Beck, 2010; Stiles et al., 2013).

Predominant social housing during infancy on the other hand is meant to embody aspects regarding past social living condition. While other factors mentioned before are more specific, providing detailed information on who provided maternal care or the presence of peers (typically referring to chimpanzees of similar age), we limit our factor to simply reflect the possibility to interact and practice social interactions with conspecifics. The absence of conspecific partners during that time also indicates an increased likelihood of higher levels of human exposure, with humans being the only social interaction partner available (Hevesi, 2023). Furthermore, this factor refers only to the first 5 years of life, rather than encompassing the whole life of a chimpanzee before arriving to a rescue center. As mentioned before, pet and entertainment chimpanzee typically change owner, location and commercial use frequently and thus categorizing long periods of their lives may not easily be done. As such, we shortened the time frame our factor refers to, to the essential development stage of an infant. We would expect chimpanzees which have lived their infancy predominantly housed with conspecifics to more likely have had less human exposure, to not or have been later deprived of maternal care, to not or have suffered less prolonged social isolation and/or have had more opportunities to learn and practice social interactions. Thus, their social environment during infancy was probably less socially depriving and more inclined to allow a certain degree of healthy social development. On the contrary, chimpanzees predominantly housed without conspecifics of any kind during infancy are expected to be socially impaired, mostly as they lacked the opportunities and experience to acquire and practice their social skills.

Indeed, we found wild-caught chimpanzees to be more selective in whom they groom and to generally engage less in social grooming, compared to captive born chimpanzees. Furthermore, chimpanzees that have been completely isolated from the grooming networks, i.e., not observed grooming others during at least four months, were always wild-caught individuals. The expected impairment, as such, is reflected as lower levels of grooming engagement and a limitation of how many individuals a chimpanzee is capable or desires to maintain relationships with. Individuals predominantly housed without conspecifics during infancy also showed to be the least active groomers, compared to those predominantly housed with conspecifics. More specifically, while captive born chimpanzee were principally more active groomers compared to wild-caught individuals, captive born chimpanzees who were predominantly housed with conspecifics were by far the most active groomers. On the contrary, wild-caught chimpanzees predominantly housed without conspecifics would score the lowest grooming activity in comparison.

Going even further into detail, we looked into the partner choice and preferred interactions types. As expected, we found both origin and predominant social housing during infancy to have an impact on grooming and other affiliative behaviors. Affiliative behavior, mostly consisting of social play and follow behaviors, was significantly more often observed between individuals that were predominantly housed with conspecifics during their infancy. It was exchanged the least often between individuals who were both predominantly housed without conspecifics during infancy. The same trend was detected for allogrooming as well, yet did not reach significance. Regarding the origin, affiliative behaviors were scored most frequently between captive born and wild-caught individuals, whereas allogrooming was exchanged most often between two captive born chimpanzees and least often between two wild-caught individuals.

These results highlight the importance of an adequate social environment during infancy, including the presence of the mother and peers among other group members to facilitate social learning and practice opportunities (Bard, 1995; Bard et al., 2014; Goodall, 1986; Plooij et al., 1984). Chimpanzees who suffered more adverse living conditions during infancy, were more likely lacking tactile stimulation from conspecifics. As a consequence, they might perceive interactions involving prolonged physical contact rather stressful and may not experience the tension-reducing and relaxing effects of allogrooming (Schino et al., 1988). On the contrary, they might be more comfortable interacting via affiliative behaviors that do not necessarily require prolonged physical contact, i.e., following each other, social play behaviors or simply remaining in close social proximity. Furthermore, while captive born chimpanzees generally exhibited higher levels of social activity, they also demonstrated certain flexibility in regard to who they are interacting with. While they mostly interacted via allogrooming with each other, they switch to affiliative behaviors, such as social play and follow when interacting with wild-caught chimpanzees. Hence, they seem to be capable to adjust to the social preferences and capacities of the interaction partner. Similar findings have been presented in former laboratory chimpanzees where later deprived individuals were argued to compensate the lack of social grooming of early deprived conspecifics by interacting via gentle social play (Kalcher-Sommersguter et al., 2013).

These findings clearly show the long-term impact of adverse living conditions on the chimpanzee's sociability, as well as the utility of the two factors used in our publications. Moreover, our results suggest that information regarding the chimpanzee's past may allow us to predict their social activity levels, patterns and even compatibility. We believe this to provide valuable insights which should be considered when evaluating or comparing the activity budgets and especially sociability of chimpanzees with different backgrounds. This might also be of great help when initiating social integration procedures, i.e., choosing early integration partners and/or destination groups or when composing new groups. Considering the stimulating effect of social company of conspecifics, a socially functioning group is considered a key factor to ensure the wellbeing of individuals in captivity, i.e., is an important factor to be considered for a welfare promoting environment (Ross, 2020). The term "socially functioning" is often misinterpreted by defining it as the absence of repeated and/or extreme aggressive interactions between group members. However, it should ideally encompass aspects such as affiliative interactions and the chimpanzee's connectivity within the social network.

Broadly speaking, we suggest that higher frequencies of affiliative interactions, including allogrooming, that are simultaneously substituting the exhibition of undesired behaviors such as high levels of inactivity or abnormal behaviors, are indicating positive welfare. It is important to state that wild living chimpanzees are often reported varying greatly in terms of social time investment, and studies often report captive social time investment to be higher (Inoue & Shimada, 2020). This, however, should not be understood as captive chimpanzees having higher levels of wellbeing than wild ranging populations. It is far more likely that higher levels of social interactions in captivity occur due to foraging and food acquisition activities being far less time-consuming and challenging, compared to the wild. Furthermore, the space limitation of captivity might also lead to an increase of affiliative interactions in order to reduce tensions, as well as a reduction of agonistic behaviors in order to avoid conflicts and risk injuries (Koyama & Aureli, 2019; Videan & Fritz, 2007). As such, higher levels of social activity in captivity might serve not only to reduce tensions and avoid conflicts, but also to stimulate and entertain oneself.

In regard to the distribution of social attention towards group members, maintaining a relationship with multiple group members in comparison to focusing on one or few social partners, is not necessarily an indication of positive welfare. However, several studies implementing social network measures centered on group cohesion (Kanngiesser et al., 2011) and social positioning (Funkhouser et al., 2018), state that central or better-connected individuals have advantages in regard to coalition formation, access to resources and mating opportunities (Feldblum et al., 2021). On the contrary, lacking social skills and/or a reduced drive to socially interact is likely to result in individuals exhibiting signs of boredom, frustration and becoming frequent victims of agonistic events. Providing an adequate social environment with compatible partners, might even be more important than the physical environment, especially for chimpanzees with social impairment (Lutz & Baker, 2023).

Decisions regarding the formation or alteration of social groups

Regarding our previously stated results, when compositing a social group, understanding the impact of their atypical past history can be very beneficial. For example, mixing captive born with wild-caught chimpanzees may serve to promote affiliative interactions with socially less active individuals. Less socially active chimpanzees with similar preferences are likely to be comfortable with each other, yet socially more active chimpanzees demonstrating flexibility in their choice of interaction types, as seen in captive born chimpanzees, have the potential to increase affiliative interactions of socially less active chimpanzees, hence may have a stimulating effect. On the long-term, this might also serve as practice opportunity for socially impaired chimpanzees, improving their social skills. However, as mentioned before, social relations and group patterns may change over time and continuous monitoring of the chimpanzee's social networks is highly recommended. Specifically, as there is a chance for socially more capable and active chimpanzees to take advantage of socially more impaired individuals, which might lead to frequent persecution, aggression and thus high levels of stress and even danger to the health and safety of the socially more impaired chimpanzees.

In order to compose a beneficial social environment, it may be necessary to modify the group composition over time. Decisions regarding alterations of social groups is in the hands of the care institution, as captive housed chimpanzees themselves are physically unable to autonomously leave or join another group. Thus, considering the chimpanzee's incapacity to verbally communicate their choice/preferences, caregivers need to be able to understand the individual's social capacities in order to make the best decisions. Being highly stimulating, changes to the social environment, can be understood as a social enrichment (Bourgeois & Brent, 2005; Keeling et al., 1991; Pruetz & McGrew, 2001) and may resemble even social fission fusion patterns seen in wild populations. However, such changes, including the separation or addition of new unfamiliar individuals might also cause a certain amount of stress and risk (Lehmann et al., 2007a). As such the short time impact can be expected to produce an important change in the chimpanzee's behavior, such as increase of agonistic events and changes to the social strategy. Furthermore, both the long- and short-term impact is not guaranteed to be beneficial to the animals and as such it is highly recommendable to conduct behavioral observations and monitor the chimpanzee's behavior and reaction not only before and during but also after the alteration.

In our long-term study, we recorded a total of 18 group alterations in two groups and found chimpanzees to change their grooming patterns in the course of several months after a group alteration occurred. All chimpanzees, regardless of their past adverse live history, would become more selective with respect to their grooming partners, but after approximately four months of adaptation time, changed back to a more equal distribution of their grooming attention. This change in grooming patterns indicates the stimulating and challenging impact of the group alteration itself, while the revolving to the more equal distribution implies their capacity to adapt and prevail to the new social environment. While we cannot draw any conclusions regarding the agonistic events, as they were recorded too seldom to analyze and discuss, we found chimpanzees to maintain the amount of time they spent on grooming, with no detectable differences between time periods categorized as stable and unstable. This might indicate that the chimpanzee's grooming activity during stable time periods, i.e., in absence of any recent group alterations, already represents the maximum amount an individual is willing to engage. It is important to remember here, that the grooming activity does differ between individuals, depending on their social capacities and preferences.

Conducting long term monitoring projects and providing care staff with the means to evaluate the chimpanzee's welfare and capacities, taking into account the individual's past and present living conditions is an extremely valuable asset, which potentially supports the efforts to create a welfare promoting environment.

Multi-layer social network analysis

When looking into these animals' social preferences and capacities, we found further evidence of their social complexity. Social grooming is the most used behavioral interaction type to interact and establish bonds, yet our results indicate that other affiliative behaviors and non-behavioral proximity-based interactions are not to be ignored. As stated before, chimpanzees have certain tendencies, and some might even feel uncomfortable being in prolonged physical contact with others. As a result, we may find individuals barely or never interacting via grooming. However, this should not lead directly to the conclusion that these individuals are not social or do not form part of the group's social network, rather they might use other interaction types better suited for their social capacities. Indeed, we found separate social networks based either on grooming, affiliative behaviors, social proximity (within arm length) and stationary vicinity (within 5 meters to another individual) to differ greatly. Each network contained information not represented by the others. This suggest that by basing evaluations on only one of these interaction types—commonly allogrooming, we are bound to lose potentially important information for their evaluation. Within our study population, we detected individuals that were isolated or barely connected in the allogrooming networks, while being well-connected and active in networks based on affiliative behaviors or proximity-based interactions types. Thus, when evaluating these animals only based on their grooming activity, they would be considered outsiders, socially not integrated and expected to have low levels of wellbeing. However, when including other interaction types, their social positioning and activity level increased drastically. Once again, making decisions regarding their social environment, only limiting evaluations and decisions on allogrooming networks, produces a high risk to overlook important bonds between individuals. Carelessly severing such bonds might produce a negative impact on the respective chimpanzee's welfare. As such, we wish to highlight the importance of carefully evaluating the chimpanzees and their relations based on all their social interactions in order to make the best choices available.

Assessing and regulating the impact of unfamiliar human exposure

Visitor programs are a commonly seen activity for institutions housing wildlife. They might even be a necessity to ensure financial stability to maintain the housed animals and/or to entertain educational activities orientated towards raising awareness and species conservation. However, it is the housing institutions' duty to ensure that any visitor programs do not negatively impact the animal's welfare. A housing institution, aiming to provide a welfare promoting environment may choose to present animals in their care as ambassadors for educational and conservation programs, yet will lose credibility and purpose, if attempting to achieve these objectives by compromising their animal's welfare in the process (Prescott, 2023).

An increasing number of studies related to human-animal interactions have been conducted over the last few decades, yet the results and conclusions are often contradicting (Davey, 2007). Whereas several studies argued visitor presence to have a negative impact, detectable as increased agonistic or stereotypical behaviors and decreased intra-group affiliations and exploration (Cooke & Schillaci, 2007; Chamove et al., 1988; Davis et al., 2005; Sekar et al., 2008), others reported no measurable effect or suggested human–animal interactions to have a positive and stimulating effect on the animals (Cook & Hosey, 1995). Although study populations and methods varied greatly, studies which reported a negative impact, mostly attributed said negative impact to the following aspects: Excessive crowding (Bonnie et al., 2016; Stoinski et al., 2012; Wells, 2005), elevated noise levels (Quadros et al., 2014), permitted proximity (Cairo-Evans et al., 2022), direct interactions and feeding attempts (Birke, 2002; Nimon & Dalziel, 1992; Pazol & Bloomsmith, 1993), continuous visibility and exposure to visitors (Blaney & Wells, 2004) and/or small ill-equipped enclosures lacking out of sight areas (Bonnie et al., 2016; Fernandez et al., 2009). Considering these factors to be the most likely causes for undesired reactions stated in previous studies, MONA offered an ideal environment to see if in absence of these variables, educational visits can be conducted without visible reducing the animals’ welfare. Fundació MONA has a strict visitor policy the primates’ welfare prevails over the visitors’ experience. In order to protect the primates from any undesired effects, all visitors are being supervised and restricted in their actions while primates are offered installations maximizing a certain amount of choice and control to avoid human exposure. Visitors may only access viewing areas at certain times and in groups, limited in size, guided and supervised by an educational guide at all times. This allows the center to control and limit the visitor’s behavior and excessive exposure, ensuring that (a) visitors may not attempt to interact with the animals, (b) noise levels to remain low and (c) that no extreme crowding events occur. On the other hand, the primates reside in large naturalistic enclosures with many structures blocking the visitor’s view. Indoor areas are off-display, and big sections of the outdoor enclosure’s surroundings are visually blocked by intentionally planted vegetation. No animal training or shows are being displayed, neither will the educational guide call animals to increase animal visibility. Guides reserve the right to ask visitors to leave in case their behavior is not in line with the centers’ visitor policies. Furthermore, visitor groups will move along if guides detect primates to exhibit indicators of being uncomfortable or stressed by the human presence or if repeated displays are directed towards the viewing areas. Indeed, we found the visitor impact to have a neutral or ambivalent impact as we could not detect any indications of any positive or negative orientated alterations in the chimpanzee’s behavior. While our study location and design does not allow us to argue which of the buffering measures described before were the most successful to mediate the visitor impact, we can confidently state that by implementing them altogether, the chimpanzees did not show any undesired reactions during or after visitor hours, indicating a reduced welfare. Thus, presential visitor programs can be implemented even at a sanctuary, housing chimpanzees potentially sensitive to unfamiliar humans, if visitor exposure and behavior are controlled and chimpanzees are provided with an environment and means to avoid exposure and visibility.

Hence, we conclude three conditions have to be met in order to reduce the likelihood of visitor programs producing a negative undesired impact on the chimpanzee's behavior:

(1) The housing organization has to provide the animals with the tools to cope with and accommodate the exposure to unfamiliar humans. This may be achieved by providing a physical environment that is complex and spacious, with plenty of areas allowing primates to exhibit their desired behaviors and activities out of the visitors' sight. However, some chimpanzees, although provided with off-sight areas might be agitated by visitors and choose to respond aggressively via repeated displays, throwing feces or other objects. Due to traumatic experiences in their past or other reasons, some individuals might never feel comfortable with unfamiliar humans in reach. Such animals need to be identified and should be assigned off-display enclosures of equal quality while remaining in their social groups.

(2) Exposure to visitors needs to be regulated and their behaviors modulated, reducing their potential negative impact to a minimum. This includes the amount of time animals are displayed, the proximity, the number of visitors that can see the animals simultaneously as well as the way visitors behave and may attempt to interact with those animals. Due to lacking knowledge and concern, we have to assume that unsupervised visitors even in the absence of bad intentions are likely to behave in a way that might disturb the animal's lives. As such visitor viewpoints and pathways should be well distanced from the chimpanzee's enclosures and should be designed to only allow a certain number of visitors at a time. Visitors may be organized in groups, which allows planning a specific schedule of human exposure and facilitates to supervise and tune their behaviors. The direct supervision of visitor groups at the center also ensures to limit and/or ideally negates any attempts to interact with the animals, or to call their attention in any way.

(3) Considering that the animal's perception and reactions towards humans might change over time, it is highly recommended to conduct repeated observations and evaluating the visitor impact regularly on all displayed animals.

Welfare promoting environment

The concept of a welfare promoting environment is rather grand and ambitious, as it encompasses the totality of all up-to-date validated aspects regarding captive care and environment, here focused on chimpanzees. Rather than a stagnant definition, it is necessary to maintain it as a flexible ever-changing concept that keeps evolving based on the growing body of knowledge, interdisciplinary professionals keep accumulating. In its most essential part, housing institutions striving towards providing a welfare promoting environment need to continuously consult the latest findings regarding animal welfare and captive care, to train care-staff consistently and to invest the available resources accordingly.

This thesis is meant to expand on the current scientific knowledge regarding animal welfare and captive care in chimpanzees, especially those with an extreme history of human induced adversities in their past lives. Special attention was given to the unique nature of each chimpanzee, considering that their life history shaped their identity over time.

Considering that chimpanzees are highly social animals (Goodall, 1973), the social environment is an important factor influencing the chimpanzees' welfare potential. However, the chimpanzees capacity to take advantage and strive in a specific social environment does not only depend on the provided social environment itself (Fitch et al., 1989; Webb et al., 2019), but also on the chimpanzees social skill set, their capacity to cope (Veenema et al., 2003) as well as perceive (Veissier et al., 2012; Veissier & Boissy, 2007) social interactions and social opportunities, which can be understood as both stressful as well as stimulating (Fultz et al., 2022). As such we aimed to add to the current understanding of social complexity as well as highlighted the importance of adverse living conditions during infancy, i.e., during an essential developing stage of the chimpanzee's social skills, to be considered in welfare assessments and when aiming for a welfare promoting environment.

Housing institutions, striving to provide a welfare promoting environment for their chimpanzees, often entertain visitor programs with the objective to cover animal care expanses as well as to promote education and conservation efforts. However, several studies suggest that visitor programs may be conflicting with animal care and welfare efforts, as the visitor exposure and activity may produce a undesired impact on the animals' behavior and welfare (Cooke & Schillaci, 2007; Chamove et al., 1988; Davis et al., 2005; Sekar et al., 2008). Considering the importance to cover the necessary expanses of housing these animals, as well as the value of education and conservation efforts, ceasing to entertain visitor programs in order to eliminate a potentially negative welfare impact might not be the best course of action. Thus, we strived to provide data, suggesting data visitor program may be entertained without producing a negative impact on the chimpanzees' welfare, as long as certain criteria, previously explained, are met.

4.2 Conclusion

In conclusion, we could show that: (1) Early traumatic life events and adverse living conditions during infancy, affect the social capacities and preferences of former pet and entertainment chimpanzees in the long term. Wild-caught individuals and those predominantly housed without conspecifics during infancy demonstrated certain social impairments, visible in their activity and distribution of grooming and other affiliative behaviors. We found individuals to preferably interact with group members with more similar past adversities, but also saw individuals that were predominantly housed with conspecifics during infancy to demonstrate certain flexibility and capacity to adapt to the preferred interaction types of their partners.

(2) Former pet and entertainment chimpanzees, regardless of their past lives, reacted similarly to alterations of group composition. Unexpectedly, they would not change the amount of time spent on grooming but would adapt their grooming distribution, becoming more restricted in the choice of their grooming partners during unstable periods. Furthermore,

after a few months, all chimpanzees reverted to a more even distribution, indicating their capacity to successfully adapt over time to group alterations.

(3) Using Multiplex analysis, we could demonstrate the social complexity of chimpanzees and the importance of other affiliative and proximity-based interactions, besides social grooming. Using reducibility analysis and analyzing the chimpanzee's interactions types separately as well as within the multiplex network, allowed us to highlight the information gain obtained through multiplex analysis. Clearly, grooming remains the most prominent and important means to socialize in chimpanzees, yet they use a variety of other social behaviors as well as proximity-based interactions to navigate their social networks. Taking this into account allowed us to tune and correct potentially misleading evaluations of chimpanzees' social capacities and preferences, bringing us closer to a more objective evaluation of their sociability.

(4) Well managed visitor programs can be entertained without negatively impacting the chimpanzees' behavior and welfare. Institutions such as licensed zoos and sanctuaries have a massive potential to raise awareness and promote conservation efforts, yet require strict monitoring and regulation of visitor activities to ensure the animals' welfare does not get compromised. The potentially negative visitor impact depends greatly on both the actions of the visitors and the capacity and possibilities of the animals to control human exposure and visibility.

We believe our results to be a valuable addition to the current knowledge, in being hopefully helpful to improve our capacities to care for chimpanzees in captivity and further evolve welfare promoting environments. We sincerely hope our findings to be of direct help to Fundació MONA where all three studies were conducted, but also to reach and support other housing institutions in their efforts to strive towards providing welfare promoting environments for chimpanzees in captivity.

4.3 Limitations & Future directions

Throughout the time frame of this thesis, I experienced a steady learning curve, with every new project and publication adding to my skill set. Now, looking back at the initial planning stage, I can definitely see there was room for improvement which could have led to more detailed results. However, there is one particular aspect I cannot help but lament. Initially, we planned to expand the study populations by including observations from other primate sanctuaries, housing chimpanzees with different past life adversities. In the end, however, partially due to my earlier inexperience to not have started earlier, but mostly due to the Covid-19 pandemic, we were unable to do so. Although I do believe our general findings would not have changed greatly, the weight and importance would have increased in the process. This being said, one of my objectives after this thesis is to continue with these projects and to reproduce our findings in other study populations in Europe and the USA.

In general, working on this thesis and its publications expanded my horizon greatly. Eventually, rather than finding answers, I ended up unearthing even more questions that need to be asked and areas that still need to be explored. As such, it was an extremely stimulating experience which helped me formulate and plan many future projects and studies, some of them already starting to get implanted before this thesis ended. Particularly, some critics received by reviewers made me realize how much information we are still lacking regarding the lives of chimpanzees in captivity.

Aging chimpanzee populations

Partially due to the improving living conditions in captivity, we find more and more chimpanzees reaching the stage of seniors, i.e., exceeding the average life span of chimpanzees. Moreover, chimpanzees in captivity are likely to get older than their wild counterparts. However, we still lack knowledge regarding these senior chimpanzees in terms of understanding their behavioral activity budget as well as to how to best care for them.

Assessing activity budgets

Although, much research is based on chimpanzee behavior, there are no published thresholds of how ideal behavioral time distribution should look like in captivity. It is hardly recommendable to compare captive activity budgets with those of their wild counterparts, as the circumstances and environment differs greatly. Hence, it might make more sense to study and compare tendencies found in captivity, while considering the chimpanzees' behavioral profile as well as captive environment.

For example, it is broadly accepted that inactivity levels should be low, but there is no specific percentage of time or range recommended that would indicate positive wellbeing. As such, if the average inactivity of a captive population would lie at approximately 40%, subjectively some might see this as positive while others would label this as an indicator of reduced welfare. The same can be said for any other registered behavior, such as self-directed behaviors or social activity.

Rehabilitation and conditions at rescue onset

Research activities and assessments are often tied to a specific moment in time, with very few projects in captivity being conducted to look into the progression of behavioral activity budgets or individual wellbeing. As such, very few projects provide information regarding the rehabilitation of rescued chimpanzees or how improved living conditions might affect these animals on the long term. Additionally, it is necessary to take the onset conditions into account, i.e., the physical, psychological and emotional state of the animals at the time of their rescue or relocation. While we can find reports written by caregivers and veterinarians, there is close to nothing published that would allow us to cite pooled and scientifically validated information regarding their rescue onset state nor their progression over time.

Although we keep learning more about these and other animals on a daily basis, there still is a need to concentrate on very basic, fundamental but crucial information regarding their lives in captivity. We are well aware that this type of research is not perceived as the most impressive or dazzling within the scientific community, yet wish to highlight its importance.

Chimpanzees in captivity should not be used for research,

rather research should be used for the chimpanzees' sake!

References

Altman, J. D. (1998). Animal activity and visitor learning at the zoo. *Anthrozoös, 11*(1), 12-21. https://doi.org/10.1080/08927936.1998.11425083

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour, 49*(3/4), 227-267. https://doi.org/10.1163/156853974x00534

American Psychiatric Association. (2013). *Diagnostic and statistical manual of mental disorders: DSM-5™ (5th ed.)*. VA: American Psychiatric Publishing, Inc. https://doi.org/10.1176/appi.books.9780890425596

Ancrenaz, M., Barton, C., Riger, P., & Wich, S. (2018). Building relationships: how zoos and other partners can contribute to the conservation of wild orangutans Pongo spp. *International Zoo Yearbook*, *52*(1), 164-172. https://doi.org/10.1111/izy.12184

Anderson, D. P., Nordheim, E. V., Boesch, C., & Moermond, T. C. (2002). Factors influencing fission-fusion grouping in chimpanzees in the Taï National Park, Côte d'Ivoire. In C. Boesch & G. Hohmann (Eds.), *Behavioural Diversity in Chimpanzees and Bonobo* (pp. 90-102). Cambridge University Press. https://doi.org/10.1207/S15327604JAWS0502_03

Anderson, U. S., Benne, M., Bloomsmith, M. A., & Maple, T. L. (2002). Retreat space and human visitor density moderate undesirable behavior in petting zoo animals. *Journal of Applied Animal Welfare Science, 5*(2), 125-137. https://doi.org/10.1207/s15327604jaws0502_03

Arcus Foundation. (2014). *Extractive industries and ape conservation (State of the Apes)*. Cambridge University Press. https://doi.org/10.1017/CBO9781107590274

Arcus Foundation. (2015). *Industrial agriculture and ape conservation (State of the Apes)*. Cambridge University Press. https://doi.org/10.1017/CBO9781316488959

Arcus Foundation. (2018). *Infrastructure development and ape conservation (State of the Apes)*. Cambridge University Press. https://doi.org/10.1017/9781108436427

Arcus Foundation. (2021). *Killing, capture, trade and ape conservation* (Vol. 4). Cambridge University Press. https://doi.org/DOI: 10.1017/9781108768351

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., . . . Schaik, C. (2008). Fission-Fusion Dynamics. *Current Anthropology, 49*(4), 627-654. https://doi.org/10.1086/586708

Aureli, F., & Schino, G. (2019). Social complexity from within: how individuals experience the structure and organization of their groups. *Behavioral Ecology and Sociobiology, 73*(1), 6. https://doi.org/10.1007/s00265-018-2604-5

Baker, K. C. (2004). Benefits of positive human interaction for socially-housed chimpanzees. *Animal Welfare, 13*(2), 239-245. https://doi.org/10.1017/S0962728600026981

Baker, K. R., & Farmer, H. L. (2023). The welfare of primates in zoos. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman primate welfare: From history, science, and ethics to practice* (pp. 79-96). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_4

Baker, S. E., Cain, R., van Kesteren, F., Zommers, Z. A., D'Cruze, N., & Macdonald, D. W. (2013). Rough trade: Animal welfare in the global wildlife trade. *BioScience, 63*(12), 928-938. https://doi.org/10.1525/bio.2013.63.12.6

Baldwin, P. J., McGrew, W. C., & Tutin, C. E. G. (1982). Wide-ranging chimpanzees at Mt. Assirik, Senegal. *International Journal of Primatology, 3*(4), 367-385. https://doi.org/10.1007/BF02693739

Baratay, E., & Hardouin-Fugier, E. (2004). *Zoo: A history of zoological gardens in the West.* Reaktion books.

Bard, K. A. (1995). Parenting in primates. In M. Bornstein (Ed.), *Handbook of parenting: biology and ecology of parenting* (Vol. 2, pp. 27-58). Lawrence Erlbaum Associates.

Bard, K. A., Dunbar, S., Maguire-Herring, V., Veira, Y., Hayes, K. G., & McDonald, K. (2014). Gestures and social-emotional communicative development in chimpanzee infants. *American Journal of Primatology*, *76*(1), 14-29. https://doi.org/10.1002/ajp.22189

Bard, K. A., & Hopkins, W. D. (2018). Early socioemotional intervention mediates long-term effects of atypical rearing on structural covariation in gray matter in adult chimpanzees. *Psychological Science*, *29*(4), 594-603. https://doi.org/10.1177/0956797617740685

Bard, K. A., & Nadler, R. D. (1983). The effect of peer separation in young chimpanzees (Pan troglodytes). *American Journal of Primatology, 5*(1), 25-37. https://doi.org/https://doi.org/10.1002/ajp.1350050104

Barrett, L., Henzi, P. S., & Lusseau, D. (2012). Taking sociality seriously: the structure of multi-dimensional social networks as a source of information for individuals. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1599), 2108-2118. https://doi.org/10.1098/rstb.2012.0113

Barton, K. (2018). *MuMIn: Multi-Model inference.* In (Version R package version 1.42.1.) https://CRAN.R-project.org/package=MuMIn

Basabose, K. A. (2005). Ranging patterns of chimpanzees in a Montane Forest of Kahuzi, Democratic Republic of Congo. *International Journal of Primatology*, *26*(1), 33-54. https://doi.org/10.1007/s10764-005-0722-1

Bashaw, M. J., Gullott, R. L., & Gill, E. C. (2010). What defines successful integration into a social group for hand-reared chimpanzee infants? *Primates*, *51*(2), 139-147. https://doi.org/10.1007/s10329-009-0176-8

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Battiston, F., Nicosia, V., & Latora, V. (2013). Structural measures for multiplex networks. *arXiv*. https://doi.org/10.1103/PhysRevE.89.032804

Beck, B. (2010). Chimpanzee orphans: sanctuaries, reintroduction, and cognition. In E. Lonsdorf, S. Ross, & T. Matsuzawa (Eds.), *The mind of the chimpanzee: Ecological and experimental perspectives* (pp. 332–346). University of Chicago Press.

Becker, E. S., Rinck, M., Margraf, J., & Roth, W. T. (2001). The emotional Stroop effect in anxiety disorders: General emotionality or disorder specificity? *Journal of Anxiety Disorders*, *15*(3), 147-159. https://doi.org/https://doi.org/10.1016/S0887-6185(01)00055-X

Beisner, B. A., Jin, J., Fushing, H., & McCowan, B. (2015). Detection of social group instability among captive rhesus macaques using joint network modeling. *Current Zoology*, *61*(1), 70-84. https://doi.org/10.1093/czoolo/61.1.70

Beisner, B. A., & McCowan, B. (2014). Social networks and animal welfare. In J. Krause, R. James, D. Franks, & D. Croft (Eds.), *Animal social networks* (pp. 111-121). Oxford University Press.

Benbow, S. M. P. (2004). Death and Dying at the Zoo. *Journal of Popular Culture*, *37*(3), 379-398. https://doi.org/10.1111/j.0022-3840.2004.00074.x

Bessa, J., Sousa, C., & Hockings, K. J. (2015). Feeding ecology of chimpanzees (Pan troglodytes verus) inhabiting a forest-mangrove-savanna-agricultural matrix at Caiquene-Cadique, Cantanhez National Park, Guinea-Bissau. *American Journal of Primatology*, *77*(6), 651-665. https://doi.org/10.1002/ajp.22388

Bethell, E. J., & Pfefferle, D. (2023). Cognitive bias tasks: A new set of approaches to assess welfare in nonhuman primates. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman Primate Welfare: From History, Science, and Ethics to Practice* (pp. 207-230). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_9

Birke, L. (2002). Effects of browse, human visitors and noise on the nehaviour of naptive orang utans. *Animal Welfare*, *11*(2), 189-202. https://doi.org/10.1017/S0962728600028141

Birkett, L. P., & Newton-Fisher, N. E. (2011). How abnormal is the behaviour of captive, zoo-living chimpanzees? *Plos ONE*, *6*(6). https://doi.org/10.1371/journal.pone.0020101

Blaney, E. C., & Wells, D. L. (2004). The influence of a camouflage net barrier on the behaviour, welfare and public perceptions of zoo-housed gorillas. *Animal Welfare*, *13*(2), 111-118. https://doi.org/10.1017/S0962728600026841

Bloomsmith, M. A., Baker, K. C., Ross, S. R., & Lambeth, S. P. (2006). Early rearing conditions and captive chimpanzee behavior: some surprising findings. In G. P. Sackett, G. C. Ruppentahal, & K. Elias (Eds.), *Nursery Rearing of Nonhuman Primates in the 21st Century* (pp. 289-312). Springer Nature. https://doi.org/10.1007/978-0-387-25640-5_15

Bloomsmith, M. A., Pazol, K. A., & Alford, P. L. (1994). Juvenile and adolescent chimpanzee behavioral development in complex groups. *Applied Animal Behaviour Science*, *39*(1), 73-87. https://doi.org/10.1016/0168-1591(94)90017-5

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution*. Oxford University Press.

Boesch, C., Bolé, C., Eckhardt, N., & Boesch, H. (2010). Altruism in forest chimpanzees: The Case of Adoption. *Plos ONE*, *5*(1). https://doi.org/10.1371/journal.pone.0008901

Bogart, S. L., Bennett, A. J., Schapiro, S. J., Reamer, L. A., & Hopkins, W. D. (2014). Different early rearing experiences have long-term effects on cortical organization in captive chimpanzees (Pan troglodytes). *Developmental Science*, *17*(2), 161--174. https://doi.org/10.1111/desc.12106

Bonacich, P. (2007). Some unique properties of eigenvector centrality. *Social Networks*, *29*(4), 555-564. https://doi.org/10.1016/j.socnet.2007.04.002

Bonnie, K. E., Ang, M. Y. L., & Ross, S. R. (2016). Effects of crowd size on exhibit use by and behavior of chimpanzees (Pan troglodytes) and Western lowland gorillas (Gorilla gorilla) at a zoo. *Applied Animal Behaviour Science*, *178*, 102-110. https://doi.org/https://doi.org/10.1016/j.applanim.2016.03.003

Borner, M. (2009). The rehabilitated chimpanzees of Rubondo Island. *Oryx*, *19*(3), 151-154. https://doi.org/10.1017/S003060530002531X

Bos, K., Zeanah, C. H., Fox, N. A., Drury, S. S., McLaughlin, K. A., & Nelson, C. A. (2011). Psychiatric outcomes in young children with a history of institutionalization. *Harvard Review of Psychiatry*, *19*(1), 15. https://doi.org/10.3109/10673229.2011.549773

Bourgeois, S. R., & Brent, L. (2005). Modifying the behaviour of singly caged baboons: evaluating the effectiveness of four enrichment techniques. *Animal Welfare*, *14*, 71-81. https://doi.org/10.1017/S0962728600028943

Bowden, R., MacFie, T. S., Myers, S., Hellenthal, G., Nerrienet, E., Bontrop, R. E., . . . Mundy, N. I. (2012). Genomic tools for evolution and conservation in the chimpanzee: Pan troglodytes ellioti is a genetically distinct population. *PLoS Genetics*, *8*(3). https://doi.org/10.1371/journal.pgen.1002504

Bradshaw, G. A., Capaldo, T., Lindner, L., & Grow, G. (2008). Building an inner sanctuary: complex PTSD in chimpanzees. *Journal of Trauma Dissociation*, *9*, 57-69. https://doi.org/10.1080/15299730802073619

Bradshaw, G. A., Capaldo, T., Lindner, L., & Grow, G. (2009). Developmental context effects on bicultural posttrauma self repair in chimpanzees. *Developmental Psychology*, *45*(5), 1376–1388. https://doi.org/10.1037/a0015860

Brambell, F. W. (1965). *Report of the technical committee to enquire into the welfare of animals kept under intensive livestock husbandry systems*. Her Majesty's Stationery Office.

Brando, S., & Buchanan-Smith, H. M. (2017). The 24/7 approach to promoting optimal welfare for captive wild animals. *Behavioural Processes*, *156*, 83-95. https://doi.org/10.1016/j.beproc.2017.09.010

Brashares, J. S., Arcese, P., Sam, M. K., Coppolillo, P. B., Sinclair, A. R. E., & Balmford, A. (2004). Bushmeat hunting, wildlife declines, and fish supply in West Africa. *Science*, *306*(5699), 1180-1183. https://doi.org/10.1126/science.1102425

Bray, J., Feldblum, J. T., & Gilby, I. C. (2021). Social bonds predict dominance trajectories in adult male chimpanzees. *Animal Behaviour*, *179*, 339-354. https://doi.org/https://doi.org/10.1016/j.anbehav.2021.06.031

Brent, L. (2001). *The care and management of captive chimpanzees* (Vol. 2). American Society of Primatologists. https://books.google.es/books?id=hubaAAAACAAJ

Brent, L., Lee, D. R., & Eichberg, J. W. (1989). The effects of single caging on chimpanzee behavior. *Laboratory animal science*, *39*(4), 345--346.

Breuer, T., Manguette, M., & Groenenberg, M. (2018). Gorilla Gorilla spp conservation – from zoos to the field and back: examples from the Mbeli Bai Study. *International Zoo Yearbook*, *52*(1), 137-149. https://doi.org/10.1111/izy.12181

Briere, J., & Spinazzola, J. (2005). Phenomenology and psychological assessment of complex posttraumatic states. *Journal of Traumatic Stress*, *18*(5), 401--412. https://doi.org/10.1002/jts.20048

Broom, D. M. (2011). A History of Animal Welfare Science. *Acta Biotheoretica*, *59*(2), 121-137. https://doi.org/10.1007/s10441-011-9123-3

Brull, J. (2022). *Primates proteccion bienestar y derechos*. Universitat de Barcelona.

Bründl, A. C., Tkaczynski, P. J., Kohou, G., Boesch, C., Wittig, R. M., & Crockford, C. (2020). Systematic mapping of developmental milestones in wild chimpanzees. *Developmental Science*. https://doi.org/10.1111/desc.12988

Bründl, A. C., Tkaczynski, P. J., Nohon Kohou, G., Boesch, C., Wittig, R. M., & Crockford, C. (2021). Systematic mapping of developmental milestones in wild chimpanzees. *Developmental Science*, *24*(1), e12988. https://doi.org/https://doi.org/10.1111/desc.12988

Brüne, M., Brüne-Cohrs, U., & McGrew, W. C. (2004). Psychiatric treatment for great apes? *Science*, *306*(5704), 2039-2039. https://doi.org/doi:10.1126/science.306.5704.2039b

Brüne, M., Brüne-Cohrs, U., McGrew, W. C., & Preuschoft, S. (2006). Psychopathology in great apes: Concepts, treatment options and possible homologies to human psychiatric disorders. *Neuroscience \& Biobehavioral Reviews*, *30*(8), 1246--1259. https://doi.org/10.1016/j.neubiorev.2006.09.002

Cairo-Evans, A., Wierzal, N. K., Wark, J. D., & Cronin, K. A. (2022). Do zoo-housed primates retreat from crowds? A simple study of five primate species. *American Journal of Primatology*, *84*(10), e23386. https://doi.org/https://doi.org/10.1002/ajp.23386

Caldecott, J. O., & Miles, L. (2005). *World atlas of great apes and their conservation* (Vol. 2005). University of California Press. https://www.biodiversitylibrary.org/item/119223

Cano, R. (2014). *Use of natural resources by sanctuary chimpanzees (Pan troglodytes): understanding the significance of naturalistic environments* Hedmark University College].

Cantin, S., & Prescott, J. (1980). Survey of animal popularity at Quebec Zoo. *International Zoo News*, *167*, 114-116.

Capitanio, J. P., Vandeleest, J., & Hannibal, D. L. (2023). Physiological measures of welfare. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman Primate Welfare: From History, Science, and Ethics to Practice* (pp. 231-254). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_10

Carlsen, F., de Jongh, T., & Pluháčková, J. (2022). *EAZA best practice guidelines for chimpanzees (Pan troglodytes)* (1 st edition ed.). European Association of Zoos and Aquariums.

Carne, C., Semple, S., Morrogh-Bernard, H., Zuberbühler, K., & Lehmann, J. (2014). The risk of disease to great apes: simulating disease spread in orang-utan (Pongo pygmaeus wurmbii) and chimpanzee *(Pan troglodytes schweinfurthii)* association networks. *Plos ONE*, *9*(4). https://doi.org/10.1371/journal.pone.0095039

Carr, N., & Cohen, S. (2011). The public face of zoos: Images of entertainment, education and conservation. *Anthrozoos: A Multidisciplinary Journal of The Interactions of People & Animals*, *24*(2), 175-189. https://doi.org/10.2752/175303711X12998632257620

Caws, C., & Aureli, F. (2003). Chimpanzees cope with temporary reduction of escape opportunities. *International Journal of Primatology*, *24*(5), 1077-1091. https://doi.org/10.1023/A:1026280329544

Clark, C. (1977). A preliminary report on weaning among chimpanzees of the Gombe National Park, Tanzania. In S. Chevalier-Skolinkoff & F. Poirer (Eds.), *Primate biosocial development: biological, social and ecological determinants* (pp. pp 235–260). Garland.

Clark, F. E. (2011). Space to choose: network analysis of social preferences in a captive chimpanzee community, and implications for management. *American Journal of Primatology*, *73*(8), 748-757. https://doi.org/10.1002/ajp.20903

Clay, A. W., Bard, K. A., & Bloomsmith, M. A. (2018). Effects of sex and early rearing condition on adult behavior, health, and well-being in captive chimpanzees (Pan troglodytes). *Behavioural Processes*, *156*, 58--76. https://doi.org/10.1016/j.beproc.2017.06.011

Clay, A. W., Bloomsmith, M. A., Bard, K. A., Maple, T. L., & Marr, M. J. (2015). Long-term effects of infant attachment organization on adult behavior and health in nursery-reared, captive chimpanzees *(Pan troglodytes)*. *Journal of Comparative Psychology*, *129*(2), 145-159. https://doi.org/10.1037/a0038901

Cloitre, M., Miranda, R., Stovall-McClough, C. K., & Han, H. (2005). Beyond PTSD: Emotion regulation and interpersonal problems as predictors of functional impairment in survivors of childhood abuse. *Behavior Therapy*, *36*(2), 119-124. https://doi.org/10.1016/S0005-7894(05)80060-7

Coe, J. C. (2003). Steering the ark toward Eden: design for animal well-being. *Journal of the American Veterinary Medical Association*, *223*(7), 977-980. https://doi.org/10.2460/javma.2003.223.977

Collins, C. K., & Marples, N. M. (2016). The effects of zoo visitors on a group of Western lowland gorillas Gorilla gorilla gorilla before and after the birth of an infant at Dublin Zoo. *International Zoo Yearbook*, *50*(1), 183-192. https://doi.org/10.1111/izy.12111

Conde, D. A., Flesness, N., Colchero, F., Jones, O. R., & Scheuerlein, A. (2011). An emerging role of zoos to conserve biodiversity. *Science*, *331*(6023), 1390 LP-1391. https://doi.org/10.1126/science.1200674

Conti, G., Hansman, C., Heckman, J. J., Novak, M. F., Ruggiero, A., & Suomi, S. J. (2012). Primate evidence on the late health effects of early-life adversity. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(23), 8866-8871. https://doi.org/10.1073/pnas.1205340109

Cook, S., & Hosey, G. R. (1995). Interaction sequences between chimpanzees and human visitors at the Zoo. *Zoo biology*, *14*(5), 431-440. https://doi.org/10.1002/zoo.1430140505

Cooke, C. M., & Schillaci, M. A. (2007). Behavioral responses to the zoo environment by white handed gibbons. *Applied Animal Behaviour Science*, *106*(1-3), 125-133. https://doi.org/10.1016/j.applanim.2006.06.016

Cordoni, G., & Palagi, E. (2011). Ontogenetic trajectories of chimpanzee social play: similarities with humans. *Plos ONE*, *6*(11), e27344. https://doi.org/10.1371/journal.pone.0027344

Cowlishaw, G. (1999). Predicting the pattern of decline of african primate diversity: an extinction debt from historical deforestation. *Conservation Biology*, *13*(5), 1183-1193. https://doi.org/10.1046/j.1523-1739.1999.98433.x

Crailsheim, D., Stüger, H. P., Kalcher-Sommersguter, E., & Llorente, M. (2020). Early life experience and alterations of group composition shape the social grooming networks of former pet and entertainment chimpanzees (Pan troglodytes). *Plos ONE*, *15*(1). https://doi.org/10.1371/journal.pone.0226947

Crockford, C., Deschner, T., Ziegler, T. E., & Wittig, R. M. (2014). Endogenous peripheral oxytocin measures can give insight into the dynamics of social relationships: a review. *Frontiers in Behavioral Neuroscience*, *8*(68). https://doi.org/10.3389/fnbeh.2014.00068

Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J., & James, R. (2009). Behavioural trait assortment in a social network: patterns and implications. *Behavioral Ecology and Sociobiology*, *63*(10), 1495-1503. https://doi.org/10.1007/s00265-009-0802-x

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems*, 1695. http://igraph.org

Chamove, A. S., Hosey, G. R., & Schaetzel, P. (1988). Visitors excite primates in zoos. *Zoo biology*, *7*(4), 359-369. https://doi.org/10.1002/zoo.1430070407

Chapman, C. A., & Wrangham, R. W. (1993). Range use of the forest chimpanzees of Kibale: Implications for the understanding of chimpanzee social organization. *American Journal of Primatology*, *31*(4), 263-273. https://doi.org/10.1002/ajp.1350310403

Che-Castaldo, J., Havercamp, K., Watanuki, K., Matsuzawa, T., Hirata, S., & Ross, S. R. (2021). Comparative survival analyses among captive chimpanzees (Pan troglodytes) in America and Japan. *PeerJ*, *9*(e11913). https://doi.org/10.7717/peerj.11913

Cheyne, S. M. (2009). Challenges and opportunities of primate rehabilitation—gibbons as a case study. *Endangered Species Research*, *9*, 159-165. https://doi.org/10.3354/esr00216

ChimpCare Licoln Park Zoo. (2023). *Chimpanzees in the U.S.* Retrieved 22/06/2023 from https://chimpcare.org/map

Chugani, H. T., Behen, M. E., Muzik, O., Juhász, C., Nagy, F., & Chugani, D. C. (2001). Local brain functional activity following early deprivation: A study of postinstitutionalized romanian orphans. *NeuroImage*, *14*(6), 1290-1301. https://doi.org/10.1006/nimg.2001.0917

Darren, E. M., Lindsay, T., Daniel, H. G., Ashley, C., Jessica, S., Richard, E., . . . Brenda, M. (2011). Human-directed contra-aggression training using positive reinforcement with single and multiple trainers for indoor-housed rhesus macaques. *Applied Animal Behaviour Science*, *132*(3), 178-186. https://doi.org/https://doi.org/10.1016/j.applanim.2011.04.009

Davenport, R. K., & Rogers, C. M. (1970). Differential rearing of the chimpanzee. A project survey. In G. H. Bourne (Ed.), *The chimpanzee* (Vol. 3, pp. 337-360). S. Karger.

Davey, G. (2006). Relationships between exhibit naturalism, animal visibility and visitor interest in a Chinese Zoo. *Applied Animal Behaviour Science*, *96*(1), 93-102. https://doi.org/10.1016/j.applanim.2005.04.018

Davey, G. (2007). Visitors' effects on the welfare of animals in the zoo: A Review. *Journal of Applied Animal Welfare Science*, *10*(2), 169-183. https://doi.org/10.1080/10888700701313595

Davis, L. H. (2008). Self-consciousness in chimps and pigeons. *Philosophical Psychology*, *2*(3), 249--259. https://doi.org/10.1080/09515088908572977

Davis, N., Schaffner, C. M., & Smith, T. E. (2005). Evidence that zoo visitors influence HPA activity in spider monkeys (Ateles geoffroyii rufiventris). *Applied Animal Behaviour Science*, *90*(2), 131-141. https://doi.org/10.1016/j.applanim.2004.08.020

De Domenico, M., Nicosia, V., Arenas, A., & Latora, V. (2014). Layer aggregation and reducibility of multilayer interconnected networks. *arXiv*. https://doi.org/10.1038/ncomms7864

De Domenico, M., Nicosia, V., Arenas, A., & Latora, V. (2015). Structural reducibility of multilayer networks. *Nature Communications*, *6*(1), 6864. https://doi.org/10.1038/ncomms7864

De Domenico, M., Porter, M. A., & Arenas, A. (2015). MuxViz: a tool for multilayer analysis and visualization of networks. *Journal of Complex Networks*, *3*(2), 159-176. https://doi.org/10.1093/comnet/cnu038

De Domenico, M., Solé-Ribalta, A., Cozzo, E., Kivelä, M., Moreno, Y., Porter, M. A., . . . Arenas, A. (2013). Mathematical formulation of multilayer networks. *Physical Review X*, *3*(4), 41022. https://doi.org/10.1103/PhysRevX.3.041022

De Domenico, M., Solé-Ribalta, A., Omodei, E., Gómez, S., & Arenas, A. (2015). Ranking in interconnected multilayer networks reveals versatile nodes. *Nature Communications*, *6*(1), 6868. https://doi.org/10.1038/ncomms7868

de Waal, F. (1997). The chimpanzee's service economy: Food for grooming. *Evolution and Human Behavior*, *18*(6), 375-386. https://doi.org/10.1016/S1090-5138(97)00085-8

de Waal, F. B. (1989). The myth of a simple relation between space and aggression in captive primates. *Zoo Biology*, *8*(S1), 141-148. https://doi.org/10.1002/zoo.1430080514

de Waal, F. B. M. (1996). Chimpanzee's adaptive potential: A comparison of social life under captive and wild conditions. In R. W. Wrangham, W. C. McGrew, F. B. de Waal, & B. G. Heltne (Eds.), *Chimpanzee cultures* (pp. 243-260). Harvard University Press.

de Waal, F. B. M. (2011). What is an animal emotion? *Annals of the New York Academy of Sciences*, *1224*(1), 191-206. https://doi.org/https://doi.org/10.1111/j.1749-6632.2010.05912.x

Devaux, C. A., Mediannikov, O., Medkour, H., & Raoult, D. (2019). Infectious disease risk across the growing human-non human primate interface: A review of the evidence. *Frontiers in Public Health*, *7*. https://doi.org/10.3389/fpubh.2019.00305

Dobson, A. (2001). An introduction to generalized linear models, Second Edition. *An Introduction to Generalized Linear Models, Second Edition*, *20011128*. https://doi.org/10.1201/9781420057683

Doyle, C. (2017). Captive wildlife sanctuaries: Definition, ethical considerations and public perception. *Animal Studies Journal*, *6*(2), 55-85. https://ro.uow.edu.au/asj/vol6/iss2/5

Doyle, R. E., Lee, C., Deiss, V., Fisher, A. D., Hinch, G. N., & Boissy, A. (2011). Measuring judgement bias and emotional reactivity in sheep following long-term exposure to unpredictable and aversive events. *Physiology & Behavior*, *102*(5), 503-510. https://doi.org/https://doi.org/10.1016/j.physbeh.2011.01.001

Dufour, V., Sueur, C., Whiten, A., & Buchanan-Smith, H. M. (2011). The impact of moving to a novel environment on social networks, activity and wellbeing in two new world primates. *American Journal of Primatology*, *73*(8), 802-811. https://doi.org/10.1002/ajp.20943

Dunbar, R. I. M. (1991). Functional significance of social grooming in primates. *Folia Primatologica*, *57*(3), 121-131. https://doi.org/10.1159/000156574

Duncan, I. J. H. (2019). Animal welfare: A brief history. In S. Hild & L. Schweitzer (Eds.), *Animal Welfare: From Science to Law* (pp. 13-19). La Fondation Droit Animal, Éthique et Sciences (LFDA).

EARS. (2019). *European Alliance of Rescue centres and Sanctuaries: The role of rescue centres and sanctuaries*. Retrieved 05/05/2019 from http://ears.org/about-ears/the-role-of-rescue-centres-and-sanctuaries

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E. C., Di Fiore, A., . . . Li, B. G. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, *3*(1). https://doi.org/10.1126/sciadv.1600946

Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, *84*(5), 1144-1163. https://doi.org/10.1111/1365-2656.12418

Farm Animal Welfare Council. (1993). *Second Report on Priorities for Research and Development in Farm Animal Welfare*. DEFRA.

Feldblum, J. T., Krupenye, C., Bray, J., Pusey, A. E., & Gilby, I. C. (2021). Social bonds provide multiple pathways to reproductive success in wild male chimpanzees. *iScience*, *24*(8), 102864. https://doi.org/https://doi.org/10.1016/j.isci.2021.102864

Feliu, O., Masip, M., Maté, C., Sánchez-López, S., Crailsheim, D., & Kalcher-Sommersguter, E. (2022). Behavioural development of three former pet chimpanzees a decade after arrival at the MONA Sanctuary. *Animals*, *12*(2), 138. https://doi.org/10.3390/ani12020138

Ferdowsian, H., & Merskin, D. (2012). Parallels in sources of trauma, pain, distress, and suffering in humans and nonhuman animals. *Journal of Trauma & Dissociation*, *13*(4), 448-468. https://doi.org/10.1080/15299732.2011.652346

Ferdowsian, H. R., Durham, D. L., Johnson, C. M., Brüne, M., Kimwele, C., Kranendonk, G., . . . Ajarova, L. (2012). Signs of generalized anxiety and compulsive disorders in chimpanzees. *Journal of Veterinary Behavior*, *7*(6), 353-361. https://doi.org/https://doi.org/10.1016/j.jveb.2012.01.006

Ferdowsian, H. R., Durham, D. L., Kimwele, C., Kranendonk, G., Otali, E., Akugizibwe, T., . . . Johnson, C. M. (2011). Signs of mood and anxiety disorders in chimpanzees. *Plos ONE*, *6*(6). https://doi.org/10.1371/journal.pone.0019855

Fernandez, E. J., Tamborski, M. A., Pickens, S. R., & Timberlake, W. (2009). Animal–visitor interactions in the modern zoo: Conflicts and interventions. *Applied Animal Behaviour Science*, *120*(1-2), 1--8. https://doi.org/10.1016/j.applanim.2009.06.002

Field, T. (1985). Attachment as psychobiological attunement: Being on the same wavelength. In M. Reite & T. Field (Eds.), *The psychobiology of attachment and separation* (pp. 415-454). Academic Press.

Finn, K. R., Silk, M. J., Porter, M. A., & Pinter-Wollman, N. (2019). The use of multilayer network analysis in animal behaviour. *Animal Behaviour, 149,* 7-22. https://doi.org/10.1016/j.anbehav.2018.12.016

Fitch, A. L., Merhalski, J. J., & Bloomsmith, M. A. (1989). Social housing for captive adult male chimpanzees: Comparing single-male and multi-male social groups. *American Journal of Primatology*, *Suppl 1*, 87-91.

Flack, J. C., Jeannotte, L. A., & de Waal, F. (2004). Play signaling and the perception of social rules by juvenile chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *118*(2), 149. https://doi.org/10.1037/0735-7036.118.2.149

Fontsere, C., Kuhlwilm, M., Morcillo-Suarez, C., Alvarez-Estape, M., Lester, J. D., Gratton, P., . . . Marques-Bonet, T. (2022). Population dynamics and genetic connectivity in recent chimpanzee history. *Cell Genomics*, *2*(6), 100133. https://doi.org/https://doi.org/10.1016/j.xgen.2022.100133

Fox, J., & Weisberg, S. (2011). *An {R} companion to applied regression* (Second ed.). Sage Publications, Inc. http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Fragaszy, D. M., & Mitchell, G. (1974). Infant socialization in primates. *Journal of Human Evolution*, *3*(6), 563--574. https://doi.org/10.1016/0047-2484(74)90017-7

Fraser, O. N., & Aureli, F. (2008). Reconciliation, consolation and postconflict behavioral specificity in chimpanzees. *American Journal of Primatology*, *70*(12), 1114-1123. https://doi.org/10.1002/ajp.20608

Freeman, H. D., & Ross, S. R. (2014). The impact of atypical early histories on pet or performer chimpanzees. *PeerJ*, *2*. https://doi.org/10.7717/peerj.579

Freeman, H. D., Weiss, A., & Ross, S. R. (2016). Atypical early histories predict lower extraversion in captive chimpanzees. *Developmental Psychobiology*, *58*(4), 519-527. https://doi.org/10.1002/dev.21395

Fultz, A. (2017). A guide for modern sanctuaries with examples from a captive chimpanzee sanctuary. *Animal Studies Journal*, *6*(2), 9-29.

Fultz, A., Yanagi, A., Breaux, S., & Beaupre, L. (2022). Aggressive, submissive, and affiliative behavior in sanctuary chimpanzees (pan troglodytes) during social integration. *Animals*, *12*(18), 2421. https://doi.org/10.3390/ani12182421

Funkhouser, J. A., Mayhew, J. A., & Mulcahy, J. B. (2018). Social network and dominance hierarchy analyses at Chimpanzee Sanctuary Northwest. *Plos ONE*, *13*(2). https://doi.org/10.1371/journal.pone.0191898

Funkhouser, J. A., Mayhew, J. A., Mulcahy, J. B., & Sheeran, L. K. (2020). Human caregivers are integrated social partners for captive chimpanzees. *Primates*. https://doi.org/10.1007/s10329-020-00867-6

Gartner, M. C. (2023). Questionnaires and their use in primate welfare. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman Primate Welfare: From History, Science, and Ethics to Practice* (pp. 255-264). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_11

Gartner, M. C., & Weiss, A. (2018). Studying primate personality in zoos: implications for the management, welfare and conservation of great apes. *International Zoo Yearbook*, *52*(1), 79-91. https://doi.org/10.1111/izy.12187

Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., & Pusey, A. E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, *67*(3), 373-381. https://doi.org/10.1007/s00265-012-1457-6

Gilmer, W. S., & McKinney, W. T. (2003). Early experience and depressive disorders: human and non-human primate studies. *Journal of Affective Disorders*, *75*(2), 97-113. https://doi.org/10.1016/S0165-0327(03)00046-6

Glatston, A. R., Geilvoet-Soeteman, E., Hora-Pecek, E., & Van Hooff, J. A. (1984). The influence of the zoo environment on social behavior of groups of cotton-topped tamarins,Saguinus oedipus oedipus. *Zoo biology*, *3*(3), 241-253. https://doi.org/10.1002/zoo.1430030307

Gluckman, P. D., & Hanson, M. A. (2004). Living with the Past: Evolution, Development, and Patterns of Disease. *Science*, *305*(5691), 1733-1736. https://doi.org/10.1126/science.1095292

Godinez, A. M., & Fernandez, E. J. (2019). What is the zoo experience? How zoos impact a visitor’s behaviors, perceptions, and conservation efforts. *Frontiers in Psychology*, *10*, 1746. https://doi.org/10.3389/fpsyg.2019.01746

Gonder, M., Locatelli, S., Ghobrial, L., Mitchell, M. W., Kujawski, J. T., Lankester, F. J., . . . Tishkoff, S. A. (2011). Evidence from Cameroon reveals differences in the genetic structure and histories of chimpanzee populations. *Proceedings of the National Academy of Sciences*, *108*(12), 4766-4771. https://doi.org/10.1073/pnas.1015422108

Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, *1*, 161-311. https://doi.org/10.1016/S0066-1856(68)80003-2

Goodall, J. (1973). The behavior of chimpanzees in their natural habitat. *American Journal of Psychiatry*, *130*(1), 1-12. https://doi.org/10.1176/ajp.130.1.1

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Harvard University Press.

Goodall, J. (1996). *Great Ape Societies*. Cambridge University Press. https://doi.org/10.1017/CBO9780511752414

Goodall, J., Bandora, A., Bermann, E., Busse, C., Matama, H., Mpongo, E., . . . Riss, D. (1979). Intercommunity interactions in the chimpanzee population of the Gombe National Park. In D. A. Hamburg & E. R. McCown (Eds.), *The Great Apes* (pp. 13-53). Benjamin/Cummings Publishing Company.

Google Maps. (2023). *Fundació MONA*. Satellite image. Retrieved from https://earth.google.com/web/@41.9026426,2.81718445,91.82353933a,212.65964273d,35y,115.42521748h,0t,0r/data=OgMKATA

Goossens, B., Setchell, J. M., Tchidongo, E., Dilambaka, E., Vidal, C., Ancrenaz, M., & Jamart, A. (2005). Survival, interactions with conspecifics and reproduction in 37 chimpanzees released into the wild. *Biological Conservation*, *123*(4), 461-475. https://doi.org/https://doi.org/10.1016/j.biocon.2005.01.008

Great Ape Information Network. (2023). *Chimpanzees in Japan*. Retrieved 22/06/2023 from https://shigen.nig.ac.jp/gain/ViewIndividualList.do?chim=true&livingOnly=&japan=true

Green, S. J., Boruff, B. J., Niyigaba, P., Ndikubwimana, I., & Grueter, C. C. (2020). Chimpanzee ranging responses to fruit availability in a high-elevation environment. *American Journal of Primatology*, *82*(5), e23119. https://doi.org/https://doi.org/10.1002/ajp.23119

Grimm, D. (2017). Chimps in waiting. *Science*, *356*(6343), 1114 LP-1117. https://doi.org/10.1126/science.356.6343.1114

Gross, M. (2023). Human population at the crossroads. *Current Biology*, *33*(1), R1-R3. https://doi.org/https://doi.org/10.1016/j.cub.2022.12.030

Grueter, C. C., Bissonnette, A., Isler, K., & van Schaik, C. P. (2013). Grooming and group cohesion in primates: implications for the evolution of language. *Evolution and Human Behavior*, *34*(1), 61-68. https://doi.org/10.1016/j.evolhumbehav.2012.09.004

Hamada, Y., Udono, T., Teramoto, M., & Sugawara, T. (1996). The growth pattern of chimpanzees: Somatic growth and reproductive maturation inPan troglodytes. *Primates*, *37*(3), 279-295. https://doi.org/10.1007/BF02381860

Hannah, A. C., & McGrew, W. C. (1991). Rehabilitation of captive chimpanzees. In B. H.O. (Ed.), *Primate responses to environmental change*. Springer. https://doi.org/10.1007/978-94-011-3110-0_9

Harding, E. J., Paul, E. S., & Mendl, M. (2004). Cognitive bias and affective state. *Nature*, *427*(6972), 312-312. https://doi.org/doi.org/10.1038/427312a

Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, *59*(4), 771--785. https://doi.org/10.1006/anbe.1999.1377

Harrison, R. (1964). *Animal Machines: The New Factory Farming Industry*. Vincent Stuart Ltd.

Hayashi, M., & Matsuzawa, T. (2017). Mother-infant interactions in captive and wild chimpanzees. *Infant Behav Dev*, *48*(Pt A), 20-29. https://doi.org/10.1016/j.infbeh.2016.11.008

Haynes, R. P. (2011). Competing conceptions of animal welfare and their ethical implications for the treatment of non-human animals. *Acta Biotheor*, *59*(2), 105-120. https://doi.org/10.1007/s10441-011-9124-2

Hemelrijk, C. K. (1994). Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*(48), 479-481. https://doi.org/10.1006/anbe.1994.1264

Herbinger, I., Boesch, C., & journal of primatology, R.-H. (2001). Territory characteristics among three neighboring chimpanzee communities in the Taï National Park, Côte d'Ivoire. *International Journal of Primatology*. https://link.springer.com/article/10.1023/A:1005663212997

Herman, J. L. (1992). Complex PTSD: A syndrome in survivors of prolonged and repeated trauma. *Journal of Traumatic Stress*, *5*(3), 377--391. https://doi.org/10.1002/jts.2490050305

Hevesi, R. (2023). The welfare of primates kept as pets and entertainers. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman primate welfare: From history, science, and ethics to practice* (pp. 121-144). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_6

Hicks, T. C., Darby, L., Hart, J., Swinkels, J., January, N., & Menken, S. (2010). Trade in orphans and bushmeat threatens one of the Democratic Republic of the Congo's most important populations of Eastern Chimpanzees *(Pan troglodytes schweinfurthii)*. *African Primates*, *7*(1), 1-18. http://dare.uva.nl/document/2/83525

Hill, K., Boesch, C., Goodall, J., Pusey, A., Williams, J., & Wrangham, R. (2001). Mortality rates among wild chimpanzees. *Journal of Human Evolution*, *40*(5), 437-450. https://doi.org/10.1006/jhev.2001.0469

Hiraiwa-Hasegawa, M., Hasegawa, T., & Nishida, T. (1984). Demographic study of a large-sized unit-group of chimpanzees in the mahale mountains, Tanzania: A preliminary report. *Primates*, *25*(4), 401-413. https://doi.org/10.1007/BF02381663

Hirata, S. (2020). Chimpanzee Kanako. *Primates*, *61*(5), 635-638. https://doi.org/10.1007/s10329-020-00856-9

Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *Plos Biology*, *12*(9). https://doi.org/10.1371/journal.pbio.1001960

Hobson, E. A. (2019). Differences in social information are critical to understanding aggressive behavior in animal dominance hierarchies. *Current opinion in psychology*, *33*, 209-215. https://doi.org/10.1016/j.copsyc.2019.09.010

Hobson, E. A., Ferdinand, V., Kolchinsky, A., & Garland, J. (2019). Rethinking animal social complexity measures with the help of complex systems concepts. *Animal Behaviour*, *155*, 287-296. https://doi.org/10.1016/j.anbehav.2019.05.016

Hockings, K. J. (2009a). Best practice guidelines for the prevention and mitigation of conflict between humans and great apes. *Occasional Paper of the IUCN Species Survival Commission,*(37), 40. https://doi.org/10.2305/IUCN.CH.2009.SSC-OP.37.en

Hockings, K. J. (2009b). Living at the interface: Human–chimpanzee competition, coexistence and conflict in Africa. *Interaction Studies*, *10*(2), 183-205. https://doi.org/10.1075/is.10.2.05hoc

Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2009). Use of wild and cultivated foods by chimpanzees at Bossou, Republic of Guinea: feeding dynamics in a human-influenced environment. *American Journal of Primatology*, *71*(8), 636-646. https://doi.org/10.1002/ajp.20698

Hopkins, W. D., Russell, J. L., Remkus, M., Freeman, H., & Schapiro, S. J. (2007). Handedness and grooming in Pan troglodytes: comparative analysis between findings in captive and wild individuals. *International Journal of Primatology*, *28*(6), 1315-1326.

Hosey, G. (2008). A preliminary model of human–animal relationships in the zoo. *Applied Animal Behaviour Science*, *109*(2-4), 105-127. https://doi.org/10.1016/j.applanim.2007.04.013

Hosey, G. (2023). The history of primates in zoos. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman Primate Welfare: From History, Science, and Ethics to Practice* (pp. 3-29). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_1

Hosey, G., Melfi, V., Formella, I., Ward, S. J., Tokarski, M., Brunger, D., . . . Hill, S. P. (2016). Is wounding aggression in zoo-housed chimpanzees and ring-tailed lemurs related to zoo visitor numbers? *Zoo Biology*, *35*(3), 205-209. https://doi.org/10.1002/zoo.21277

Hosey, G. R. (2000). Zoo animals and their human audiences: What is the visitor effect? *Animal Welfare*, *9*(4), 343-357. https://doi.org/10.1017/S0962728600022946

Hosey, G. R. (2005). How does the zoo environment affect the behaviour of captive primates? *Applied Animal Behaviour Science*, *90*(2), 107--129. https://doi.org/10.1016/j.applanim.2004.08.015

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*(3), 346-363. https://doi.org/10.1002/bimj.200810425

Humle, T., Colin, C., Laurans, M., & Raballand, E. (2011). Group release of sanctuary chimpanzees (pan troglodytes) in the Haut Niger National Park, Guinea, West Africa: Ranging patterns and lessons so far. *International Journal of Primatology*, *32*(2), 456-473. https://doi.org/10.1007/s10764-010-9482-7

Humle, T., Maisels, F., Oates, J. F., Plumptre, A., & Williamson, E. A. (2016). *Pan troglodytes. The IUCN Red List of Threatened Species 2016*. T. I. R. L. o. T. Species.

Inoue, N., & Shimada, M. (2020). Comparisons of activity budgets, interactions, and social structures in captive and wild chimpanzees (pan troglodytes). *Animals*, *10*(6), 1063. https://doi.org/10.3390/ani10061063

Inoue, S., & Matsuzawa, T. (2007). Working memory of numerals in chimpanzees. *Current Biology*, *17*(23), R1004--R1005. https://doi.org/10.1016/j.cub.2007.10.027

Institute of Medicine and National Research Council. (2011). *Chimpanzees in biomedical and behavioral research: Assessing the necessity*. National Academies Press (US). https://doi.org/10.17226/13257

Itani, J., & Suzuki, A. (1967). The social unit of chimpanzees. *Primates*, *8*(4), 355-381. https://doi.org/10.1007/BF01792020

Jacobs, A., & Petit, O. (2011). Social network modeling: A powerful tool for the study of group scale phenomena in primates. *American Journal of Primatology*, *73*(8), 741-747. https://doi.org/10.1002/ajp.20932

Jacobson, S. L., Freeman, H. D., Santymire, R. M., & Ross, S. R. (2017). Atypical experiences of captive chimpanzees *(Pan troglodytes)* are associated with higher hair cortisol concentrations as adults. *Royal Society Open Science*, *4*(12), 170932. https://doi.org/10.1098/rsos.170932

Jamieson, D. (2008). Against zoos. *Revista Brasileira de Direito Animal*, *3*(4).

Jeffries, M. J. (2006). *Biodiversity and conservation* (2n ed. ed.). Routledge. https://books.google.es/books?id=PdW5AaoZo9IC

Jensvold, M. L. A. (2008). Chimpanzee (pan troglodytes) responses to caregiver use of chimpanzee behaviors. *Zoo Biology*, *27*(5), 345-359. https://doi.org/10.1002/zoo.20194

Johnsen, D. O., Johnson, D. K., & Whitney, R. A. (2012). History of the use of nonhuman primates in biomedical research. In C. R. Abee, K. Mansfield, S. D. Tardif, & T. Morris (Eds.), *Nonhuman Primates in Biomedical Research: Biology and Management* (pp. 1-33). Academic Press. https://doi.org/10.1016/B978-0-12-381365-7.00001-7

Kabasawa, A. (2011). The chimpanzees of West Africa: From “man-like beast” to “our endangered cousin”. In T. Matasuzawa, T. Humle, & Y. Sugiyama (Eds.), *The chimpanzees of Bossou and Nimba* (pp. 45-57). Springer. https://doi.org/10.1007/978-4-431-53921-6_6

Kagan, R. (2017). Sanctuaries. Zoos of the future? In J. Donahuem (Ed.), *Increasing legal rights for zoo animals* (pp. 131-146). Lexington Books.

Kahlenberg, S. M., Thompson, M., Muller, M. N., & Wrangham, R. W. (2008). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behaviour*, *76*(5), 1497-1509. https://doi.org/10.1016/j.anbehav.2008.05.029

Kalcher-Sommersguter, E., Franz-Schaider, C., Crailsheim, K., & Preuschoft, S. (2013). Social competence of adult chimpanzees (Pan troglodytes) with severe deprivation history: A relational approach. *International Journal of Comparative Psychology*, *26*, 136-157.

Kalcher-Sommersguter, E., Preuschoft, S., Crailsheim, K., & Franz, C. (2011). Social competence of adult chimpanzees *(Pan troglodytes)* with severe deprivation history: I. An individual approach. *Developmental Psychology*, *47*(1), 77-90. https://doi.org/10.1037/a0020783

Kalcher-Sommersguter, E., Preuschoft, S., Franz-Schaider, C., Hemelrijk, C. K., Crailsheim, K., & Massen, J. J. M. (2015). Early maternal loss affects social integration of chimpanzees throughout their lifetime. *Scientific Reports*, *5*(1). https://doi.org/10.1038/srep16439

Kalcher, E., Franz, C., Crailsheim, K., & Preuschoft, S. (2008). Differential onset of infantile deprivation produces distinctive long-term effects in adult ex-laboratory chimpanzees *(Pan troglodytes)*. *Developmental Psychobiology*, *50*, 777-788. https://doi.org/10.1002/dev.20330

Kanngiesser, P., Sueur, C., Riedl, K., Grossmann, J., & Call, J. (2011). Grooming network cohesion and the role of individuals in a captive chimpanzee group. *American Journal of Primatology*, *73*(8), 758-767. https://doi.org/10.1002/ajp.20914

Kano, F., Yamanashi, Y., & Tomonaga, M. (2012). Emotion as intervening variable in understanding the cognitive and social complexity and well-being of chimpanzees. *Psychologia*, *55*(1), 9-20. https://doi.org/10.2117/psysoc.2012.9

Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. *Primates*, *50*(4), 343-356. https://doi.org/10.1007/s10329-009-0153-2

Kawai, N., & Matsuzawa, T. (2000). Numerical memory span in a chimpanzee. *Nature*, *403*(6765), 39-40. https://doi.org/10.1038/47405

Keeling, M. E., Alford, P. L., & Bloomsmith, M. A. (1991). Decision analysis for developing programs of psychological well-being: A bias-for-action approach. In *Through the looking glass: Issues of psychological well-being in captive nonhuman primates.* (pp. 57-65). American Psychological Association. https://doi.org/10.1037/10080-007

Kerr, G. R., Chamove, A. S., & Harlow, H. F. (1969). Environmental deprivation: its effect on the growth of infant monkeys. *The Journal of Pediatrics*, *75*(5), 833-837. https://doi.org/10.1016/S0022-3476(69)80307-0

King, N. E., & Mellen, J. D. (1994). The effects of early experience on adult copulatory behavior in zoo-born chimpanzees (Pan troglodytes). *Zoo Biology*, *13*(1), 51-59. https://doi.org/https://doi.org/10.1002/zoo.1430130107

King, T., Chamberlan, C., & Courage, A. (2012). Assessing initial reintroduction success in long-lived primates by quantifying survival, reproduction, and dispersal parameters: Western Lowland Gorillas (Gorilla gorilla gorilla) in Congo and Gabon. *International Journal of Primatology*, *33*(1), 134--149. https://doi.org/10.1007/s10764-011-9563-2

Kisling, V. N. (2000). *Zoo and Aquarium History: Ancient Animal Collections to Zoological Gardens*. CRC Press.

Kivela, M., Arenas, A., Barthelemy, M., Gleeson, J. P., Moreno, Y., & Porter, M. A. (2014). Multilayer networks. *Journal of Complex Networks*, *2*(3), 203-271. https://doi.org/10.1093/comnet/cnu016

Koene, P., & Ipema, B. (2014). Social networks and welfare in future animal management. *Animals*, *4*(1), 93-118. https://doi.org/10.3390/ani4010093

Kolk, B. A. v. d., Roth, S., Pelcovitz, D., Sunday, S., & Spinazzola, J. (2005). Disorders of extreme stress: The empirical foundation of a complex adaptation to trauma. *Journal of Traumatic Stress*, *18*(5), 389--399. https://doi.org/10.1002/jts.20047

Kormos, R., Boesch, C., Bakarr, M. I., & Butynski, T. M. (2003). *West African Chimpanzees: Status survey and conservation action plan*. IUCN/SSC Primate Specialist Group.

Koski, S. E., de Vries, H., van de Kraats, A., & Sterck, E. H. M. (2012). Stability and change of social relationship quality in captive chimpanzees *(Pan troglodytes)*. *International Journal of Primatology*, *33*(4), 905-921. https://doi.org/10.1007/s10764-012-9623-2

Koyama, N. F., & Aureli, F. (2019). Social network changes during space restriction in zoo chimpanzees. *Primates*, *60*(3), 203-211. https://doi.org/10.1007/s10329-018-0675-6

Kraemer, G. W. (1997). Psychobiology of early social attachment in rhesus monkeys clinical implications. *Annals of the New York Academy of Sciences*, *807*(1), 401--418. https://doi.org/10.1111/j.1749-6632.1997.tb51935.x

Kreger, M. D., & Mench, J. A. (1995). Visitor—animal interactions at the zoo. *Anthrozoos: A Multidisciplinary Journal of The Interactions of People & Animals*, *8*(3), 143-158. https://doi.org/10.2752/089279395787156301

Kreppner, J. M., O'Connor, T. G., & Rutter, M. (2001). Can inattention/overactivity be an institutional deprivation syndrome? *Journal of Abnormal Child Psychology*, *29*(6), 513-528. https://doi.org/10.1023/a:1012229209190

Kret, M. E., Muramatsu, A., & Matsuzawa, T. (2018). Emotion processing across and within species: A comparison between humans (Homo sapiens) and chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *132*, 395-409. https://doi.org/10.1037/com0000108

Krief, S., Cibot, M., Bortolamiol, S., Seguya, A., Krief, J.-M., & Masi, S. (2014). Wild chimpanzees on the edge: Nocturnal activities in croplands. *Plos ONE*, *9*(10). https://doi.org/10.1371/journal.pone.0109925

Kummrow, M. (2021). Diagnostic and therapeutic guidelines to abnormal behavior in captive nonhuman primates. *Veterinary Clinics of North America: Exotic Animal Practice*, *24*(1), 253--266. https://doi.org/10.1016/j.cvex.2020.09.012

Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences*, *104*(19), 7786-7790. https://doi.org/10.1073/pnas.0611449104

Langergraber, K. E., Rowney, C., Schubert, G., Crockford, C., Hobaiter, C., Wittig, R., . . . Vigilant, L. (2014). How old are chimpanzee communities? Time to the most recent common ancestor of the Y-chromosome in highly patrilocal societies. *Journal of Human Evolution*, *69*, 1-7. https://doi.org/https://doi.org/10.1016/j.jhevol.2013.12.005

Laurence, H., Kumar, S., Owston, M. A., Lanford, R. E., Hubbard, G. B., & Dick Jr., E. J. (2017). Natural mortality and cause of death analysis of the captive chimpanzee (Pan troglodytes): A 35-year review. *Journal of Medical Primatology*, *46*(3), 106-115. https://doi.org/https://doi.org/10.1111/jmp.12267

Leavens, D. A., & Hopkins, W. D. (1998). Intentional communication by chimpanzees: a cross-sectional study of the use of referential gestures. *Developmental Psychology*, *34*(5), 813-822. https://doi.org/10.1037//0012-1649.34.5.813

Lehmann, J., & Boesch, C. (2004). To fission or to fusion: effects of community size on wild chimpanzee *(Pan troglodytes verus)* social organisation. *Behavioral Ecology and Sociobiology*, *56*(3), 207-216. https://doi.org/10.1007/s00265-004-0781-x

Lehmann, J., & Boesch, C. (2008). Sexual differences in chimpanzee sociality. *International Journal of Primatology*, *29*(1), 65-81. https://doi.org/10.1007/s10764-007-9230-9

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007a). Fission–fusion social systems as a strategy for coping with ecological constraints: a primate case. *Evolutionary Ecology*, *21*(5), 613-634. https://doi.org/10.1007/s10682-006-9141-9

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007b). Group size, grooming and social cohesion in primates. *Animal Behaviour*, *74*(6), 1617-1629. https://doi.org/10.1016/j.anbehav.2006.10.025

Leroy, E. M., Rouquet, P., Formenty, P., Souquière, S., Kilbourne, A., Froment, J.-M., . . . Rollin, P. E. (2004). Multiple ebola virus transmission events and rapid decline of central African wildlife. *Science*, *303*(5656), 387-390. https://doi.org/doi:10.1126/science.1092528

Lester, J. D., Vigilant, L., Gratton, P., McCarthy, M. S., Barratt, C. D., Dieguez, P., . . . Arandjelovic, M. (2021). Recent genetic connectivity and clinal variation in chimpanzees. *Commun Biol*, *4*(1), 283. https://doi.org/10.1038/s42003-021-01806-x

Levé, M., Sueur, C., Petit, O., Matsuzawa, T., & Hirata, S. (2016). Social grooming network in captive chimpanzees: does the wild or captive origin of group members affect sociality? *Primates*, *57*(1), 73-82. https://doi.org/10.1007/s10329-015-0494-y

Lewis, A., Berntsen, D., & Call, J. (2019). Long-term memory of past events in great apes. *Current Directions in Psychological Science*, *28*, 117-123. https://doi.org/10.1177/0963721418812781

Lewton, K. L. (2017). The effects of captive versus wild rearing environments on long bone articular surfaces in common chimpanzees (Pan troglodytes). *PeerJ*, *5*. https://doi.org/10.7717/peerj.3668

Lindsey, P., Balme, G., Becker, M., Begg, C., Bento, C., Bocchino, C., . . . Zisadza-Gandiwa, P. (2013). The bushmeat trade in African savannas: Impacts, drivers, and possible solutions. *Biological Conservation*, *160*, 80-96. https://doi.org/10.1016/j.biocon.2012.12.020

Littleton, J. (2005). Fifty years of chimpanzee demography at Taronga Park Zoo [https://doi.org/10.1002/ajp.20185]. *American Journal of Primatology*, *67*(3), 281-298. https://doi.org/https://doi.org/10.1002/ajp.20185

Loibooki, M., Hofer, H., Campbell, K. L. I., & East, M. L. (2002). Bushmeat hunting by communities adjacent to the Serengeti National Park, Tanzania: the importance of livestock ownership and alternative sources of protein and income. *Environmental Conservation*, *29*(3), 391-398. https://doi.org/10.1017/S0376892902000279

Lonsdorf, E. V. (2013). The role of mothers in the development of complex skills in chimpanzees. In K. B. H. Clancy, K. Hinde, & J. N. Rutherford (Eds.), *Building Babies: Primate Development in Proximate and Ultimate Perspective* (pp. 303-318). Springer New York. https://doi.org/10.1007/978-1-4614-4060-4_14

Lonsdorf, E. V., Ross, S. R., Matsuzawa, T., & Goodall, J. (2010). *The mind of the chimpanzee: Ecological and experimental perspectives*. University of Chicago Press. https://books.google.es/books?id=UCbW-Y37Tp0C

Lonsdorf, E. V., Ross, S. R., Matsuzawa, T., & Goodall, J. (2012). Socialization and development of behavior. In R. A. Palombit, J. C. Mitani, & J. Call (Eds.), *The evolution of primate societies* (pp. 245–268). The University of Chicago Press.

Lonsdorf, E. V., Stanton, M. A., Pusey, A. E., & Murray, C. M. (2019). Sources of variation in weaned age among wild chimpanzees in Gombe National Park, Tanzania. *American Journal of Physical Anthropology*, *171*(3), 419-429. https://doi.org/10.1002/ajpa.23986

Lopresti-Goodman, S. M., Bezner, J., & Ritter, C. (2015). Psychological distress in chimpanzees rescued from laboratories. *Journal of Trauma & Dissociation: the Official Journal of the International Society for the Study of Dissociation*, *16*(4), 349-366. https://doi.org/10.1080/15299732.2014.1003673

Lopresti-Goodman, S. M., Kameka, M., & Dube, A. (2013). Stereotypical behaviors in chimpanzees rescued from the african bushmeat and pet trade. *Behavioural Sciences*, *3*(1), 1-20. https://doi.org/10.3390/bs3010001

Lowenstine, L. J., McManamon, R., & Terio, K. A. (2016). Comparative pathology of aging great apes: Bonobos, chimpanzees, gorillas, and orangutans. *Veterinary Pathology*, *53*(2), 250-276. https://doi.org/10.1177/0300985815612154

Lutz, C. K., & Baker, K. C. (2023). Using behavior to assess primate welfare. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman Primate Welfare: From History, Science, and Ethics to Practice* (pp. 171-205). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_8

Llorente, M. (2020). Coronavirus, primates y extinción. *Boletín de la Asociación Primatológica Española*, *27*(1), 12-23. https://issuu.com/apespain/docs/boletinape_27_1__2020

Llorente, M., Armisen, S., & Feliu, O. (2014). New postgraduate programme in primatology: Enhancing learning through research and practice. *Folia Primatologica*, *85*(1), 67-68.

Llorente, M., & Campi, A. (2014). Is 'tool use' a welfare tool? Using an artificial ant-fishing task as environmental enrichment in naturalistically housed chimpanzees from the Fundacio Mona. *Folia Primatologica*, *85*(1), 68-68.

Llorente, M., Riba, D., Ballesta, S., Feliu, O., & Rostán, C. (2015). Rehabilitation and socialization of chimpanzees *(Pan troglodytes)* used for entertainment and as pets: An 8-Year Study at Fundació Mona. *International Journal of Primatology*, *36*(3), 605-624. https://doi.org/10.1007/s10764-015-9842-4

Llorente, M., Riba, D., Mosquera, M., Ventura, M., & Feliu, O. (2012). Hunting activity among naturalistically housed chimpanzees (*Pan troglodytes*) at the Fundació Mona (Girona, Spain). Predation, occasional consumption and strategies in rehabilitated animals. *Animals*, *2*, 363-376. https://doi.org/10.3390/ani2030363.

Maki, S., Fritz, J., & England, N. (1993). An assessment of early differential rearing conditions on later behavioral development in captive chimpanzees. *Infant Behavior and Development*, *16*(3), 373-381. https://doi.org/https://doi.org/10.1016/0163-6383(93)80042-7

Maple, T. L., & Perdue, B. M. (2013). Designing for animal welfare. In T. Maple & B. M. Perdue (Eds.), *Zoo Animal Welfare* (pp. 139-165). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-35955-2_8

Marsden, S. B., Marsden, D., & Thompson, M. E. (2006). Demographic and female life history parameters of free-ranging chimpanzees at the chimpanzee rehabilitation project, River Gambia National Park. *International Journal of Primatology*, *27*(2), 391--410. https://doi.org/10.1007/s10764-006-9029-0

Martin, C. F., Bhui, R., Bossaerts, P., Matsuzawa, T., & Camerer, C. (2014). Chimpanzee choice rates in competitive games match equilibrium game theory predictions. *Scientific Reports*, *4*(1), 5182. https://doi.org/10.1038/srep05182

Martin, J. E. (2005). The effects of rearing conditions on grooming and play behaviour in captive chimpanzees. *Animal Welfare*, *14*(2), 125-133. https://doi.org/10.1017/S0962728600029122

Martin, P., & Bateson, P. (1993). *Measuring behaviour: An introductory guide* (Second edition ed.). Cambridge University Press.

Martínez-Íñigo, L., Baas, P., Klein, H., Pika, S., & Deschner, T. (2021). Intercommunity interactions and killings in central chimpanzees (Pan troglodytes troglodytes) from Loango National Park, Gabon. *Primates*, *62*(5), 709-722. https://doi.org/10.1007/s10329-021-00921-x

Mason, G., & Mendi, M. (2023). Why is there no simple way of measuring animal welfare? *Animal Welfare*, *2*(4), 301-319. https://doi.org/10.1017/S0962728600016092

Massen, J., Antonides, A., Arnold, A. M. K., Bionda, T., & Koski, S. E. (2013). A behavioral view on chimpanzee personality: Exploration tendency, persistence, boldness, and tool-orientation measured with group experiments. *American Journal of Primatology*, *75*(9), 947-958. https://doi.org/10.1002/ajp.22159

Massen, J., & Koski, S. E. (2014). Chimps of a feather sit together: chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior*, *35*(1), 1-8. https://doi.org/10.1016/j.evolhumbehav.2013.08.008

Matsumoto-Oda, A., Hosaka, K., Huffman, M. A., & Kawanaka, K. (1998). Factors affecting party size in chimpanzees of the Mahale Mountains. *International Journal of Primatology*, *19*(6), 999-1011. https://doi.org/10.1023/A:1020322203166

Matsumoto-Oda, A., & Oda, R. (1998). Changes in the activity budget of cycling female chimpanzees. *American Journal of Primatology*, *46*(2), 157-166. https://doi.org/10.1002/(SICI)1098-2345(1998)46:2<157::AID-AJP5>3.0.CO;2-V

Matsumoto-Oda, A. (1999). Mahale chimpanzees: Grouping patterns and cycling females. *American Journal of Primatology*, *47*(3), 197-207. https://doi.org/10.1002/(SICI)1098-2345(1999)47:3<197::AID-AJP2>3.0.CO;2-3

Matsumoto, T. (2017). Developmental changes in feeding behaviors of infant chimpanzees at Mahale, Tanzania: Implications for nutritional independence long before cessation of nipple contact. *American Journal of Physical Anthropology*, *163*(2), 356-366. https://doi.org/10.1002/ajpa.23212

Matsuzawa, T. (2006). Sociocognitive sevelopment in chimpanzees: A synthesis of laboratory work and fieldwork. In T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds.), *Cognitive development in chimpanzees* (pp. 3-33). Springer. https://doi.org/10.1007/4-431-30248-4_1

Matsuzawa, T. (2009). *Primate origins of human cognition and behavior*. Springer.

McEwen, B. S. (2003). Early life influences on life-long patterns of behavior and health. *Mental Retardation and Developmental Disabilities Research Reviews*, *9*(3), 149-154. https://doi.org/10.1002/mrdd.10074

McFarland, D. S. M., Nowak, M., & Westwood, S. J. (2010). *Social network analysis labs in R.* Stanford University.

McGoron, L., Gleason, M., Smyke, A. T., Drury, S. S., Nelson, C. A., Gregas, M. C., . . . Zeanah, C. H. (2012). Recovering from early deprivation: Attachment mediates effects of caregiving on psychopathology. *Journal of the American Academy of Child & Adolescent Psychiatry*, *51*(7), 683-693. https://doi.org/10.1016/j.jaac.2012.05.004

McLennan, M. R. (2013). Diet and feeding ecology of chimpanzees (pan troglodytes) in Bulindi, Uganda: Foraging strategies at the forest–farm interface. *International Journal of Primatology*, *34*(3), 585-614. https://doi.org/10.1007/s10764-013-9683-y

McLennan, M. R., & Hill, C. M. (2010). Chimpanzee responses to researchers in a disturbed forest-farm mosaic at Bulindi, western Uganda. *American Journal of Primatology*, *72*(10), 907-918. https://doi.org/10.1002/ajp.20839

McMillan, F. D., & Yeates, J. W. (2020). The problems with well-being terminology. In F. D. McMillan (Ed.), *Mental health and well-being in animals* (pp. 8-20). CABI Books. https://doi.org/10.1079/9781786393401.0008

Mellor, D. J. (2016). Updating animal welfare thinking: Moving beyond the "Five Freedoms" towards "A Life Worth Living". *Animals*, *6*(3), 21. https://doi.org/10.3390/ani6030021

Mellor, D. J., & Beausoleil, N. J. (2015). Extending the 'Five Domains' model for animal welfare assessment to incorporate positive welfare states. *Animal Welfare*, *24*(3), 241-253. https://doi.org/10.7120/09627286.24.3.241

Mellor, D. J., Beausoleil, N. J., Littlewood, K. E., McLean, A. N., McGreevy, P. D., Jones, B., & Wilkins, C. (2020). The 2020 five domains model: Including human–animal interactions in assessments of animal welfare. *Animals*, *10*(10). https://doi.org/10.3390/ani10101870

Milner-Gulland, E. J., Bennett, E. L., & the Group, S. C. B. (2003). Wild meat: the bigger picture. *Trends in ecology & evolution*, *18*(7), 351-357. https://doi.org/10.1016/S0169-5347(03)00123-X

Miller, C., Bard, K. A., Juno, C. J., & Nadler, R. D. (1990). Behavioral responsiveness to strangers in young chimpanzees (Pan troglodytes). *Folia Primatologica*, *55*(3-4), 142--155. https://doi.org/10.1159/000156510

Mitani, J., & Amsler, S. (2003). Social and spatial aspects of male subgrouping in a community of wild chimpanzees. *Behaviour*, *140*(7), 869-884.

Mitani, J. C., & Watts, D. P. (2005). Correlates of territorial boundary patrol behaviour in wild chimpanzees. *Animal Behaviour*, *70*(5), 1079-1086. https://doi.org/10.1016/j.anbehav.2005.02.012

Mitchell, G., Obradovich, S. D., Herring, F. H., Dowd, B., & Tromborg, C. (1991). Threats to observers, keepers, visitors, and others by zoo mangabeys (Cercocebus galeritus chrysogaster). *Primates*, *32*(4), 515-522. https://doi.org/10.1007/BF02381942

Molina-Vacas, G., Muñoz-Mas, R., Amarasekaran, B., & Garriga, R. M. (2023). Reaffirming the Loma Mountains National Park in Sierra Leone as a critical site for the conservation of West African chimpanzee (Pan troglodytes verus) [https://doi.org/10.1002/ajp.23469]. *American Journal of Primatology*, *n/a*(n/a), e23469. https://doi.org/https://doi.org/10.1002/ajp.23469

Morris, D. (1962). *The biology of art: A study of the picture-making behaviour of the great apes and its relationship to human art*. Knopf. http://books.google.es/books?id=QO4NAAAAQAAJ

Moss, A., & Esson, M. (2010). Visitor interest in zoo animals and the implications for collection planning and zoo education programmes. *Zoo Biology*, *29*(6), 715-731. https://doi.org/https://doi.org/10.1002/zoo.20316

Muller, M. N., & Wrangham, R. W. (2014). Mortality rates among Kanyawara chimpanzees. *Journal of Human Evolution*, *66*, 107-114. https://doi.org/10.1016/j.jhevol.2013.10.004

Murray, C. M., Lonsdorf, E. V., Stanton, M. A., Wellens, K. R., Miller, J. A., Goodall, J., & Pusey, A. E. (2014). Early social exposure in wild chimpanzees: Mothers with sons are more gregarious than mothers with daughters. *Proceedings of the National Academy of Sciences*, *111*(51), 18189--18194. https://doi.org/10.1073/pnas.1409507111

Negrey, J. D., Reddy, R. B., Scully, E. J., Phillips-Garcia, S., Owens, L. A., Langergraber, K. E., . . . Goldberg, T. L. (2019). Simultaneous outbreaks of respiratory disease in wild chimpanzees caused by distinct viruses of human origin. *Emerging Microbes & Infections*, *8*(1), 139-149. https://doi.org/10.1080/22221751.2018.1563456

Newman, M. E. J. (2004). Analysis of weighted networks. *Physical Review E*, *70*(5), 56131. https://doi.org/10.1103/PhysRevE.70.056131

Nimon, A. J., & Dalziel, F. R. (1992). Cross-species interaction and communication: a study method applied to captive siamang (Hylobates syndactylus) and long-billed corella (Cacatua tenuirostris) contacts with humans. *Applied Animal Behaviour Science*, *33*(2), 261-272. https://doi.org/https://doi.org/10.1016/S0168-1591(05)80013-9

Nishida, T. (1988). Development of social grooming between mother and offspring in wild chimpanzees. *Folia Primatologica*, *50*(1-2), 109-123. https://doi.org/10.1159/000156335

Nishida, T. (1990). *The chimpanzees of the Mahale mountains: sexual and life history strategies*. University of Tokyo Press. https://books.google.es/books?id=3aI_AAAAYAAJ

Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., . . . Zamma, K. (2003). Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology*, *59*(3), 99-121. https://doi.org/10.1002/ajp.10068

Ongman, L., Colin, C., Raballand, E., & Humle, T. (2013). The "Super Chimpanzee": The ecological dimensions of rehabilitation of orphan chimpanzees in Guinea, West Africa. *Animals*, *3*(1), 109-126. https://doi.org/10.3390/ani3010109

Ordaz-Németh, I., Arandjelovic, M., Boesch, L., Gatiso, T., Grimes, T., Kuehl, H. S., . . . Junker, J. (2017). The socio-economic drivers of bushmeat consumption during the West African Ebola crisis. *PLOS Neglected Tropical Diseases*, *11*(3). https://doi.org/10.1371/journal.pntd.0005450

Ortin, S., Parera, J., & Llorente, M. (2014). Changes in group dynamics of an already established social group as a result of the integration of a new chimpanzee. *Folia Primatologica*, *85*(1), 69-69.

Ortín, S., Úbeda, Y., Garriga, R. M., & Llorente, M. (2019). Bushmeat trade consequences predict higher anxiety, restraint, and dominance in chimpanzees. *Developmental Psychobiology*, *61*(6), 874-887. https://doi.org/10.1002/dev.21853

Padrell, M., Llorente, M., & Amici, F. (2021). Invasive research on non-human primates - Time to turn the page. *Animals*, *11*(10), 2999. https://doi.org/10.3390/ani11102999

Padrell, M., Riba, D., Úbeda, Y., Amici, F., & Llorente, M. (2020). Personality, cognition and behavior in chimpanzees: a new approach based on Eysenck’s model. *PeerJ*, *8*, e9707. https://doi.org/10.7717/peerj.9707

Parker, E. N., Bramley, L., Scott, L., Marshall, A. R., & Slocombe, K. E. (2018). An exploration into the efficacy of public warning signs: A zoo case study. *PLOS ONE*, *13*(11). https://doi.org/10.1371/journal.pone.0207246

Parker, K. J., & Maestripieri, D. (2011). Identifying key features of early stressful experiences that produce stress vulnerability and resilience in primates. *Neuroscience & Biobehavioral Reviews*, *35*(7), 1466-1483. https://doi.org/10.1016/j.neubiorev.2010.09.003

Pasquaretta, C., Leve, M., Claidiere, N., van de Waal, E., Whiten, A., MacIntosh, A. J., . . . Sueur, C. (2014). Social networks in primates: smart and tolerant species have more efficient networks. *Scientific Reports*, *4*. https://doi.org/10.1038/srep07600

Pasquaretta, C., Levé, M., Claidière, N., van de Waal, E., Whiten, A., MacIntosh, A. J. J., . . . Sueur, C. (2015). Social networks in primates: smart and tolerant species have more efficient networks. *Scientific Reports*, *4*(1), 7600. https://doi.org/10.1038/srep07600

Patrick, P. G., Matthews, C. E., Ayers, D. F., & Tunnicliffe, S. D. (2007). Conservation and education: Prominent themes in zoo mission statements. *The Journal of Environmental Education*, *38*(3), 53-60. https://doi.org/10.3200/JOEE.38.3.53-60

Pazol, K. A., & Bloomsmith, M. A. (1993). The development of stereotyped body rocking in chimpanzees (pan troglodytes) reared in a variety of nursery settings. *Animal Welfare*, *2*(2), 113-129. https://doi.org/10.1017/S0962728600015657

Pechtel, P., & Pizzagalli, D. A. (2011). Effects of early life stress on cognitive and affective function: an integrated review of human literature. *Psychopharmacology*, *214*(1), 55-70. https://doi.org/10.1007/s00213-010-2009-2

Pereira, A. S., Rebelo, I. D., Casanova, C., Lee, P. C., & Louca, V. (2020). The multidimensionality of female mandrill sociality—A dynamic multiplex network approach. *Plos ONE*, *15*(4). https://doi.org/10.1371/journal.pone.0230942

Pérez-Galicia, S., Miranda-Anaya, M., Canales-Espinosa, D., & Muñoz-Delgado, J. (2017). Visitor effect on the behavior of a group of spider monkeys (Ateles geoffroyi) maintained at an island in Lake Catemaco, Veracruz/Mexico. *Zoo biology*, *36*(6), 360-366. https://doi.org/10.1002/zoo.21384

Perkins, L. A. (1992). Variables that influence the activity of captive orangutans. *Zoo Biology*, *11*(3), 177-186. https://doi.org/10.1002/zoo.1430110306

Peterson, D., & Goodall, J. (2000). *Visions of Caliban: on chimpanzees and people*. University of Georgia Press.

Picton, H. (1889). A Chimpanzee's Humour. *Nature*, *40*(1027), 224-224. https://doi.org/10.1038/040224c0

Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., de Silva, S., . . . McDonald, D. B. (2014). The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behavioral Ecology*, *25*(2), 242-255. https://doi.org/10.1093/beheco/art047

Plooij, F. X. (1984). *The behavioral development of free-living chimpanzee babies and infants*. Rijksuniversiteit te Groningen. https://books.google.es/books?id=c-XaAAAAMAAJ

Plooij, F. X., Lipsitt, L. P., Bygott, D., & Sackett, G. P. (1984). *The behavioral development of free-living chimpanzee babies and infants*. Ablex Publishing Corporation. https://books.google.es/books?id=c-XaAAAAMAAJ

Poirier, C., & Bateson, M. (2017). Pacing stereotypies in laboratory rhesus macaques: Implications for animal welfare and the validity of neuroscientific findings. *Neuroscience & Biobehavioral Reviews*, *83*, 508-515. https://doi.org/10.1016/j.neubiorev.2017.09.010

Polgár, Z., Wood, L., & Haskell, M. J. (2017). Individual differences in zoo-housed squirrel monkeys' (Saimiri sciureus) reactions to visitors, research participation, and personality rating. *American Journal of Primatology*, *79*(5), e22639-e22639. https://doi.org/https://doi.org/10.1002/ajp.22639

Pomerantz, O., & Terkel, J. (2009). Effects of positive reinforcement training techniques on the psychological welfare of zoo-housed chimpanzees (Pan troglodytes). *American Journal of Primatology*, *71*(8), 687--695. https://doi.org/10.1002/ajp.20703

Porges, S. W. (2003). Social engagement and attachment. A phylogenetic perspective. *Annals of the New York Academy of Sciences*, *1008*(1), 31-47. https://doi.org/10.1196/annals.1301.004

Potts, K. B., Watts, D. P., & Wrangham, R. W. (2011). Comparative feeding ecology of two communities of chimpanzees (pan troglodytes) in Kibale National Park, Uganda. *International Journal of Primatology*, *32*(3), 669-690. https://doi.org/10.1007/s10764-011-9494-y

Poulsen, J. R., Clark, C. J., Mavah, G., & Elkan, P. W. (2009). Bushmeat supply and consumption in a tropical logging concession in Northern Congo. *Conservation Biology*, *23*(6), 1597-1608. https://doi.org/10.1111/j.1523-1739.2009.01251.x

Prescott, M. J. (2023). Using primates in captivity: Research, conservation, and education. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman Primate Welfare: From History, Science, and Ethics to Practice* (pp. 57-78). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_3

Pruetz, J. D. E., & McGrew, W. C. (2001). What does a chimpanzee need? Using natural behavior to guide the care and management of captive populations. In L. Brent (Ed.), *The care and management of captive chimpanzees* (Vol. Volume 2, pp. 16-37). American Society of Primatologists.

Pusey, A. E. (1983). Mother-offspring relationships in chimpanzees after weaning. *Animal Behaviour, 31*(2), 363-377. https://doi.org/10.1016/S0003-3472(83)80055-4

QGIS Development Team. (2016). *QGIS Geographic Information System*. In Open Source Geospatial Foundation. http://qgis.org

Quadros, S., Goulart, V. D. L., Passos, L., Vecci, M. A. M., & Young, R. J. (2014). Zoo visitor effect on mammal behaviour: Does noise matter? *Applied Animal Behaviour Science*, *156*, 78-84. https://doi.org/https://doi.org/10.1016/j.applanim.2014.04.002

Queiroz, M. B., & Young, R. J. (2018). The different physical and behavioural characteristics of zoo mammals that influence their response to visitors. *Animals*, *8*(8), 139. https://doi.org/10.3390/ani8080139

R Core Team. (2018). *R: A language and environment for statistical computing*. In R Foundation for Statistical Computing. https://www.R-project.org

Rajagopal, T., Archunan, G., & Sekar, M. (2011). Impact of zoo visitors on the fecal cortisol levels and behavior of an endangered species: Indian blackbuck (Antelope cervicapra L.). *Journal of Applied Animal Welfare Science*, *14*(1), 18-32. https://doi.org/10.1080/10888705.2011.527598

Rapaport, L. G., & Brown, G. R. (2008). Social influences on foraging behavior in young nonhuman primates: Learning what, where, and how to eat. *Evolutionary Anthropology: Issues, News, and Reviews*, *17*(4), 189--201. https://doi.org/10.1002/evan.20180

Redshaw, M. E., & Mallinson, J. J. C. (1991). Stimulation of natural patterns of behaviour: studies with golden lion tamarins and gorillas. In H. O. Box (Ed.), *Primate responses to environmental change* (pp. 217-238). Springer. https://doi.org/10.1007/978-94-011-3110-0_12

Reimers, M., Schwarzenberger, F., & Preuschoft, S. (2007). Rehabilitation of research chimpanzees: Stress and coping after long-term isolation. *Hormones and Behavior*, *51*(3), 428-435. https://doi.org/10.1016/j.yhbeh.2006.12.011

Rennie, A. E., & Buchanan-Smith, H. M. (2006). Refinement of the use of non-human primates in scientific research. Part II: housing, husbandry and acquisition. *Animal Welfare*, *15*(3), 215-238. http://scholar.google.com/scholar?q=Refinement of the use of non-human primates in scientific research. Part II: housing, husbandry and acquisition&btnG=&hl=en&num=20&as_sdt=0%2C22

Reyno, V., & Reynolds, F. (1965). Chimpanzees of the Budongo Forest. In I. DeVore (Ed.), *Primate Behaviour. Field Studies of Monkeys and Apes* (pp. 368-424). Rinehart and Winston.

Roberts, A. I., & Roberts, S. G. B. (2019). Social bonding, gestural complexity and displacement behaviour of wild chimpanzee. *bioRxiv*, 678805. https://doi.org/10.1101/678805

Robinson, L. M., & Weiss, A. (2023a). *Nonhuman primate welfare: From history, science, and ethics to practice*. Springer Cham. https://doi.org/https://doi.org/10.1007/978-3-030-82708-3

Robinson, L. M., & Weiss, A. (2023b). Primate personality and welfare. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman primate welfare: From history, science, and ethics to practice* (pp. 395-411). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_17

Rodrigues, F. A. (2019). Network centrality: An introduction. In E. Macau (Ed.), *A mathematical modeling approach from nonlinear dynamics to complex systems. Nonlinear systems and complexity* (Vol. 22). Springer. https://doi.org/10.1007/978-3-319-78512-7_10

Rodrigues, M. A., & Boeving, E. R. (2019). Comparative social grooming networks in captive chimpanzees and bonobos. *Primates*, *60*(3), 191-202. https://doi.org/10.1007/s10329-018-0670-y

Rodriguez Escalada, L., Riba, D., Llorente, M., & Mosquera, M. (2014). Social learning mechanisms in chimpanzees (pan troglodytes): An experimental study through two manipulative tasks. *Folia Primatologica*, *85*(1), 71-71.

Ross, M. R., Niemann, T., Wark, J. D., Heintz, M. R., Horrigan, A., Cronin, K. A., . . . Gillespie, K. (2016). *ZooMonitor (Version 1)*. [Mobile application software]. Available from https://zoomonitor.org

Ross, S. R. (2020). Chimpanzee welfare in the context of science, policy, and practice. In M. H. Lydia & R. R. Stephen (Eds.), *Chimpanzees in context* (pp. 552-582). University of Chicago Press. https://doi.org/doi:10.7208/9780226728032-027

Ross, S. R., Joshi, P. B., Terio, K. A., & Gamble, K. C. (2022). A 25-year retrospective review of mortality in chimpanzees (Pan troglodytes) in accredited U.S. zoos from a management and welfare perspective. *Animals*, *12*(15), 1878. https://doi.org/10.3390/ani12151878

Ross, S. R., & Shender, M. A. (2016). Daily travel distances of zoo-housed chimpanzees and gorillas: implications for welfare assessments and space requirements. *Primates*, *57*(3), 395-401. https://doi.org/10.1007/s10329-016-0530-6

Rushmore, J., Caillaud, D., Matamba, L., Stumpf, R. M., Borgatti, S. P., & Altizer, S. (2013). Social network analysis of wild chimpanzees provides insights for predicting infectious disease risk. *Journal of Animal Ecology*, *82*(5), 976-986. https://doi.org/10.1111/1365-2656.12088

Sachser, N., Hennessy, M. B., & Kaiser, S. (2011). Adaptive modulation of behavioural profiles by social stress during early phases of life and adolescence. *Neuroscience \& Biobehavioral Reviews*, *35*(7), 1518--1533. https://doi.org/10.1016/j.neubiorev.2010.09.002

Sachser, N., Kaiser, S., & Hennessy, M. B. (2013). Behavioural profiles are shaped by social experience: when, how and why. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1618), 20120344. https://doi.org/10.1098/rstb.2012.0344

Sakura, O. (1994). Factors affecting party size and composition of chimpanzees (Pan troglodytes verus) Bossou, Guinea. *International Journal of Primatology*, *15*(2), 167-183. https://doi.org/10.1007/BF02735272

Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R. M., & Crockford, C. (2018). Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proceedings of the Royal Society B*, *285*(1888). https://doi.org/10.1098/rspb.2018.1643

Sauquet, T., Ubeda, Y., & Llorente, M. (2014). Long-term use of sensorial enrichment in chimpanzees (Pan troglodytes) : is it really powerful or just ineffective? *Folia Primatologica*, *85*(1), 73-73.

Scott, K., Heistermann, M., Cant, M. A., & Vitikainen, E. I. K. (2017). Group size and visitor numbers predict faecal glucocorticoid concentrations in zoo meerkats. *Royal Society Open Science*, *4*(4), 161017. https://doi.org/10.1098/rsos.161017

Schino, G. (2006). Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, *18*(1), 115-120. https://doi.org/10.1093/beheco/arl045

Schino, G., Scucchi, S., Maestripieri, D., & Turillazzi, P. G. (1988). Allogrooming as a tension-reduction mechanism: a behavioral approach. *American Journal of Primatology*, *16*(1), 43-50. https://doi.org/10.1002/ajp.1350160106

Schulte-Herbrüggen, B., Cowlishaw, G., Homewood, K., & Rowcliffe, M. J. (2013). The importance of bushmeat in the livelihoods of West African cash-crop farmers living in a faunally-depleted landscape. *Plos ONE*, *8*(8). https://doi.org/10.1371/journal.pone.0072807

Seal, U. S., & Flesness, N. R. (1986). Captive chimpanzee populations—Past, present, and future. In K. Benirschke, *Primates* New York, NY.

Segarra, S., & Ribeiro, A. (2014). Stability and continuity of centrality measures in weighted graphs. *arXiv*(1410.5119). https://doi.org/10.48550/arXiv.1410.5119

Sekar, M., Rajagopal, T., & Archunan, G. (2008). Influence of zoo visitor presence on the behavior of captive Indian gaur (Bos gaurus gaurus) in a zoological park. *Journal of Applied Animal Welfare Science*, *11*(4), 352-357. https://doi.org/10.1080/10888700802330093

Sherwen, S. L., Harvey, T. J., Magrath, M. J. L., Butler, K. L., Fanson, K. V., & Hemsworth, P. H. (2015). Effects of visual contact with zoo visitors on black-capped capuchin welfare. *Applied Animal Behaviour Science*, *167*, 65-73. https://doi.org/10.1016/J.APPLANIM.2015.03.004

Shimada, M., & Sueur, C. (2014). The importance of social play network for infant or juvenile wild chimpanzees at Mahale Mountains National Park, Tanzania. *American Journal of Primatology*, *76*(11), 1025-1036. https://doi.org/10.1002/ajp.22289

Silk, J. B. (1982). Altruism among female *Macaca Radiata*: Explanations and analysis of patterns of grooming and coalition formation. *Behaviour*, *79*(2-4), 162-188. https://doi.org/10.1163/156853982X00238

Silk, M. J., Finn, K. R., Porter, M. A., & Pinter-Wollman, N. (2018). Can multilayer networks advance animal behavior research? *Trends in ecology & evolution*, *33*(6), 376-378. https://doi.org/https://doi.org/10.1016/j.tree.2018.03.008

Smith-Aguilar, S. E., Aureli, F., Busia, L., Schaffner, C., & Ramos-Fernández, G. (2018). Using multiplex networks to capture the multidimensional nature of social structure. *Primates*, *60*, 277-295. https://doi.org/10.1007/s10329-018-0686-3

Smith, J. J. (2016). Primates and people in the zoo: Implications of human–animal interactions and relationships BT - Ethnoprimatology: Primate conservation in the 21st century. In M. T. Waller (Ed.), (pp. 371-398). Springer International Publishing. https://doi.org/10.1007/978-3-319-30469-4_20

Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., & Struhsaker, T. T. (Eds.). (1987). *Primate societies*. University of Chicago Press.

Solá, L., Romance, M., Criado, R., Flores, J., del Amo, A., & Boccaletti, S. (2013). Eigenvector centrality of nodes in multiplex networks. *Chaos (Woodbury, N.Y.)*, *23*(3), 33131. https://doi.org/10.1063/1.4818544

Soldati, A., Fedurek, P., Dezecache, G., Call, J., & Zuberbühler, K. (2022). Audience sensitivity in chimpanzee display pant hoots. *Animal Behaviour*, *190*, 23-40.

Solé-Ribalta, A., Domenico, M., Gómez, S., & Arenas, A. (2014). Centrality rankings in multiplex networks. *Proceedings of the 2014 ACM Conference on Web Science*, 149-155. https://doi.org/10.1145/2615569.2615687

Spinelli, S., Chefer, S., Suomi, S. J., Higley, J. D., Barr, C. S., & Stein, E. (2009). Early-life stress induces long-term morphologic changes in primate brain. *Archives of General Psychiatry*, *66*(6), 658-665. https://doi.org/10.1001/archgenpsychiatry.2009.52

Stanton, M. A., Lonsdorf, E. V., Murray, C. M., & Pusey, A. E. (2020). Consequences of maternal loss before and after weaning in male and female wild chimpanzees. *Behavioral Ecology and Sociobiology*, *74*(2), 22. https://doi.org/10.1007/s00265-020-2804-7

Stanton, M. A., Lonsdorf, E. V., Pusey, A. E., & Murray, C. M. (2017). Do juveniles help or hinder? Influence of juvenile offspring on maternal behavior and reproductive outcomes in wild chimpanzees (Pan troglodytes). *Journal of Human Evolution*, *111*, 152-162. https://doi.org/10.1016/j.jhevol.2017.07.012

Stiles, D., Redmond, I., Cress, D., Nelleman, C., & Formo, R. K. (2013). *Stolen Apes. The illicit trade in chimpanzees, gorillas, bonobos and orangutans. A rapid response assessment* (U.N.E. Programme GRID-Ardenal, Issue. https://wedocs.unep.org/20.500.11822/32463

Stoinski, T. S., Jaicks, H. F., & Drayton, L. A. (2012). Visitor effects on the behavior of captive Western Lowland Gorillas: The importance of individual differences in examining welfare. *Zoo Biology*, *31*(5), 586-599. https://doi.org/10.1002/zoo.20425

Stokes, R., Tully, G., & Rosati, A. G. (2018). Pan African Sanctuary Alliance: securing a future for the African great apes. *International Zoo Yearbook*, *52*(1), 173-181. https://doi.org/10.1111/izy.12174

Stumpf, R. M., & Boesch, C. (2010). Male aggression and sexual coercion in wild West African chimpanzees, Pan troglodytes verus. *Animal Behaviour*, *79*(2), 333-342. https://doi.org/10.1016/j.anbehav.2009.11.008

Sugiyama, Y. (2004). Demographic parameters and life history of chimpanzees at Bossou, Guinea. *American Journal of Physical Anthropology*, *124*(2), 154-165. https://doi.org/10.1002/ajpa.10345

Suomi, S. J. (1997). Early determinants of behaviour: evidence from primate studies. *British Medical Bulletin*, *53*(1), 170-184. https://doi.org/10.1093/oxfordjournals.bmb.a011598

Surinova, M. (1971). An analysis of the popularity of animals. *International Zoo Yearbook*, *11*(1), 165-167. https://doi.org/10.1111/j.1748-1090.1971.tb01895.x

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, *65*(1), 13-21. https://doi.org/10.1007/s00265-010-1037-6

Terry, R. L. (1970). Primate grooming as a tension reduction mechanism. *The Journal of Psychology*, *76*(1), 129-136. https://doi.org/10.1080/00223980.1970.9916830

Thompson, M. E. (2013). Reproductive ecology of female chimpanzees. *American Journal of Primatology*, *75*(3), 222-237. https://doi.org/https://doi.org/10.1002/ajp.22084

Thunström, M., Persson, T., & Björklund, M. (2013). Integration of a hand-reared chimpanzee *(Pan troglodytes)* infant into a social group of conspecifics. *Primates*, *54*(1), 13-19. https://doi.org/10.1007/s10329-012-0319-1

Tribe, A., & Booth, R. (2003). Assessing the role of zoos in wildlife conservation. *Human Dimensions of Wildlife*, *8*(1), 65-74. https://doi.org/10.1080/10871200390180163

Troisi, A. (2003). Psychopathology. In D. Maestripieri (Ed.), *Primate psychology* (pp. 451-470). Harvard University Press.

Turner, C. H., Davenport, R. K., & Rogers, C. M. (1969). The effect of early deprivation on the social behavior of adolescent chimpanzees. *American Journal of Psychiatry*, *125*(11), 1531--1536. https://doi.org/10.1176/ajp.125.11.1531

Tutin, C. E. G., McGrew, W. C., & Baldwin, P. J. (1983). Social organization of savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Senegal. *Primates*, *24*(2), 154-173. https://doi.org/10.1007/BF02381079

Úbeda, Y., Fatjó, J., Rostán, C., Crailsheim, D., Gomara, A., Almunia, J., & Llorente, M. (2020). A preliminary investigation on the evaluation of psychopathologies in a group of ex-pet and ex-performer chimpanzees (Pan troglodytes): A rating approach based on the Diagnostic and Statistical Manual of Mental Disorders (DSM). *Journal of Veterinary Behavior*. https://doi.org/10.1016/j.jveb.2020.08.006

Úbeda, Y., & Llorente, M. (2015). Personality in sanctuary-housed chimpanzees: a comparative approach of psychobiological and penta-factorial human models. *Evolutionary Psychology*, *13*(1), 182-196. https://doi.org/10.1177/147470491501300111

van Hooff, J. A. R. A. M., Dienske, H., Jens, W., & Spijkerman, R. P. (1996). Differences in variability, interactivity and skills in social play of young chimpanzees living in peer groups and in a large family zoo group. *Behaviour*, *133*(9-10), 717-739. https://doi.org/https://doi.org/10.1163/156853996X00440

van Leeuwen, E., Mulenga, I., & Chidester, D. (2014). Early social deprivation negatively affects social skill acquisition in chimpanzees (*Pan troglodytes*). *Animal Cognition*, *17*, 407-414. https://doi.org/10.1007/s10071-013-0672-5

van Leeuwen, E. J. C., Cronin, K. A., & Haun, D. B. M. (2018). Population-specific social dynamics in chimpanzees. *Proceedings of the National Academy of Sciences*, *115*(45), 201722614. https://doi.org/10.1073/pnas.1722614115

Vandeleest, J. J., McCowan, B., & Capitanio, J. P. (2011). Early rearing interacts with temperament and housing to influence the risk for motor stereotypy in rhesus monkeys (Macaca mulatta). *Applied Animal Behaviour Science*, *132*(1-2), 81-89. https://doi.org/10.1016/j.applanim.2011.02.010

Veenema, A. H., Meijer, O. C., De Kloet, E. R., & Koolhaas, J. M. (2003). Genetic selection for coping style predicts stressor susceptibility. *Journal of Neuroendocrinology*, *15*(3), 256-267. https://doi.org/https://doi.org/10.1046/j.1365-2826.2003.00986.x

Veissier, I., Aubert, A., & Boissy, A. (2012). Animal welfare: A result of animal background and perception of its environment. *Animal Frontiers*, *2*(3), 7-15. https://doi.org/10.2527/af.2012-0043

Veissier, I., & Boissy, A. (2007). Stress and welfare: Two complementary concepts that are intrinsically related to the animal's point of view. *Physiology & Behavior*, *92*(3), 429-433. https://doi.org/https://doi.org/10.1016/j.physbeh.2006.11.008

Videan, E. N. (2006). Bed-building in captive chimpanzees (Pan troglodytes): the importance of early rearing. *American Journal of Primatology*, *68*(7), 745--751. https://doi.org/10.1002/ajp.20265

Videan, E. N., & Fritz, J. (2007). Effects of short- and long-term changes in spatial density on the social behavior of captive chimpanzees (Pan troglodytes). *Applied Animal Behaviour Science*, *102*, 95-105. https://doi.org/10.1016/j.applanim.2006.03.011

Walker, K. K., Rudicell, R. S., Li, Y., Hahn, B. H., Wroblewski, E., & Pusey, A. E. (2017). Chimpanzees breed with genetically dissimilar mates. *Royal Society Open Science*, *4*(1), 160422. https://doi.org/doi:10.1098/rsos.160422

Walker, K. K., Walker, C. S., Goodall, J., & Pusey, A. E. (2018). Maturation is prolonged and variable in female chimpanzees. *Journal of Human Evolution*, *114*, 131-140. https://doi.org/10.1016/j.jhevol.2017.10.010

Walsh, P. D., Abernethy, K. A., Bermejo, M., Beyers, R., De Wachter, P., Akou, M. E., . . . Wilkie, D. S. (2003). Catastrophic ape decline in western equatorial Africa. *Nature*, *422*(6932), 611-614. https://doi.org/10.1038/nature01566

Walsh, S., Bramblett, C. A., & Alford, P. L. (1982). A vocabulary of abnormal behaviors in restrictively reared chimpanzees. *American Journal of Primatology*, *3*(1-4), 315--319. https://doi.org/10.1002/ajp.1350030131

Waller, B. M., & Dunbar, R. I. (2005). Differential behavioural effects of silent bared teeth display and relaxed open mouth display in chimpanzees (Pan troglodytes). *Ethology*, *111*(2), 129-142. https://doi.org/10.1111/j.1439-0310.2004.01045.x

Wallis, J. (1997). A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *Journal of Reproduction and Fertility*, *109*(2), 297-307. https://doi.org/10.1530/jrf.0.1090297

Wasserman, S., & Faust, K. (1994). *Social network analysis: Methods and applications* (Vol. 8). Cambridge University Press. https://doi.org/10.1017/CBO9780511815478

Watts, D. P. (2000). Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and diversity and grooming reciprocity. *International Journal of Primatology*, *21*(2), 189-210. https://doi.org/10.1023/A:1005469302911

Watts, D. P., & Pusey, A. E. (2002). Behavior of juvenile and adolescent great apes. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile primates: life history, development, and behavior*, (2nd ed., pp. 148–167). The University of Chicago Press.

Webb, S. J. N., Hau, J., & Schapiro, S. J. (2019). Does group size matter? Captive chimpanzee (Pan troglodytes) behavior as a function of group size and composition. *American Journal of Primatology*, *81*(1), e22947. https://doi.org/10.1002/ajp.22947

Wells, D. L. (2005). A note on the influence of visitors on the behaviour and welfare of zoo-housed gorillas. *Applied Animal Behaviour Science*, *93*(1), 13-17. https://doi.org/https://doi.org/10.1016/j.applanim.2005.06.019

White, F. J. (1992). Activity Budgets, feeding behavior, and habitat use of pygmy chimpanzees at Lomako, Zaire. *American Journal of Primatology*, *26*(3), 215-223. https://doi.org/10.1002/ajp.1350260307

White, F. J., & Chapman, C. A. (1994). Contrasting chimpanzees and bonobos: nearest neighbor distances and choices. *Folia Primatologica*, *63*(4), 181-191. https://doi.org/10.1159/000156818

Whitehead, H. A. L. (1997). Analysing animal social structure. *Animal Behaviour*, *53*(5), 1053-1067. https://doi.org/10.1006/anbe.1996.0358

Wiedenmayer, C. (2010). Sensitive periods in the behavioral development of mammals. In C. M. Worthman, P. M. Plotsky, D. S. Schechter, & C. A. Cummings (Eds.), *Formative experiences: The interaction of caregiving, culture, and developmental psychobiology*. University Press. https://doi.org/10.1017/CBO9780511711879.008

Wilkie, D. S., Bennett, E. L., Peres, C. A., & Cunningham, A. A. (2011). The empty forest revisited. *Annals of the New York Academy of Sciences*, *1223*(1), 120-128. https://doi.org/10.1111/j.1749-6632.2010.05908.x

Wilson, M. L., & Wrangham, R. W. (2003). Intergroup relations in chimpanzees. *Annual Review of Anthropology*, *32*(1), 363-392. https://doi.org/10.1146/annurev.anthro.32.061002.120046

Willner, P. (2005). Chronic mild stress (CMS) revisited: Consistency and behavioural-neurobiological concordance in the effects of CMS. *Neuropsychobiology*, *52*(2), 90-110. https://doi.org/10.1159/000087097

Wolfle, T. L. (1999). Psychological well-being of nonhuman primates: A brief history. *Journal of Applied Animal Welfare Science*, *2*, 297-302. https://doi.org/10.1207/s15327604jaws0204_4

Wood, B. M., Watts, D. P., Mitani, J. C., & Langergraber, K. E. (2017). Favorable ecological circumstances promote life expectancy in chimpanzees similar to that of human hunter-gatherers. *Journal of Human Evolution*, *105*, 41-56. https://doi.org/10.1016/j.jhevol.2017.01.003

Wooddell, L. J., Hamel, A. F., Murphy, A. M., Byers, K. L., Kaburu, S., Meyer, J. S., . . . Dettmer, A. M. (2017). Relationships between affiliative social behavior and hair cortisol concentrations in semi-free ranging rhesus monkeys. *Psychoneuroendocrinology*, *84*, 109-115. https://doi.org/10.1016/j.psyneuen.2017.06.018

Wrangham, R. W. (1975). *Behavioural ecology of chimpanzees in Gombe National Park, Tanzania* Cambridge University]. Cambridge.

Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In T. H. Clutton-Brock (Ed.), *Primate Ecology* (pp. 503-538). London Academic Press. https://doi.org/10.1016/B978-0-12-176850-8.50022-6

Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. *American Journal of Physical Anthropology*, *106*(3), 283-295. https://doi.org/10.1002/(SICI)1096-8644(199807)106:3<283::AID-AJPA2>3.0.CO;2-O

Ziegler, T. E., & Crockford, C. (2017). Neuroendocrine control in social relationships in non-human primates: Field based evidence. *Hormones and Behavior*, *91*, 107-121. https://doi.org/10.1016/j.yhbeh.2017.03.004

Supplementary Tables & Figures

Table SA1

List of best models, forming part of the subset being used in the averaging process, with vertex strength centrality as dependent variable

VSC	(Int)	TP stability	Arrival Age Cat	Sex	PHC infant	Origin	df	logLik	AICc	delta	weight
Mod12	2.139			X	X	X	7	-182.688	380.4	0.00	0.452
Mod22	2.280	X		X	X	X	8	-182.569	382.4	2.06	0.161
Mod9	2.274		X	X	X	X	8	-182.620	382.5	2.16	0.153
Mod5	2.424	X	X	X	X	X	9	-182.495	384.6	4.26	0.054
Mod14	2.487			X		X	6	-185.955	384.7	4.28	0.053
Mod30	2.689	X		X		X	7	-185.686	386.4	6.00	0.023
Mod15	1.447				X	X	6	-186.858	386.5	6.08	0.022
Mod29	2.663		X	X		X	7	-185.879	386.8	6.38	0.019
Mod16	1.834					X	5	-188.119	386.8	6.38	0.019
Mod25	1.245		X		X	X	7	-186.713	388.4	8.05	0.008
Mod31	2.877	X	X	X		X	8	-185.602	388.5	8.13	0.008
Mod21	1.553	X			X	X	7	-186.782	388.6	8.19	0.008
Mod17	1.972	X				X	6	-187.959	388.7	8.28	0.007
Mod24	1.710		X			X	6	-188.067	388.9	8.5	0.006
Mod23	0.5062		X		X		6	-188.567	389.9	9.5	0.004
Mod6	0.9414		X				5	-189.826	390.2	9.8	0.003

Note. VSC models with stability of time period (TPstability), arrival age category (ArrivalAgeCat), sex, predominant housing condition during infancy (PHCinfant) and origin as fixed effects and group composition in a certain time period and ID as random factors in all models. Models are ranked according to the best *AICc*. All models considered here have a ΔAICc lower than 10 compared to the best model (first model listed). Fixed effects included in each model candidate are marked with an X.

Table SA2

List of best models, forming part of the subset being used in the averaging process, with deviation from edge weight disparity as dependent variable

DEWD	(Int)	TP stability	Arrival Age Cat	Sex	PHC infant	Origin	df	logLik	AICc	delta	weight
Mod30	0.1253	X		X		X	7	11.797	-8.4	0.00	0.205
Mod17	0.2157	X				X	6	10.425	-8.0	0.44	0.164
Mod22	0.1016	X		X	X	X	8	12.438	-7.4	1.07	0.12
Mod31	0.05551	X	X	X		X	8	12.308	-7.1	1.33	0.105
Mod21	0.2004	X			X	X	7	10.769	-6.4	2.06	0.073
Mod1	0.2656	X					5	8.221	-5.8	2.6	0.056
Mod5	0.04528	X	X	X	X	X	9	12.848	-5.8	2.65	0.054
Mod27	0.2071	X	X			X	7	10.439	-5.7	2.72	0.053
Mod2	0.2993	X	X				6	8.715	-4.6	3.86	0.03
Mod18	0.2494	X			X		6	8.543	-4.2	4.21	0.025
Mod26	0.196	X	X		X	X	8	10.733	-4.0	4.4	0.023
Mod19	0.2393	X		X			6	8.358	-3.9	4.58	0.021
Mod28	0.2838	X	X		X		7	9.109	-3.1	5.38	0.014
Mod3	0.2757	X	X	X			7	8.816	-2.5	5.96	0.01
Mod20	0.2135	X		X	X		7	8.781	-2.4	6.03	0.01
Mod14	0.2542			X		X	6	7.472	-2.1	6.35	0.009
Mod12	0.2208			X	X	X	7	8.27	-1.4	7.06	0.006
Mod16	0.3351					X	5	5.958	-1.3	7.12	0.006
Mod4	0.2497	X	X	X	X		8	9.31	-1.1	7.32	0.005
Mod29	0.1878		X	X		X	7	7.999	-0.8	7.6	0.005
Mod15	0.3088				X	X	6	6.486	-0.1	8.32	0.003
Mod9	0.1733		X	X	X	X	8	8.621	0.3	8.7	0.003
Mod24	0.3319		X			X	6	5.96	0.9	9.37	0.002

Note. DEWD models with stability of time period (TPstability), arrival age category (ArrivalAgeCat), sex, predominant housing condition during infancy (PHCinfant) and origin as fixed effects and group composition in a certain time period and ID as random factors in all models. Models are ranked according to the best *AICc*. All models considered here have a Δ*AIC*c lower than 10 compared to the best model (first model listed). Fixed effects included in each model candidate are marked with an X.

Table SA3

Results from the ANOVA post hoc test on the VSC Full-model

VSC Full-model Post Hoc:
Type III Analysis of Variance Table with Satterthwaite's method

	Sum Sq	Mean Sq	Num DF	Den DF	F value	Pr(>F)
TPstability	0.2199	0.2199	1	17.732	0.2509	0.622637
ArrivalAgeCat	0.129	0.129	1	12.71	0.1472	0.707595
Sex	10.5026	10.5026	1	15.063	11.9786	0.003473 **
PHCinfant	7.0448	7.0448	1	15.422	8.0348	0.01229 *
Origin	13.6113	13.6113	1	11.066	15.5242	0.002286 **

Note. Signif. codes: '***' ≤0.001 '**' ≤0.01 '*' ≤0.05 '.' ≤0.1 ' ' ≤1

Table SA4

Results from the ANOVA test on the extended VSC model including the interaction of Origin and Predominant housing condition during infancy (PHCinfant)

VSC Full-model including Interaction between PHCinfant and Origin:
Type III Analysis of Variance Table with Satterthwaite's method

	Sum Sq	Mean Sq	Num DF	Den DF	F value	Pr(>F)
TPstability	0.1084	0.1084	1	17.8438	0.1224	0.7305
ArrivalAgeCat	0.9008	0.9008	1	10.9216	1.0176	0.3349
Sex	12.8005	12.8005	1	13.7881	14.4595	0.0020 **
PHCinfant	10.0851	10.0851	1	13.4513	11.3922	0.0048 **
Origin	20.8679	20.8679	1	9.2476	23.5725	0.0008 ***
PHCinfant:Origin	4.3446	4.3446	1	13.2177	4.9076	0.0449 *

Interaction contrast: Tukey method for comparing the four estimates of PHCinfant: Origin

Contrast	Estimate	SE	DF	T ratio	P value
captive,with - wild,with	2.0733	0.5316	25.21	3.900	0.0033 **
captive,with - captive,without	1.4230	0.4652	27.20	3.059	0.0240 *
captive,with - wild,without	2.3718	0.5222	24.50	4.542	0.0007 ***
wild,with - captive,without	-0.6503	0.5175	24.77	-1.257	0.5980
wild,with - wild,without	0.2985	0.4487	26.49	0.665	0.9092
captive,without - wild,without	0.9488	0.5048	23.28	1.880	0.2638

Note. Results of the Interaction contrast analysis: Results are averaged over the levels of TPstability, ArrivalAgeCat, and Sex with a p-value adjustment based on Tukey method for comparing a family of 4 estimates. Signif. codes:'***' ≤0.001 '**' ≤0.01 '*' ≤0.05 '.' ≤0.1 ' ' ≤1

Table SA5

Results from the ANOVA post hoc test on the DEWD Full-model

DEWD Full-model Post Hoc:
Type III Analysis of Variance Table with Satterthwaite's method

	Sum Sq	Mean Sq	Num DF	Den DF	F value	Pr(>F)
TPstability	0.37143	0.37143	1	15.2589	10.154	0.006023 **
ArrivalAgeCat	0.03371	0.03371	1	6.9778	0.9215	0.369152
Sex	0.22219	0.22219	1	9.1780	6.0741	0.035405 *
PHCinfant	0.04208	0.04208	1	8.6841	1.1504	0.312365
Origin	0.35146	0.35146	1	6.6089	9.6081	0.018646 *

Note. Signif. codes: ‘***’ ≤0.001 ‘**’ ≤0.01 ‘*’ ≤0.05 ‘.’ ≤0.1 ‘ ’ ≤1

Table SA6

Results from the ANOVA test on the extended DEWD model including the interaction of Origin and Time Period Stability (TPstability)

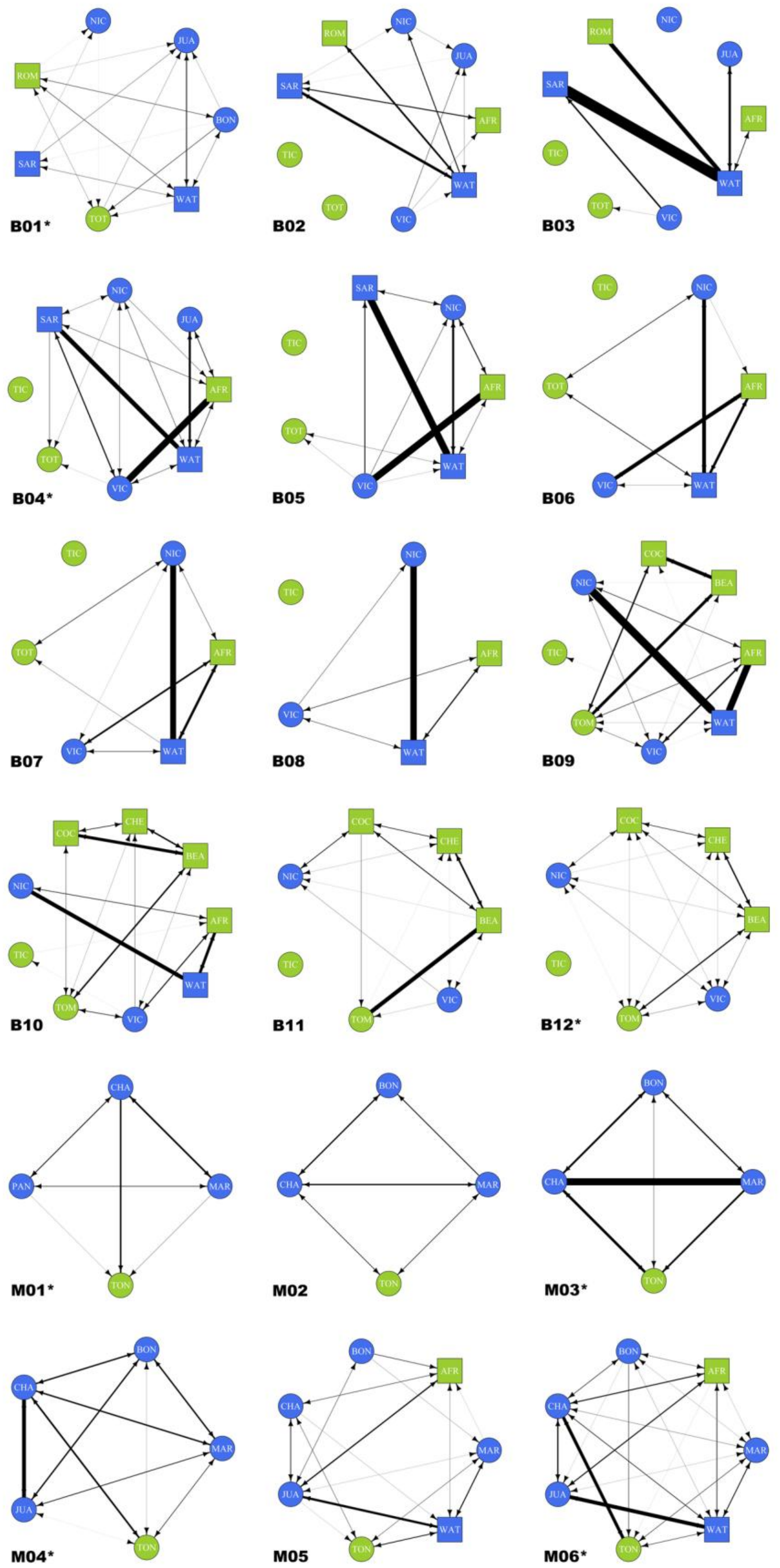
DEWD Full-model including Interaction between TPstability and Origin:
Type III Analysis of Variance Table with Satterthwaite's method

	Sum Sq	Mean Sq	Num DF	Den DF	F value	Pr(>F)
ArrivalAgeCat	0.0297	0.0297	1	7.153	0.8154	0.3959
Sex	0.2129	0.2129	1	9.255	5.8445	0.0381 *
PHCinfant	0.0437	0.0437	1	8.765	1.1986	0.3028
TPstability	0.3723	0.3723	1	16.221	10.2215	0.0055 **
Origin	0.2941	0.2941	1	8.058	8.0752	0.0216 *
TPstability:Origin	0.0053	0.0053	1	91.883	0.1463	0.7030

Note. Signif. codes: ‘***’ ≤0.001 ‘**’ ≤0.01 ‘*’ ≤0.05 ‘.’ ≤0.1 ‘ ’ ≤1

Figure SA1

Graphical representation of the weighted social grooming networks of all 18 Observation Time Periods/Group compositions for both chimpanzee groups (Bilinga B01-B12, Mutamba M01-M06) in chronological order



Note. Nodes represent group members, with green nodes being wild-caught and blue nodes being captive born chimpanzees. Node shape represents the sex, with squares being females and circles being males. Graphs marked with a * are describing stable time periods. The procedures used to create the matrices are described in the method section. Graphs were drawn using the Igraph package in R.

Figure SA2

Plot of the residual vs. fitted values for vertex strength centrality (VSC)

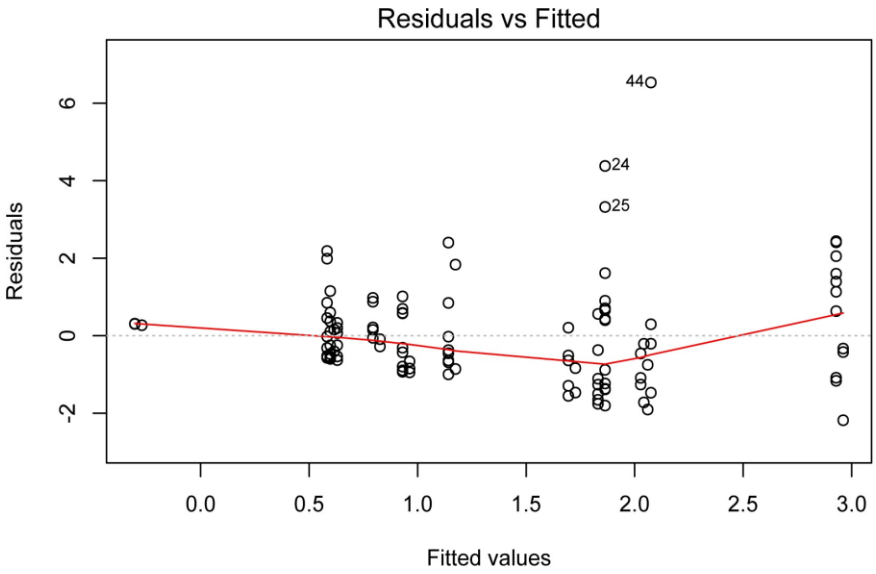


Figure SA3

Plot of the residual normality distribution for vertex strength centrality (VSC).

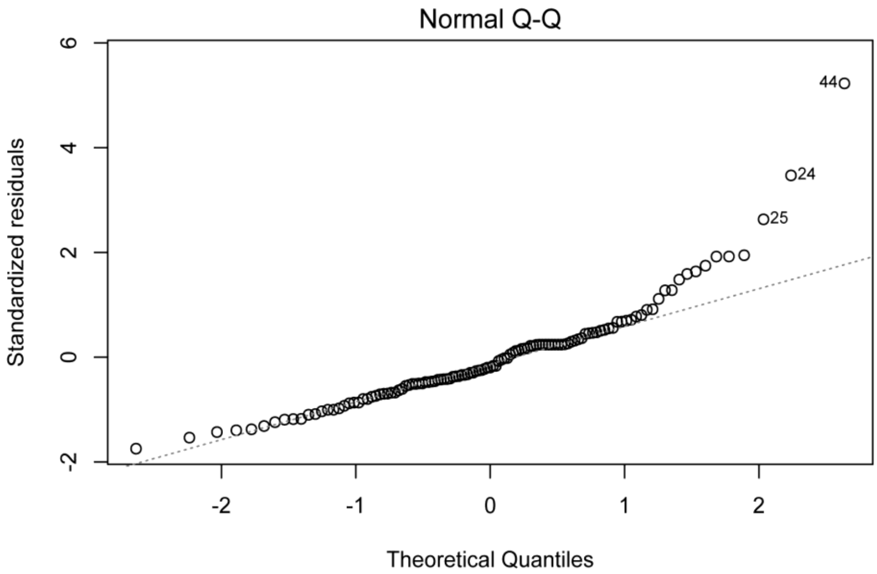


Figure SA4

Plot of the residual vs. fitted values for deviation from edge weight disparity (DEWD).

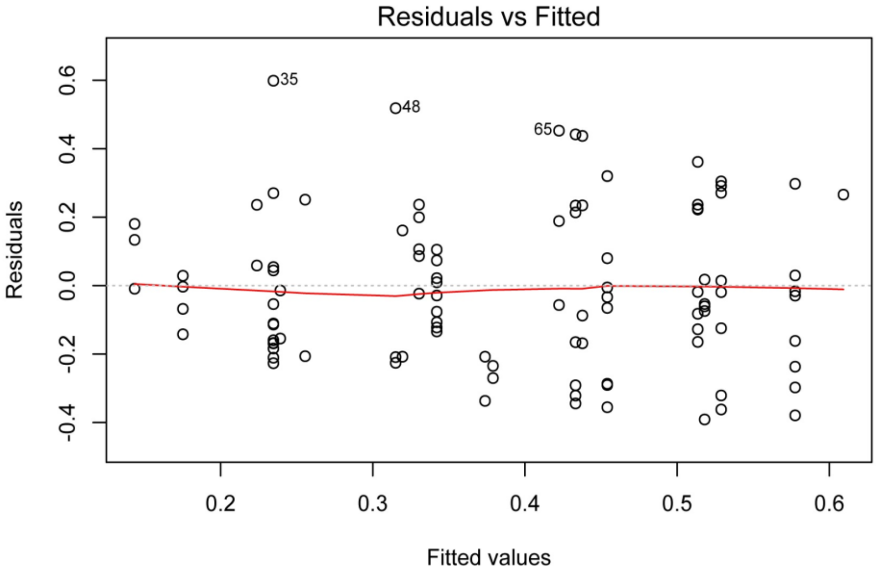


Figure SA5

Plot of the residual normality distribution for deviation from edge weight disparity (DEWD)

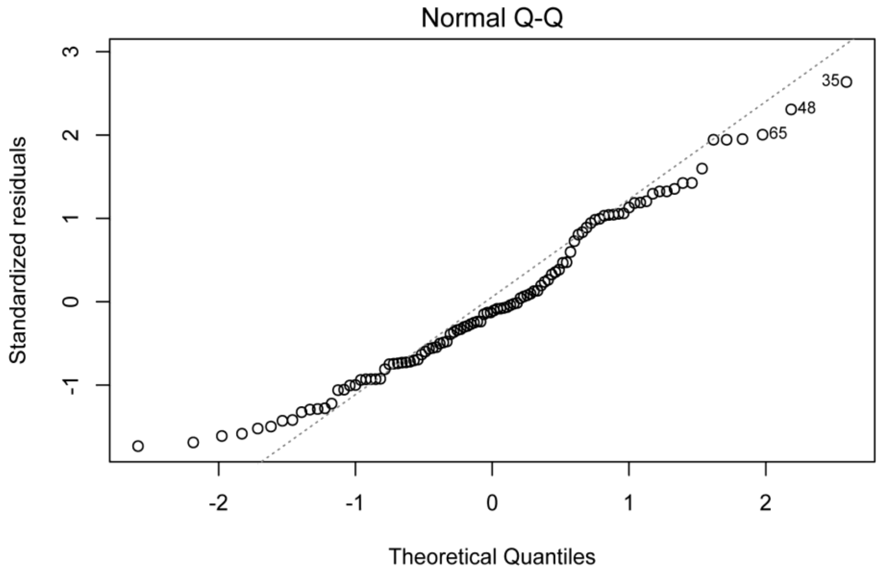


Table SB1

Descriptive information on the 4-layered multiplex networks for the two social groups (Bilinga, Mutamba)

	Multiplex layer	Mean index value	Min-max index value	Mean weighted index value	Min-max weighted index value	Nodes	Edges	Network density
Bilinga group	Stationary vicinity	0.190 ± 0.120	0.047 - 0.465	0.399 ± 0.252	0.099 - 0.980	7	42	1
	Affiliative behaviour	0.003 ± 0.003	0.000 - 0.010	0.150 ± 0.160	0.014 - 0.545	7	31	0.74
	Allogrooming	0.006 ± 0.009	0.000 - 0.038	0.066 ±0.098	0.003 - 0.418	7	24	0.57
	Passive close proximity	0.031 ± 0.031	0.001 - 0.133	0.196 ± 0.194	0.003 - 0.837	7	42	1
Mutamba group	Stationary vicinity	0.169 ± 0.143	0.031 - 0.475	0.357 ± 0.302	0.065 - 1.000	7	42	1
	Affiliative behaviour	0.005 ± 0.005	0.001 - 0.018	0.264 ± 0.257	0.055 - 1.000	7	42	1
	Allogrooming	0.014 ± 0.019	0.000 - 0.090	0.154 ± 0.213	0.002 - 1.000	7	40	0.95
	Passive close proximity	0.039 ± 0.047	0.001 -0.159	0.243 ± 0.298	0.007 - 1.000	7	42	1

Table SB2

Interlayer edge-overlap

	Mutamba	Bilinga	Group Average
Mean global edge-overlap	**0.19**	**0.10**	**0.14**
Groom - StatVic	0.54	0.17	0.36
Groom - Affil	0.54	0.49	0.51
Groom - Prox	0.61	0.32	0.47
Affil - Prox	0.54	0.62	0.58
Affil - StatVic	0.54	0.43	0.48
Prox - StatVic	0.79	0.65	0.72
STDEV	**0.10**	**0.18**	**0.12**
Average	**0.59**	**0.45**	**0.52**

Note. Fraction of shared edges between layers and mean global edge-overlap for both chimpanzee groups. Last column shows the average values over both social groups.

Table SB3

Reducibility Analysis

	Mutamba	**Bilinga**	**Group Average**
Prox - StatVic	0.102	0.117	0.110
Groom - Affil	0.289	0.173	0.231
Groom - Prox	0.197	0.338	0.268
Affil - Prox	0.344	0.291	0.318
Groom - StatVic	0.217	0.358	0.288
Affil - StatVic	0.285	0.304	0.295
Average	**0.239**	**0.264**	**0.251**
SD	**0.086**	**0.096**	**0.091**

Note. The Jensen-Shannon distances are used for the hierarchical clustering of the multiplex layers. These values defined the order of the layer reduction process (for each social group). Values range from 0 to 1 with larger values representing a greater distance (difference) between layers.

Table SB4

Eigenvector centrality and versatility values of the social groups

Bilinga							
ID	**Groom**	**Affil**	**Prox**	**StatVic**	**Aggregate**	**Multiplex**	**Versatility Rank**
TOM	0.6106	**1.000**	0.8180	**1.000**	**1.000**	**1.000**	1
BEA	**1.000**	0.9924	0.8335	0.7753	0.9899	0.9263	2
CHE	0.2489	0.6364	0.6798	0.9013	0.8414	0.8470	3
TIC	0.0008	0.0042	0.9351	0.9286	0.7562	0.8068	4
VIC	0.0777	0.5079	**1.000**	0.7325	0.7488	0.7628	5
COC	0.2354	0.6991	0.5127	0.4932	0.6010	0.5639	6
NIC	0.0745	0.2624	0.1914	0.2664	0.2706	0.2657	7
Mutamba							
ID	**Groom**	**Affil**	**Prox**	**StatVic**	**Aggregate**	**Multiplex**	**Versatility Rank**
JUA	**1.000**	0.4410	0.9662	0.9669	**1.000**	**1.000**	1
WAT	0.9572	0.4561	**1.000**	0.9189	0.9599	0.9648	2
AFR	0.5668	0.3205	0.9821	**1.000**	0.8977	0.9163	3
BON	0.1735	0.3988	0.5211	0.7550	0.5866	0.6091	4
MAR	0.3766	0.8484	0.3020	0.5578	0.5172	0.5297	5
CHA	0.4011	0.8027	0.1461	0.2005	0.3387	0.3264	6
TON	0.1786	**1.000**	0.0835	0.1914	0.2936	0.2899	7

Note. First column refers to the individual. Columns 2-5 represent the Eigenvector centralities for each layer of the multiplex network separately. Column 5 is the calculated Eigenvector of a fully aggregated network version (where all 4 layers have been aggregated to one single layer). Column 7 represents the Eigenvector versatility (multiplex equivalent to the

Eigenvector centrality) as described by De Domenico (2015). Column 8 represents the Versatility rank based on the eigenvector versatility (column 7). Rows are ranked according to the versatility rank. Within the columns, values higher than the average are highlighted in green, values lower than the average are highlighted in in purple, with the highest value written bold.

Table SB5

Linear mixed models based on each interaction type and its fully aggregated state

			Origin			
Model	**Δ AIC**	**p**	**SumSq**	**Mean Sq**	**Fvalue**	**p**
Groom	6.9	0.00309**	0.0014498	0.00048325	3.0853	0.0316077 *
Affil	15.3	0.0001209 ***	0.00013734	4.5778e-05	4.2721	0.007391 **
Prox	4.6	0.007175 **	0.0061884	0.0020628	1.8942	0.1413807
StatVic	-	-	-	-	-	-
Aggregate	-	-	-	-	-	-
			PHCinfant			
Model	**Δ AIC**	**p**	**SumSq**	**Mean Sq**	**Fvalue**	**p**
Groom	6.9	0.00309**	0.0010059	0.00033531	2.1408	0.1011569
Affil	15.3	0.0001209 ***	0.00040013	1.3338e-04	12.4470	8.211e-07 ***
Prox	4.6	0.007175 **	0.0032532	0.0010844	0.9958	0.4030339
StatVic	-	-	-	-	-	-
Aggregate	-	-	-	-	-	-
			Sex			
Model	**Δ AIC**	**p**	**SumSq**	**Mean Sq**	**Fvalue**	**p**
Groom	6.9	0.00309**	0.0028343	0.00094477	6.0319	0.0009025 ***
Affil	15.3	0.0001209 ***	0.00009298	3.0993e-05	2.8923	0.040094 *
Prox	4.6	0.007175 **	0.0213231	0.0071077	6.5267	0.0008248 ***
StatVic	-	-	-	-	-	-
Aggregate	-	-	-	-	-	-

Table SB6

Post hoc test results of the linear mixed models

Model	Fixed Factor			Estimate	Std. Erroer	Z value	p-value
Groom	**Sex**	F > M	F > F	-0.009772	0.005516	-1.771	0.152990
		M > F	F > F	-0.011541	0.005516	-2.092	0.109257
		M > M	F > F	-0.021633	0.005718	-3.783	0.000929 ***
		M > F	F > M	-0.001770	0.004273	-0.414	0.678722
		M > M	F > M	-0.011861	0.003836	-3.092	0.009949 **
		M > M	M > F	-0.010092	0.003836	-2.630	0.034107 *
	Origin	captive > wild	captive > captive	-0.008543	0.004705	-1.816	0.2776
		wild > captive	captive > captive	-0.011767	0.004705	-2.501	0.0619 .
		wild.wild	captive.captive	-0.014765	0.005085	-2.904	0.0221 *
		wild > captive	captive > wild	-0.003224	0.004385	-0.735	0.9243
		wild > wild	captive > wild	-0.006221	0.004229	-1.471	0.4239
		wild.wild	wild > captive	-0.002997	0.004229	-0.709	0.9243
	PHCinfant	with > without	with > with	-0.007111	0.004846	-1.467	0.7115
		without > with	with > with	-0.005075	0.004846	-1.047	0.8851
		without > without	with > with	-0.010602	0.004267	-2.485	0.0778
		without > with	with > without	0.002036	0.004533	0.449	0.8851
		without > without	with > without	-0.003491	0.004281	-0.816	0.8851
		without > without	without > with	-0.005528	0.004281	-1.291	0.7866
Affil	**Sex**	F > M	F > F	-0.0037370	0.0014428	-2.590	0.0480 *
		M > F	F > F	-0.0038567	0.0014428	-2.673	0.0451 *
		M > M	F > F	-0.0029556	0.0014956	-1.976	0.1926
		M > F	F > M	-0.0001197	0.0011175	-0.107	1.0000
		M > M	F > M	0.0007814	0.0010035	0.779	1.0000
		M > M	M > F	0.0009011	0.0010035	0.898	1.0000
	Origin	captive > wild	captive > captive	0.0038393	0.0012307	3.120	0.00905 **
		wild > captive	captive > captive	0.0039185	0.0012307	3.184	0.00871 **
		wild.wild	captive.captive	0.0030425	0.0013300	2.288	0.08864 .
		wild > captive	captive > wild	0.0000792	0.0011469	0.069	1.00000
		wild > wild	captive > wild	-0.0007968	0.0011063	-0.720	1.00000
		wild.wild	wild > captive	-0.0008760	0.0011063	-0.792	1.00000
	PHCinfant	with > without	with > with	-0.0054868	0.0012676	-4.328	7.51e-05 ***
		without > with	with > with	-0.0053150	0.0012676	-4.193	0.00011 ***
		without > without	with > with	-0.0066599	0.0011161	-5.967	1.45e-08 ***
		without > with	with > without	0.0001718	0.0011855	0.145	0.88479
		without > without	with > without	-0.0011731	0.0011197	-1.048	0.68915
		without > without	without > with	-0.0013449	0.0011197	-1.201	0.68915
Prox	**Sex**	F > M	F > F	-0.0585887	0.0146360	-4.003	0.000313 ***
		M > F	F > F	-0.0588200	0.0160873	-3.656	0.001023 **
		M > M	F > F	-0.0686524	0.0165764	-4.142	0.000207 ***
		M > F	F > M	-0.0002313	0.0131409	-0.018	1.00000
		M > M	F > M	-0.0100637	0.0121463	-0.829	1.00000
		M > M	M > F	-0.0098324	0.0101732	-0.967	1.00000

Note. Multiple comparison of means with Tukey contrasts (adjusted p values with Holm-Bonferroni method). Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Figure SB1

Plot of the residual normality distribution

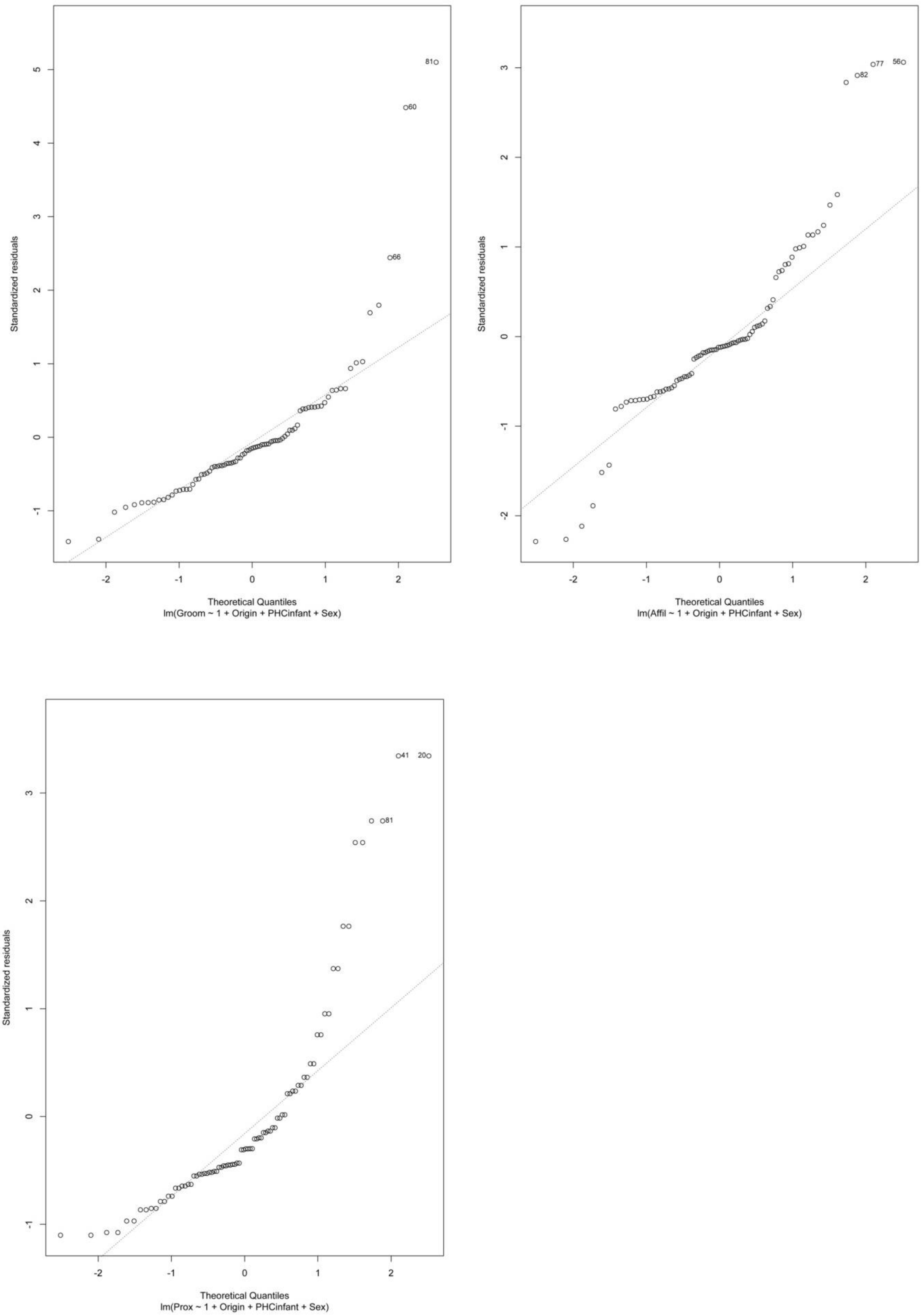


Figure SB2

Plot of the residual vs. fitted values

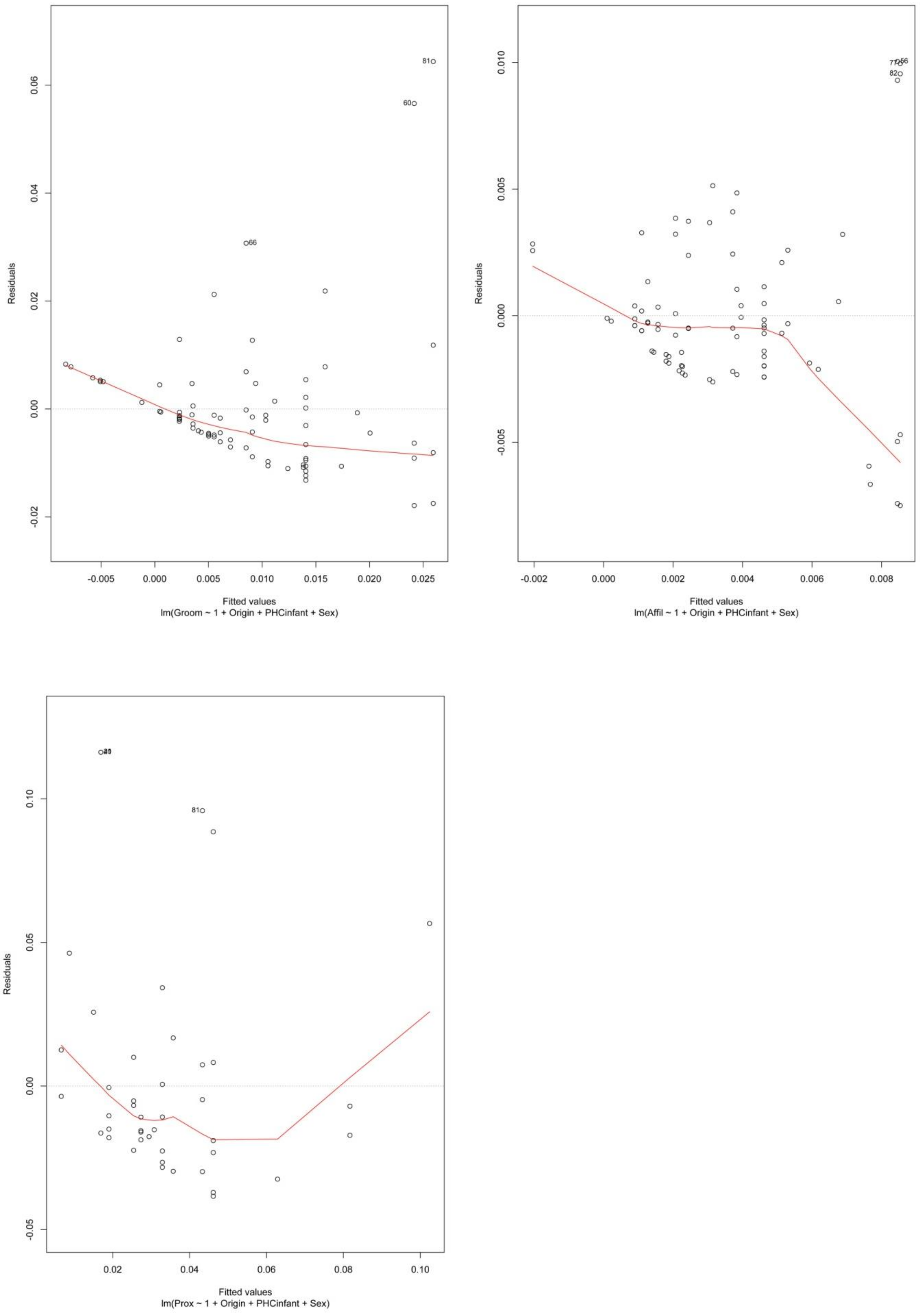


Figure SC1

QQ plot residuals model 5 locomotion

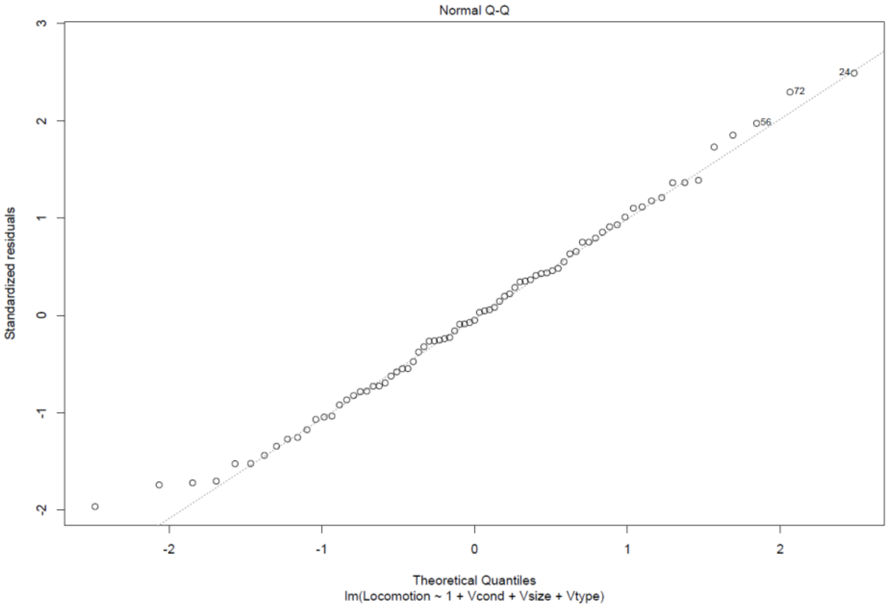


Figure SC2

QQ plot residuals model 3 human interaction