# *Endangered Childhoods - Longitudinal Socio-emotional Development of Orphaned Bonobos in the Context of Sanctuary-Based Conservation*

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**How to cite:**

KORDON, STEPHANIE (2026). *Endangered Childhoods - Longitudinal Socio-emotional Development of Orphaned Bonobos in the Context of Sanctuary-Based Conservation*, Durham e-Theses. http://etheses.dur.ac.uk/16453/

# Endangered Childhoods

## Longitudinal Socio-emotional Development of Orphaned Bonobos in the Context of Sanctuary-Based Conservation

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Thesis submitted to Durham University for the Degree of
Master of Philosophy
Research conducted with the Department of Psychology

2025

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# Acknowledgements

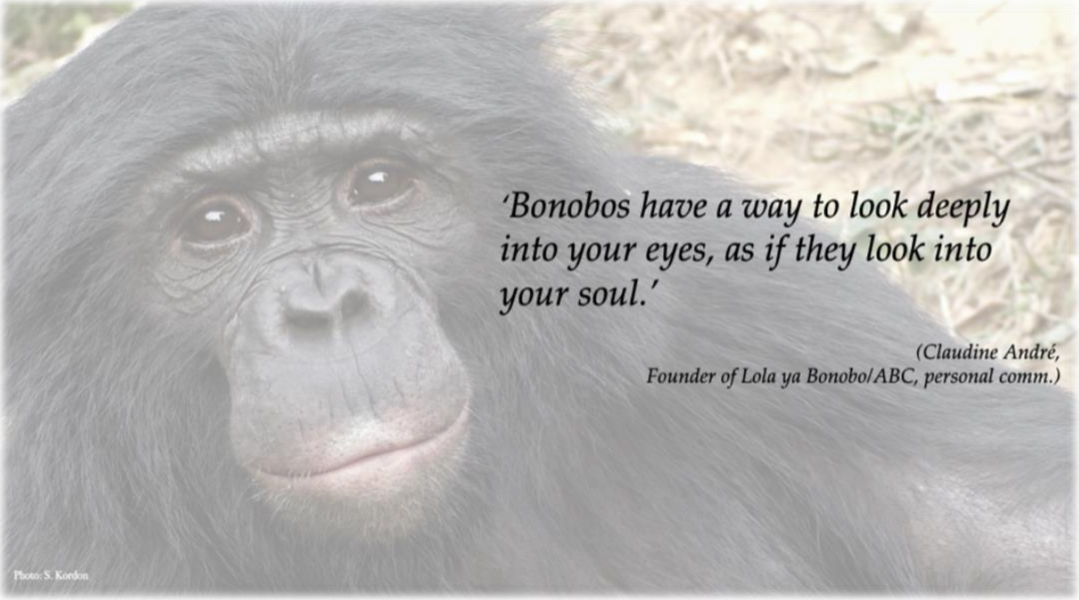
I am grateful to have had the privilege of having Zanna Clay, my mentor and supervisor, guide me on my journey to become a primatologist. A good decade ago, she opened the most precious world of bonobos for me and has supported, guided and believed in me ever since. For this, and her empathy, care and understanding I shall always be grateful. I sincerely thank my external co-supervisor Christine Webb for her patient support, and insightful, inspiring views and advice. It was an honour to have been supported by and to have worked with the late Frans de Waal, who has left behind an invaluable legacy that has paved the way for generations of primatologists to come.

Further, I'd like to thank my internal supervisor Lynda Boothroyd for her supervision during Zanna's leave. And of course, the wonderful C4D-Lab for countless lab-meetings to share helpful feedback, brainstorming, advice and help with statistics and R, and most importantly moral support: Raphaela Heesen, Georgia Sandars, Georgia Tuohy, Miranda Ventrella, Jake Brooker, Carlo Vreden, Chris Krupenye, Emma Doherty. Special thanks go to the friends within and outside our lab that came into my life in Durham and made many dark and rainy days brighter. Johanna Schechner was the wind beneath my wings when I needed it the most, I thank her for everything she has taught me. I am lucky to be surrounded by such a supportive family, who always believe in me and welcome me home to help me recharge.

I sincerely thank Heritier Izansone and Pitshou Nsele Kayanga for assistance in data collection; Claudine André, Fanny Minesi, Raphaël Belais as well as the entire Lola ya Bonobo staff who tirelessly work to save and care for the bonobos, particularly, Stany Mokando, Jean-Claude Nzumbi, Suzy Kwetuenda and Jonas Mukamba for facilitating data collection. I also thank the entire team for making Lola ya Bonobo my second home. Many thanks go to the editor, Shinya Yamamoto and two anonymous reviewers for their insightful and constructive comments on the empirical study. I thank the funders that have enabled this research:

This study has been financially supported by the Templeton World Charity Foundation: Diverse Intelligences initiative (awarded to F.B.M.d.W, Z.C., C.E.W.; grant number 0309, 2018). Funding to support this work has also been received from the European Research Council Horizon 2020 Starting Grant (802979, awarded to Z.C.) and the Fürst Dietrichstein Stiftung (awarded to S.K.). Finally, I would like to thank my viva reviewers Bruce Rawlings and Teresa Romero for their interest leading to a lively discussion, as well as their valuable input for improvement of this work.

The most precious saved for last, who will always be close to my heart, I thank the bonobos for showing us the importance of empathy, tolerance and love to enable a life in peace and harmony – let us take them as a leading example.



*'Bonobos have a way to look deeply into your eyes, as if they look into your soul.'*

*(Claudine André,*
*Founder of Lola ya Bonobo/ABC, personal comm.)*

Photo: S. Kordon

# Abstract

This thesis explores the socio-emotional development of orphaned bonobos in the context of maternal loss, sanctuary care, and long-term adaptation. It reviews the evidence from humans and non-human primates showing the importance of maternal support for primate development, shaping survival, social integration, and psychological resilience. In great apes such as chimpanzees and bonobos, mothers continue to provide protection and social opportunities well beyond infancy, shaping long-term fitness outcomes and socio-emotional development. By contrast, maternal loss can have lasting detrimental effects on physical, physiological and psychological levels such as growth, survival, fitness, stress physiology, emotion regulation, and social functioning.

Evidence suggests that rehabilitation upon maternal loss is possible in socially enriched, naturalistic environments such as accredited great ape sanctuaries. Most of the research on ape socio-emotional functioning, however, has been cross-sectional, providing just snapshots of behaviour at specific times without taking into consideration developmental trajectories over time that would be a relevant indicator of life outcomes.

To address this gap, the empirical study presented here draws on a decade of longitudinal observations of sanctuary-living bonobos, published in *Royal Society Open Science*. It investigates how rearing background, sex, and age predict variation in social tendencies and aggression risk across the life span. Results highlight the potential that ape sanctuaries like this can have by demonstrating that orphans exhibit decreased affiliative tendencies yet show social functioning that ranges within patterns of their mother-reared peers.

Given the importance of maternal support for great apes' physical and mental development, it is critical to better understand the developmental trajectories of the growing number of orphans entering sanctuaries as a result of habitat degradation and the bushmeat trade. These insights are not only scientifically significant but also practically urgent, informing the rehabilitation and long-term care of endangered apes.

# 1. General introduction

## 1.1. Social groups

Group-living non-human primates (henceforth primates) lead highly social lives in which group cohesion is an essential part of survival and reproductive fitness (Silk, 2001). There is growing evidence that strong social relationships in primates have a positive effect on individuals' fitness (Silk, 2012). For example, female yellow baboons (*Papio cynocephalus*) and chacma baboons (*Papio ursinus*) who maintain strong dyadic bonds and full social integration show higher infant survival and greater longevity themselves (Silk et al., 2003, 2010). However, a recent re-analysis did not find maternal sociality to be associated with infant survival, once the females' social behavioural shifts across reproductive phases and during the presence of an infant are taken into consideration (Creighton et al., 2025). Strong and stable male social bonds can predict reproductive success in species such as Assamese macaques (*Macaca assamensis*, Schülke et al., 2010) and chimpanzees (*Pan troglodytes*, Boesch, 2009; Constable et al., 2001; Nishida & Hosaka, 1996; Seyfarth & Cheney, 2012). Strong social relationships are hypothesized to buffer individuals from both ecological stress (e.g. nutritional access) and risks and negative consequences of social conflicts. Benefits include improved access to resources, lower predation risk due to central group positions, and enhanced stress resilience (Crockford et al., 2008; Silk et al., 2012; Wittig et al., 2008). These advantages are not only immediate but also extend into long-term health, survival and even cellular processes. Coping with stress is an important ability, particularly for females, to increase their reproductive success, as maternal distress can have detrimental effects on the longevity, growth rates and behaviour of their offspring (Silk, 2012). Recently, observations on social mammals, including primates, have demonstrated that social integration, social status, and early-life adversity predict natural life spans in the wild and molecular, physiological, and disease outcomes in experimental animal models (Snyder-Mackler et al., 2020).

## 1.2. Maternal support

In addition to broader group-level effects, maternal care is arguably the most influential relationship during the early stages of primate development of maternally dependent infants. For long-lived, slow-developing species like primates, maternal support can extend far beyond the dependency period, shaping social behaviour, rank acquisition, and emotional resilience into adolescence and adulthood (Mitani et al., 2012; Morrison et al., 2021). Beyond the nutritional advantage of maternal care, maternal influence on offspring social development is a universal and important factor across primate species (Maestripieri, 2018). Active maternal support enables offspring, including at later developmental stages, to integrate into their social groups and often increase their social rank, which is further related to survival and fitness (Morrison et al., 2021; Tung et al., 2016).

Another important component of maternal contribution to offspring fitness is the transmission of social status across generations (Maestripieri, 2018). In most baboon and macaque species where females remain in their natal groups and dominance hierarchies are steep and linear, mothers pass on their dominance rank to their male and female offspring by agonistic support (reviewed in Chapais, 1992; Maestripieri, 2018). This early advantage can shape future social opportunities and affect long-term integration within the group.

Our closest great ape cousins, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) can particularly provide important evolutionary insights into the importance of maternal support for offspring development, given their close phylogenetic relationship to us and similar life-histories to our own. In the social structure of chimpanzees and bonobos, males are philopatric and stay within their natal social groups, usually co-residing with their mothers (Gerloff et al., 1999; Mitani et al., 2002). Females on the other hand, tend to leave their natal groups prior to reproduction in both species (Kano, 1982; Pusey, 1979). Correspondingly, both chimpanzees and bonobos keep close associations to their mothers, especially sons, for extended periods beyond weaning and maternal investment often continues into adulthood (e.g. Samuni et al., 2020). For chimpanzees, research shows that time spent with the mother is positively associated with infant survival probability (e.g. Tkaczynski et al., 2020). Beyond weaning and into early adulthood, maternal presence in chimpanzees has also been shown to allow for nutritional buffering in feeding competition and benefits physical development, such that maternal presence positively influences offspring muscle mass throughout ontogeny (Samuni et al., 2020).

In bonobos, mothers play a particularly important role in enhancing the fitness outcomes of adult offspring, particularly their sons ( de Waal, 2002; Furuichi, 2011). Bonobos are unusual among primates as although they live in male-philopatric societies, females play a central role in their groups, are highly gregarious, maintain close female-female bonds, and tend to dominate males. Mothers support their sons and maintain close relationships with them throughout their lives (Surbeck et al., 2011). The presence of high-ranking bonobo mothers implies higher reproductive success of their male offspring. Mothers may even actively support their sons' reproductive success by enabling their sons to be in close proximity with oestrous females, preventing other males from interfering with their son's mating attempts and by interfering in mating attempts of other males (Surbeck et al., 2011). With the help of building coalitions with their sons, mothers enable their sons to acquire and maintain high rank positions (Furuichi, 2011). Maternal support of philopatric sons is facilitated by the high social status of females and their cooperative and tolerant structure (Toda et al., 2021), which increases both of their fitness outcomes.

While the field of maternal effects is predominated by primate research which remains the focus of the present study, effects of maternal support as well as maternal loss on long-term outcomes of survival, fitness, physiology, and behaviour are also evidenced in other long-lived mammals with complex social structures, large brains and similar stress and reproductive physiology such as hyenas (Watts et al., 2009), elephants (Lahdenperä et al., 2016), cetaceans (Foster et al., 2012) canids and ungulates (reviewed in Dettmer and Chusyd, 2023). In such species, mothers also play a critical role in offspring development, fitness and survival, where mothers provide ongoing protection, skill transmission, social integration, and access to resources well after weaning (reviewed in Zipple et al. 2024). Thus, although represented in a smaller field of research, the aforementioned and following examples of the importance of mothers do not solely refer to our species and our close primate cousins but are present across other long-lived, social mammals for which various perspectives of later life outcomes depend on maternal support.

## 1.3. Maternal loss

### 1.3.1 Effects on survival, longevity and fitness

As described, maternal support is vital for the survival, social integration, rank acquisition and fitness of primate offspring. With the critical presence of mothers for offspring outcomes, comes the extensive immediate and long-term detrimental effects associated with maternal loss.

Widespread evidence shows that maternal loss negatively affects primate survival, longevity and social and physical development. Longitudinal work on wild baboons demonstrated that cumulative early life adversities, including early maternal loss negatively affect survival in adulthood (Tung et al., 2016). Wild chimpanzee males, and most females were found to die shortly after the death of their mothers during infancy, as they are nutritionally dependent. Orphaned males died at a young age, even when being orphaned after weaning, which indicates the long-term dependency of sons on their mothers in male-philopatric societies (Nakamura et al., 2014). Similarly, a recent study by Stanton and colleagues (2020) conducted on wild chimpanzees with data from a period of 50 years stresses the importance of the mother to the survival and longevity of their dependent offspring and well beyond the age of weaning. Orphans between the age of 0-10 years had significantly lower survival and longevity probabilities than non-orphans of both sexes. However, orphaned males among chimpanzees were equally negatively affected in their survival at the age of 10-15 years, whereas females were less affected in this older age category. Philopatric male chimpanzees may continue to benefit from the mother’s ecological knowledge e.g. resources distribution, while females become more independent preparing for migration (Stanton et al., 2020). Also, males who are orphaned after weaning and before reaching sexual maturity reproduce later and less successfully (Crockford et al., 2020).

### 1.3.2 Physical and physiological consequences

Maternal loss also profoundly affects physical and physiological changes in orphan primates. Among our close ape cousins, long lasting physical costs of maternal loss were found in wild chimpanzees resulting in lower body mass and muscle growth, as measured by specific gravity and creatinine concentration of urine samples, even when orphaned after weaning (Samuni et al., 2020). Orphans may face lower physical growth due to the lack of maternal buffering. The absence of maternal agonistic support to access rich nutrients and independent travel and foraging may expose orphans to increased physical and psychological stress leading to suppression of growth and muscle development (Samuni et al., 2020).

A further example of physiological consequences of stress related to maternal loss was demonstrated in young chimpanzees in the wild (Girard-Buttoz et al., 2020): The hypothalamic pituitary adrenal (HPA) axis is involved in the internal physiological stress response and severe stressors such as early life adversities can lead to short and long-term disruptions of its functioning in humans (Girard-Buttoz et al., 2020) and rodents showing HPA-axis alternations following maternal separation (Nishi et al. 2013). Young orphaned chimpanzees, who suffered from early maternal loss, were found to have a higher HPA axis activation than non-orphans, as measured by urinary cortisol levels and diurnal urinary cortisol slopes. Equally high physiological stress response was measured in recently orphaned immatures. These findings suggest that these young orphans are facing high social and nutritional stressors when losing their mothers. Among adult males, such differences were not found anymore, suggesting that there may not be long-term alterations of physiological stress response, or that other mechanisms such as adoption may buffer these social stressors (Girard-Buttoz et al., 2020).

Deleterious long-term effects of early rearing adversities are indeed detectable in brain development of apes. Atypical rearing in the absence of socio-emotional experience can lead to changes in the structural covariation and grey matter volume in the basal forebrain in adult chimpanzees (Bard & Hopkins, 2018). Such changes in the brain can however be prevented by early socio-emotional intervention of human caretakers and peer grouping to optimize the development of species-typical behaviours in nursery-reared chimpanzees (Bard & Hopkins, 2018).

### 1.3.3 Psychological consequences

Early adversity has perhaps its biggest and most notable impact on primate psychological development and social functioning, the core topic of this research.

We know from neglected human children of early foster homes that lack of emotional stimulation from maternal deprivation negatively affects social development, behavioural and emotional regulation (De Bellis, 2005). Adoption into a family environment can improve these effects, however, social deprivation lasting longer than the first 6 months of life prior to adoption lead to persistent cognitive, socio-emotional and behavioural impairments into early adolescence (Beckett et al., 2006; Chisholm, 1998; Kreppner et al., 2007; Wismer Fries et al., 2005). The first 6 months seem to be a critical point in this aspect, as full recovery in adoptive care is possible when early deprivation does not surpass this age (Kreppner et al., 2007).

Given that most primates live in social communities with complex social networks, studies on non-human primates have been very informative on the role that early life history has on emotional and social development. Harlow and colleagues conducted pioneer studies on the impact of rearing on socio-emotional development in non-human primates, specifically rhesus macaque (*Macaca mulatta*) infants (Cross & Harlow, 1965; Harlow et al., 1965). They manipulated natural settings, exposing infants to total or partial social isolation, taken from their mothers within the first minutes of life, which had long-lasting effects on their social competences later in life. Social isolation resulted in repetitive stereotyped movements, detachment from the environment, and hostility towards others and their own body. When given the opportunity to interact with peers, primary social responsiveness was fear and emotional shock, with individuals unable to form adequate heterosexual or social attachments and hardly showing social positive or aggressive behaviour into adolescence and adulthood (Cross & Harlow, 1965; Harlow et al., 1965). Early deprivation for at least the first six months of life negatively affects socio-emotional development and leads to severe deficits in social behavioural capabilities (Harlow et al., 1965; Harlow & Suomi, 1971). Individuals who are completely isolated for six months show violent aggression when housed with more helpless 12 months deprived peers ( Harlow & Harlow, 1965). However, short periods of social isolation (≤ 3 months) may be reversible and do not lead to permanent social deficits (Harlow et al., 1965). When social contact with young peers was provided in rehabilitation situations, it was found that 6-month-old infants can recover from total social isolation (Harlow & Suomi, 1971).

While research on the impacts of maternal loss is important for theories of psychological development, investigating rearing effects in such a highly invasive and unethical manner is highly problematic and obsolete, as investigations in more naturalistic and unmanipulated settings show. More recent studies which have not entailed unethical rearing manipulations have also pointed out the importance of maternal rearing and the presence of a social network for the development of primate social skills: Adolescent rhesus macaques for instance, who were mother-reared only during the first year of life and subsequently peer-reared (i.e. reared with conspecifics but without the mother) were found to show higher rates of submissive and stereotypic behaviour and more aggression in nonthreatening contexts as compared to non-deprived individuals (Kempes et al., 2008). Studies on rehabilitated ex-laboratory chimpanzees (*Pan troglodytes*) have revealed that early maternal loss and long-term deprivation in solitary housing in over 20 years leads to long-term social deficits in adulthood even after rehabilitation. In these studies, it was shown that early deprived chimpanzees are less closely associated with group members and show less grooming activity (or even none at all) than socially reared chimpanzees (Kalcher-Sommersguter et al., 2015). Furthermore, chimpanzees who suffered earlier deprivation at the age of 1-2 years and spent more years solitary housed in the laboratory were found to be more frightful, less socially active, less dominant and showed higher stress response during rehabilitation than individuals who were deprived at the age of 3-4 years and were peer reared for one year before being isolated in the laboratory setting (Reimers et al., 2007). Orphaned juvenile chimpanzees housed at a sanctuary showed more frequent play behaviours, however less ability to sustain social play compared to mother-reared juveniles. It was also found that play bouts are more prone to turn into aggressive behaviours in orphans than in mother-reared chimpanzees (van Leeuwen et al., 2014). Studies on resocialized chimpanzees with different rearing backgrounds also revealed that individuals who have been hand-reared by humans only, or peer-reared without their mothers, show higher levels of abnormal behaviours later in life than mother-reared individuals (Martin, 2002). However, their social skills were not found to be significantly affected by these rearing backgrounds, apart from social initiations that were found to be less successful in hand-reared chimpanzees (Martin, 2005). In rehabilitated chimpanzees, rescued from the pet and entertainment industry with different life-histories (wild-caught and captive-born) it was also found that adverse early life experiences affect social interaction such as affiliative behaviour and allogrooming (Crailsheim, Romani, et al., 2020). Wild-caught (i.e. orphaned) individuals were reported to be more selective towards grooming partner choice and showed less grooming activity as compared to their captive-born peers (Crailsheim, Stüger, et al., 2020).

As part of the adverse psychological impacts of maternal loss, the development of empathy, attachment and emotion regulation are highly negatively affected, as known from human children (De Bellis, 2005). While much less is known in this respect in our close non-human primate cousins, existing studies on bonobos provide evidence for rearing effects on the development of empathy and socio-emotional competence (Clay & de Waal, 2013a, 2013b).

Empathy is considered to be a key form of socio-emotional competence. It entails the capacity to be affected by and share the emotional state of others and underlies sympathetic concern (de Waal, 2008). “Sympathetic concern is the concern about another’s state and the attempt to ameliorate this state” (de Waal, 2008, p. 283). This may require a higher cognitive ability to encounter an other’s emotions while differentiating them from one's own (Clay & de Waal, 2013a; Preston & de Waal, 2002), though, more recent work on rodents challenges the view that empathy depends on higher-order cognition (Bartal et al., 2011; Burkett et al., 2016; Langford et al., 2006; Meyza et al., 2017). A marker of sympathetic concern is consolation, which is defined as offered contact by a third party that implies the function of reducing the distress of a distressed party such as an aggressed victim (Clay & de Waal, 2013b; de Waal, 2008; de Waal & van Roosmalen, 1979). Evidence for stress alleviation, a crucial function of consolation, in non-human primates was thus far found in chimpanzees (Fraser et al., 2008), bonobos (Clay & de Waal, 2013a, 2013b, 2015; Palagi & Norscia, 2013) and tonkean macaques (*Macaca tonkeana*) (Palagi et al., 2014).

As mentioned above, sympathetic concern is indicated by other-oriented behaviour. This contrasts to personal-distress, which instead is a self-focussed reaction to the emotional state of a distressed party and mimics the distress of the other individual (Pérez-Manrique & Gomila, 2018). Emotion regulation is an important key factor of socio-emotional competence that differentiates between sympathetic concern and personal distress (Pérez-Manrique & Gomila, 2018). It is the ability to regulate one's own emotions to adequately respond to arousing situations by e.g. modifying, inhibiting and evaluating internal states and reactions (Clay & de Waal, 2013b).

Studies by Clay and de Waal (2013a, 2013b) investigated the socio-emotional capacities of mother-reared and orphaned juvenile bonobos, focusing on behaviours such as post-conflict reconciliation, consolation, emotion regulation, and broader social competence. Their findings revealed that consolatory behaviours emerge early in development, with juveniles more likely to console than adults. Importantly, rearing background significantly influenced this tendency: mother-reared juveniles were more likely to console distressed group members than orphaned peers (Clay & de Waal, 2013a). Moreover, mother-reared juveniles also showed shorter latencies to cease distress-related behaviours in post-distress periods—an indication of more effective emotion regulation (Clay & de Waal, 2013b). These two capacities—emotion regulation and empathic response—were found to be correlated, particularly in mother-reared individuals, suggesting that the ability to manage one's own distress may facilitate responding to the distress of others. Beyond empathy, mother-reared juveniles also demonstrated greater overall social competence: they had a significantly higher number of close affiliative partners, initiated and sustained play more frequently, and showed stronger social bonding as measured by affinity scores within the group's upper quartile.

Taken together, these findings underscore the role of maternal presence in shaping not just emotional recovery but also the development of key prosocial behaviours in juvenile bonobos.

### 1.3.4 Adaptive consequences of early adversity?

Although early adversity including maternal loss can have long-term costs, these experiences can sometimes conversely lead to the development of cognitive, social and emotional skills, adaptive to stressful adverse conditions. This notion of the resilience building effects of adversity is described in the 'hidden talents framework' (reviewed in Ellis et al. 2023) which builds on the evolutionary-development perspective to consider stress adaptation in regard to fitness outcome where adaptive traits can be costly, yet adaptive in specific (here stressful) circumstances (Ellis et al. 2023, Ellis & Del Giudice, 2014, 2019). The field of developmental psychopathology often emphasizes that behavioural responses shaped by early adversity may support immediate survival while being costly in later, more stable contexts. The *hidden talents framework* extends this view by suggesting that early stress can also positively shape stress-adapted skills that remain functional beyond the immediate context in which they emerge (reviewed in Ellis et al. 2023). For example, human children raised in adverse circumstances do not necessarily underperform on social and cognitive tasks compared to those from more stable conditions. Instead, their abilities may be enhanced in specific areas that align with the skills required in coping with challenging, unpredictable circumstances. For example, the ability to identify and recall negative emotions (e.g., quick danger identification), make reward-oriented decisions, problem solving, empathic accuracy and emotion recognition, collaborative skills, and executive functions such as attention shifting and working memory maintenance (reviewed in Ellis et al. 2003). Although not highlighted within the framework, a recent study on orphaned mountain gorillas (*Gorilla beringei beringei*), reported an increase in social integration and relationship strength following maternal loss, indicating surprising adaptation after a severely stressful life-event (Morrison et al., 2021).

Thus, despite the presence of negative consequences of maternal loss, early adversity can simultaneously foster resilience through the development of stress-adapted skills that can be beneficial in certain challenging environments.

## 1.4. Rehabilitation and recovery in sanctuaries

The Pan-African Sanctuary Alliance (PASA, 2025) is the largest network of primate sanctuaries in Africa, with 23 member organizations across 13 countries (PASA, 2023). Its mission is to provide enriched physical and social environments that facilitate recovery from the trauma of maternal loss and capture (Farmer, 2002). Studies suggest that PASA-accredited sanctuaries meet this goal effectively: orphaned bonobos and chimpanzees do not show major abnormalities in behaviour, cognition, or stress profiles (Wobber & Hare, 2011). Range country sanctuary settings can offer a rare opportunity to explore whether and how socio-emotional functioning can be supported following early adversity. Such institutions accredited by the Pan African Sanctuary Alliance (PASA) provide socially rich, environmentally enriched contexts for orphaned great apes. Here, rescued individuals receive surrogate human care, form peer relationships, and engage in species-typical activities such as nest-building, foraging, and social play (André et al., 2008; Wobber & Hare, 2011).

***Figure 1.*** *Surrogate mother Mme. Yvonne Vela with rescued bonobo infants at Lola ya Bonbobo. Photo by S. Kordon*

Sanctuaries like Lola ya Bonobo, where the current research was conducted, not only provide physical and emotional care to rescued infant bonobos—who often arrive malnourished and injured—but also contribute to conservation by helping enforce wildlife protection laws and countering illegal trade (André et al., 2008). Education is central to this mission, with schoolchildren and local visitors learning about bonobo behaviour, biodiversity, and environmental stewardship through sanctuary outreach programs (André et al., 2008). Finally, successful rewilding efforts are pursued to return rehabilitated bonobos into protected natural rainforest habitats.

Although some impairments may persist, studies show that sanctuary-living orphans can achieve levels of behavioural and cognitive competence comparable to mother-reared peers (Bard & Hopkins, 2018; Crailsheim, Stüger, et al., 2020). Peer interaction and group cohesion may buffer some of the social costs of maternal loss, allowing orphans to develop adaptive strategies in the absence of kin support. Nonetheless, certain socio-emotional capacities—such as empathy or stress regulation—may remain subtly affected, particularly if they depend on early attachment experiences.

Whether and how orphans continue to improve over time, however, remains less understood. Some individuals may show gains in socio-emotional functioning as they age, while others continue to face persistent deficits. Longitudinal observation is thus essential for assessing trajectories of adaptation, compensation, or recovery following early life trauma. This perspective raises critical questions about developmental plasticity and the potential limits—and promise—of rehabilitation in socially enriched settings like sanctuaries.

## 1.5. Research context and objectives

While the long-term consequences of maternal loss are well-documented, fewer studies have systematically investigated how these outcomes evolve across development. In apes, much of the existing research has concentrated on survival or reproductive outcomes, with fewer studies addressing long-term psychological impairments linked to early-life adversity. Where such impairments have been explored in apes mostly specific time points at an older age have been addressed. Yet to fully assess how socio-emotional competencies unfold as a function of rearing history, it is critical to examine behaviour across different developmental stages across the life span. Longitudinal approaches are essential to understanding whether, how, and for whom recovery is possible. This thesis contributes to this line of inquiry.

Social integration is essential for the survival and fitness of highly social species, including humans and other primates. As reviewed here, maternal support plays a central role in shaping not only the physical development but also the psychological resilience of offspring—particularly in slow-developing species like great apes. With mounting pressures from habitat loss and the bushmeat trade, the number of orphaned apes entering sanctuaries is increasing. Understanding the long-term developmental trajectories of these individuals is therefore both scientifically and practically urgent. Expanding our insight into the psychological and social challenges faced by sanctuary-living orphans across their lifespan can help inform evidence-based management strategies that support their successful rehabilitation and, ultimately, reintroduction into protected habitats.

In the following empirical study, I present a longitudinal investigation of sanctuary-living bonobos, examining how rearing background, sex, and age influence differences in social affiliation, consolation, and conflict exposure. The study, now published in *Royal Society Open Science*, draws on a decade of behavioural data collected at Lola ya Bonobo sanctuary. It builds on the themes discussed here by tracing the developmental trajectories of orphaned and mother-reared bonobos in a semi-natural, socially rich environment, offering new insights into the long-term socio-emotional consequences of early life adversity. Note that the following study includes amendments to the published version to comply with the present thesis.

# 2. Empirical study

## Factors shaping socio-emotional trajectories in sanctuary-living bonobos: a longitudinal approach

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**Cite this article:** Kordon S, Webb CE, Brooker JS, de Waal FBM, Clay Z. 2024 Factors shaping socio-emotional trajectories in sanctuary-living bonobos: a longitudinal approach. *R. Soc. Open Sci.* **11**: 240435.

### 2.1. Abstract

Early maternal loss can have lasting detrimental effects on primate social development. While many rehabilitation settings provide enriching environments to buffer against such effects in orphans, previous research indicates that young bonobo (*Pan paniscus*) orphans exhibit striking deficiencies in socio-emotional competence compared to their mother-reared peers. However, such studies are generally cross-sectional, without accounting for changes across the lifespan. We conducted longitudinal observations in bonobos living in an accredited African ape sanctuary to examine how rearing background, sex and age predict social tendencies including affiliation, consolation and aggression risk. Affiliative tendencies increased in females and decreased in males with age but were overall lower in orphans compared to mother-reared bonobos. Consolation tendencies decreased with age in mother-reared bonobos, while orphans showed consistently lower consolation (akin to levels of older mother-reared individuals). Young and male bonobos were more likely to receive aggression, while mother-reared and older females were more likely aggressors. Our study highlights the potential that ape sanctuaries like this can have by demonstrating that orphans exhibit decreased affiliative tendencies yet show social functioning ranging within patterns of their mother-reared peers. We discuss these results in the context of bonobos' natural social ecology and ongoing rehabilitation efforts in this species.

## 2.2. Introduction

As with other mammals, early maternal loss in primates can have both immediate as well as lasting detrimental effects that persist into adulthood. Longitudinal studies on wild primate populations— including baboons (*Papio cynocephalus*) in Amboseli, Kenya (Tung et al., 2016) and chimpanzees (*Pan troglodytes*) in Mahale and Gombe, Tanzania (Nakamura et al., 2014; Stanton et al., 2020)— reveal that losing a mother early in life can lead to a variety of negative fitness consequences (e.g. survival and longevity - reviewed above). Moreover, the nature and severity of these fitness consequences vary according to the sex of the infant and the age when they lost their mother. For instance, compared to females, chimpanzee male survival is more affected by maternal loss after the age of weaning and into adolescence. This may reflect the paramount importance of maternal support for chimpanzee males, a philopatric species, who continue to benefit from their mother's ecological knowledge (e.g. about resource distribution) into adulthood, while females become more independent upon preparing for dispersal (Nakamura et al., 2014; Stanton et al., 2020). Moreover, male chimpanzees orphaned at an immature age after weaning subsequently reproduce later and less successfully than non-orphaned males (Crockford et al., 2020).

A close cousin of the chimpanzee, the bonobo (*Pan paniscus*) is another male philopatric species where maternal bonds appear to play an especially important role in offering sons life-long maternal support (Surbeck et al., 2011). Through building strong and enduring coalitions with their mothers, sons can acquire and maintain high-rank positions (Furuichi, 2011), while also themselves benefitting through kin selection as well as enhanced coalitionary strength. The high social status of bonobo females and the characteristic cooperative and tolerant structure among female group members facilitate maternal support of philopatric sons (Toda et al., 2021), which in turn increases the fitness outcomes of both (Surbeck et al., 2011).

In addition to promoting offspring survival and reproductive success, research in humans and other animals shows that maternal support facilitates healthy social and emotional functioning. Research on neglected human children from orphanages and early foster homes suggests that maternal deprivation can negatively affect social development, including behavioural and emotional regulation (see de Bellis, 2005). While adoption into a family environment often helps mitigate these effects, prolonged social deprivation beyond the first six months of life prior to adoption often leads to persistent cognitive, socio-emotional and behavioural challenges into early adolescence (Beckett et al., 2006; Chisholm, 1998; Kreppner et al., 2007; Wismer Fries et al., 2005). However, such outcomes are not necessarily inevitable or uniform across all individuals. Recovery is also possible, especially when deprivation does not extend beyond the first six months of life (Kreppner et al., 2007); moreover, various individual and environmental factors, such as genetic predispositions and the quality of subsequent caring environments, also serve as both protective and risk factors.

Although less studied, early life maternal deprivation and subsequent adverse social environments can also negatively affect the development of social competence (i.e. adequate social functioning within a social group) in other primates. Likewise, however, such effects may be buffered by social support along with other factors (e.g. Morrison et al., 2021; see below). Studies on ex-laboratory chimpanzees, who suffered early maternal loss along with long-term deprivation in solitary housing for over 20 years, showed long-term deficits in grooming and social closeness to their peers into adulthood (Kalcher-Sommersguter et al., 2015). Captive chimpanzees who were maternally deprived in infancy (1–2 years) and socially isolated for longer were more fearful and less socially active, with higher stress responses during rehabilitation as compared to later deprived individuals (3–4 years) who were peer-reared for one year pre-laboratory isolation (Reimers et al., 2007). In former pet and entertainment chimpanzees in a primate rescue and rehabilitation centre in Spain, wild-caught individuals who additionally experienced early life adversities prior to their captive lives (such as the transfer from wild to species-inappropriate isolated captive life and potential maltreatment and malnutrition) were socially impaired, including reduced affiliative behaviour and grooming activity compared to their captive-born peers (Crailsheim, Romani, et al., 2020; Crailsheim, Stüger, et al., 2020). The play behaviour of orphaned juvenile chimpanzees (rescued victims of the illegal pet and bushmeat trades) in a naturalistic African sanctuary environment was also negatively affected; the orphans were unable to sustain play and more frequently became aggressive as compared to mother-reared juveniles (van Leeuwen et al., 2014).

Socio-emotional skills encompass a wide range of competencies related to how individuals build and maintain relationships, function socially within a group, and understand and regulate emotions (Napolitano et al., 2021). Of such skills, empathy represents a key socio-emotional ability that appears to be compromised by maternal loss in humans (De Bellis, 2005) and non-human primates (Clay et al., 2022). We use the term empathy here to broadly refer to the capacity to share, understand, or respond with concern to the emotional state of others ( de Waal, 2008; Decety, 2012). Consolation—the offering of friendly contact by a third party to a distressed individual (such as after a fight) is considered a reliable behavioural marker of empathy (de Waal & van Roosmalen, 1979). Crucially, consolation has a stress-reducing function for the recipient (de Waal, 2008) without any obvious benefits to the actor, supportive of its prosocial function. Among primates, the stress-alleviating effect of being consoled has been demonstrated in several species, including bonobos (Clay & de Waal, 2013a, 2013b, 2015; Palagi & Norscia, 2013), chimpanzees (Fraser et al., 2008) and Tonkean macaques (*Macaca tonkeana*) (Palagi et al., 2014). Research conducted with bonobos housed at the facility where the present study took place revealed that compared to mother-reared peers, orphan juveniles show lower consolation tendencies and reduced socio-emotional competence, as measured by the number of close affiliative partners, tendency to initiate and sustain play behaviour, and ability to cope with emotional distress (Clay & de Waal, 2013a, 2013b). Evidence that immature apes engage in consolation suggests that the behaviour may not depend on sophisticated cognitive mechanisms, and there are broader, ongoing debates about levels of cognitive complexity involved in empathetic responses (Batson, 2009; de Waal, 2008). However, as consolation requires the ability to attend to others' states, it can indicate investment in social relation- ships and thus is used here as a proxy for social functioning.

Despite the broadly detrimental effects of early maternal loss, opportunities for peer interaction may provide social buffering to support the development of social skills. A recent study of wild mountain gorillas (*Gorilla beringei beringei*) found that, against predictions, orphans did not face pronounced social adversity or fitness costs following maternal loss. Rather, a subsequent increase in their social integration and relationship strength suggested they were able to cope with maternal loss through social group buffering (Morrison et al., 2021). Morrison and colleagues also found that while early life adversity (including parental loss) predicts high mortality in early life, it had no effect on the adult longevity of mountain gorillas (Morrison et al., 2023). In captive settings, rehabilitation from the early life trauma of maternal loss is possible through surrogacy and nursery rearing practices. For instance, research with captive chimpanzees revealed that behavioural and social deficits of orphans (who required nursery-rearing to survive) might be partially mitigated by modern nursery-rearing practices that include receiving surrogate care by human carers along with experiencing social interactions within a stimulating peer-group environment, where they are offered the chance to engage in physical activity in more complex outdoor enclosures (reviewed in Bloomsmith et al., 2006). Such rehabilitative environments may even prevent changes in neural structures that can otherwise occur following adverse early rearing experiences (Bard & Hopkins, 2018).

Lola ya Bonobo is an African primate centre, accredited to the Pan African Sanctuary Alliance (PASA) (PASA, 2016) that rescues and rehabilitates orphaned bonobos, victims of the illegal bushmeat and pet trade. It provides a naturalistic environment including large, forested enclosures and social groups that favour the adoption of species-typical behaviour and follows high-standard sanctuary requirements (e.g. housing, welfare, management and others) as a member of PASA (PASA, 2016). We stress that we hence- forth refer to a 'sanctuary' in compliance with the aforementioned criteria, as one cannot generalize the conditions, procedures, facilities, aims and circumstances of all great ape centres in Africa, but also in European, Asian and American locations which may self-identify as sanctuaries.

African great ape sanctuaries like Lola ya Bonobo offer a unique opportunity to investigate the effects of social rearing in more ecologically valid environments than can be afforded in captivity. Importantly, such settings combine early surrogate human care of orphaned infants with extensive nutritional and veterinary support, followed by supported integration into socially and environmentally enriching groups. This nurturing setting may thus facilitate rehabilitation processes including improved social functioning over time. Compared to other captive settings, such as zoos, home-range sanctuaries are typically more similar to the wild environment and climate and enable apes to live in large social groups and express species-typical behaviours including foraging and nest-building in large forested enclosures (André et al., 2008; Rosati et al., 2013; Wobber & Hare, 2011). Such potential rehabilitation in sanctuaries of this kind has recently been suggested for chimpanzees, where orphans that experienced early life trauma did not vary in their later-life social integration from their mother-reared counterparts born in the sanctuary (van Leeuwen et al., 2022). A study on sanctuary-living bonobos and chimpanzees also found that orphans from juvenility to adulthood performed equally well on various cognitive tasks as mother-reared peers and did not show abnormalities in behaviour or stress levels (Wobber & Hare, 2011). An example of a European primate rescue centre that follows high standards and is a member of European Alliance of Rescue Centres and Sanctuaries (EARS) is a study on ex-pet and performance chimpanzees that suggests that rehabilitation is possible over time, indicated by increasing social competence and welfare and decreasing abnormal behaviours (Llorente et al., 2015).

Thus far, most research on ape social and/or emotional functioning in similar settings has been cross-sectional. Although there are two studies with chimpanzees that provide a rare longitudinal approach (Llorente et al., 2015; van Leeuwen et al., 2022), they still do not entail observations across early social development, as their study individuals were observed from adolescence or adulthood. In the study by Llorente et al., 2015, chimpanzees were rescued either at adolescence or (mostly) adulthood, while the study by van Leeuwen et al., 2022 only investigated effects from adolescence or adulthood, even if some were rescued at a younger age. Although this provides relevant snapshots in time, it fails to account for potential developmental trajectories over time; moreover, single timepoints might not be representative of later life stages or outcomes. To address this limitation, the present study examined the socio-emotional development of sanctuary-living bonobos using a longitudinal approach including all age classes. Building upon and extending existing cross-sectional findings revealing rearing effects from this population (Clay & de Waal, 2013a, 2013b), behavioural observations were compiled across five independent periods of data collection spanning a decade. Analyses explored how rearing, sex and age interact to predict three behavioural markers of socio-emotional functioning: affiliation tendencies, consolation tendencies and the likelihood of being a victim or aggressor in social conflicts. As this sanctuary comprises both wild-born orphans (whose rehabilitation process started at a young age) and mother-reared individuals (who were born at the sanctuary), this setting provides a unique opportunity to investigate longitudinally the impact of rearing on socio-emotional development in an environmentally controlled context. Furthermore, the semi-wild housing provides a more valid social and ecological environment than can be afforded in captivity while still maintaining good degrees of observation visibility and large sample size, thus making it a good compromise between wild and captive environments, as these kinds of observations are challenging to achieve in the wild.

Despite providing unique and precious insights into hominid life histories, longitudinal studies of great ape social development are rare. By taking a longitudinal approach, this study aimed to enhance understanding of factors shaping primate socio-emotional development, and to examine the outcomes of sanctuary rehabilitation efforts for endangered species, including bonobos. Lastly, for conservation efforts the majority of the study site's bonobos may be released and some already have been released into the wild; therefore, we also aimed to expand the knowledge about their ability to perform vital healthy social functioning.

Social competence is broadly defined as the ability to effectively assess social situations and respond to them in a species-appropriate way, enabling adequate functioning within a social group (e.g Kempes et al. 2008b). Although healthy social functioning can be measured in various different ways, we focussed on the following three indicators of socio-emotional competence: Affiliative tendencies, consolation tendencies and risk of social conflict (actor and victim). These metrics and the following predictions are informed from the comparative and human developmental literature, as well as being derived from the most systematic and substantial measures of our data set.

*Affiliative tendencies*: Given that bonobos are a male-philopatric species in which males depend on sustained maternal support for fitness outcomes (Surbeck et al., 2011), we predicted that orphaned male bonobos would exhibit more persistent social deficiencies than their female counterparts or mother-reared peers. Furthermore, wild female bonobos migrate at adolescence and integrate into a new group, facilitated by investing in female–female relationships with recently migrated and older resident females of high-ranking positions (Furuichi, 1989, 2011; Idani, 1991; Toda & Furuichi, 2022), leading to our prediction that female bonobos would be less affected by a lack of maternal support with age. Males show less intra-sexual bonding and instead typically build coalitions with their mothers and other females to receive support in acquiring and maintaining high rank positions (Furuichi, 2011; Surbeck et al., 2011). Thus, we predicted that with age, males would exhibit decreased affiliative tendencies, whereas females would exhibit increased affiliative tendencies. Finally, we predicted that affiliative tendencies in orphaned compared to mother-reared bonobos would persist at a lower level across age, based on evidence that chimpanzee social phenotypes are relatively stable across the life-span (Tkaczynski et al., 2020). Alternatively, if the sanctuary provides a rehabilitative setting for improved social functioning (e.g. van Leeuwen et al., 2022; Wobber & Hare, 2011), we would expect an increase in affiliation across age within the orphans particularly.

*Consolation tendencies*: Previous research, including in chimpanzees (Webb et al.,

2017) and in bonobos in this study population (Clay & de Waal, 2013a, 2013b), found that infants and juveniles console more often than their older counterparts. Based on these findings, we anticipated a similar overall developmental decline in consolation behaviour. Chimpanzee consolation tendencies were also found to be relatively stable across the lifespan (Webb et al., 2017). We, therefore, investigated whether the lower consolation tendencies observed in juvenile orphans (compared to mother-reared bonobos) in this study population (Clay & de Waal, 2013a, 2013b) would persist with age, or if the orphans' empathic tendencies would improve over time. Again, based on species-typical patterns, we would expect female orphans to increasingly align with mother-reared bonobos with age, whereas male orphans would exhibit a consistent disparity with their mother-reared counterparts into adulthood. Research on sex differences in consolation remains limited and inconsistent, with conflicting results reported in great apes (Clay & de Waal, 2013a; Cordoni et al., 2006; Romero et al., 2010; Webb et al., 2017). We, therefore, did not have a strong directional prediction regarding sex differences.

*Social conflict risk:* Last, we investigated the likelihood of being a victim or aggressor in social conflicts. Again, based on the species' natural social ecology, we predicted that older females—the high-ranking core of the group (Furuichi, 1997)—would be the most likely aggressors. Furthermore, we expected that aggression would be primarily directed at young bonobos, especially male orphans, who are at a disadvantage when trying to integrate into a social group in the absence of maternal support.

## 2.3. Methods

### 2.3.1. Study site and subjects

Observations were conducted at Lola ya Bonobo sanctuary in Kinshasa, Democratic Republic of Congo. Groups at Lola ya Bonobo consist primarily of orphaned victims of the illegal bushmeat and pet trade. Most wild-caught orphans have experienced some form of trauma, poor health, and malnourishment owing to maltreatment prior to their rescue at an estimated minimum age of 2–3 years. Age at the rescue is estimated by dental and weight estimates by the veterinarians of the sanctuary (Wobber & Hare, 2011). Along with orphans, groups include some bonobos who were born and mother-reared at the study site, where limited reproduction is allowed to promote naturalistic social settings of mixed-age social groups (following strict guidelines for primate release programmes e.g. by IUCN, PASA).

Alongside rescuing and housing orphaned bonobos at Lola ya Bonobo, Amis des Bonobos du Congo (ABC) manages a reintroduction site called Ekolo ya Bonobo, where fully rehabilitated individuals are released into a protected wild habitat. For eligibility for reintroduction, individuals pass through a series of stages upon rescue (see appendix: supplementary material, box 1). The study site at Lola ya Bonobo features three separate outdoor enclosures that provide a semi-wild environment composed of secondary rainforest, grasslands and swampy areas with ad libitum access to water (by means of a lake, floating stream or a pool). Observations were conducted on all individuals from the three social groups (henceforth G1, G2, G3); these include orphaned as well as mother-reared individuals of all age and sex classes across different time points (G3 was observed in 2016 only). As observational data were collected across multiple years (see below), there are fluctuations in observed individuals (across a total of $n = 83$) and group compositions based on births, deaths, reintroductions into the wild and transfer between groups following veterinary and management decisions (Appendix: supplementary material, table 1).

***Figure 2. Satellite view of the three outdoor enclosures of group 1, 2, and 3 at Lola ya Bonobo.*** *Enclosure area sizes: 1 (Group 1) = 10 ha; 2 (Group 2) = 15 ha; 3 (Group 3) = 5 ha. Satellite image obtained through Google Maps and edited in Adobe Photoshop by J.S. Brooker*

***Figure 3. Image of the enclosure of group 2 at Lola ya Bonobo;*** *showing the naturalistic environment composed of primary rainforest, grassland, small river and lake. Photo by S. Kordon*

### 2.3.2. Data collection and processing

Data were collected over a decade during five time points in the years 2011, 2012, 2016, 2019 and 2021, respectively. Each time point comprised 2–3-month observation periods (Appendix: supplementary material, table 2). Observations were led by Z.C. (2011, 2012) and S.K. (2016, 2019, 2021) with assistance of Pitshou Nsele Kayanga (2011, 2012) and Heritier Izansone (2019, 2021). Across all observation periods, consistent methods of data collection and ethograms were applied (see below for a deviation regarding affiliation scans in 2019). Observations included social affiliation scan sampling, all-occurrences of post-conflict/post-distress (hereafter PC/PD) focal video sampling and all-occurrences of agonistic conflicts followed by an identifiable victim response. PC/PD recordings were prioritized over scan sampling if they occurred simultaneously. The identities of the aggressor and victim as well as the type of aggression were recorded on a dyadic level per group and observation period (see appendix: supplementary material for ethogram and definitions). Observations of social affiliations only began with the presence of at least one-quarter of the group members to allow for sufficient opportunities to engage in social interactions to estimate socializing. All instances of aggressions were recorded when at least the aggressor and victim were visible.

### 2.3.3. Affiliation scans

Instantaneous scan samples of all visible social affiliations at the group level were recorded throughout the day, outside of feeding times (when PC/PD recordings were the primary focus, and to avoid overestimation of proximities influenced by food location). The presence of each individual as well as dyadic proximities and interactions of state behaviours were recorded at each scan point (i.e. contact sit, within arm's reach, play, groom, sexual contact; see appendix: supplementary material, table 6 for an ethogram). Intervals between scan points remained consistent within each observation period, but differed between some periods, that is, affiliation scans were conducted every 10 min in observation periods 2011 and 2012, and every 20 min in 2016 and 2021. The data collection in 2019 deviated modestly from other years; however, the resulting raw data remained constant. In 2019, social affiliation was recorded using a 10 min focal scan (Altmann, 1974), consisting of ten 1 min scan points whereby affiliative behaviours (equal to all observation periods) the focal was involved in were recorded. A mean dyadic affiliation score was calculated per individual and observation period and controlled for overall social tendencies per group and observation period, that is, (*N* scan points a dyad interacted/*N* scan points a dyad was present) divided by the group mean across individual dyadic affiliation scores per observation period (adapted from Clay & de Waal, 2013a; Silk et al., 2003). As all behaviours required body contact or proximity of one arm's length, they were all combined into the affiliation score, representing dyadic proximities. Across all study periods, we collected a total of *n* = 6337 social affiliation scans (see appendix: supplementary material, table 7).

### 2.3.4. Post-conflict and post-distress focals

To measure consolation, PC and PD focal observations were collected on victims of aggression with high-definition hand-held camcorders. As conflicts occurred spontaneously, we conducted all occurrence-focal sampling (Altmann, 1974) on individuals of all age classes. The victim was identified as the recipient of aggression resulting in clear victim response behaviours such as a high-pitched distress scream (see appendix: supplementary material, table 3). In case of a spontaneous tantrum, or when the conflict occurred out of sight, the focal recording was marked as a PD observation. Previous observations at this study site demonstrated that consolation behaviour mostly occurred within the first 5 min of a PC/PD (70.7% within the first 2 min, 84.6% within the first 5 min; (Clay & de Waal, 2013a), indicating that 5 min PC/PD focal follows were sufficiently long. Henceforth, a PC period was defined as a period of 5 min after the onset of a conflict between two opponents leading to a clear losing party of the conflict (i.e. the victim, see appendix: supplementary material, data collection). A PD period did not include a conflict but started with a spontaneous outburst of distress and was observed for 5 min as well. During behavioural coding (supplementary material, methods), consolation was defined as the first spontaneous affiliative body contact offered by a third party bystander to the victim of a conflict or spontaneous distress during the PC/PD period (Clay & de Waal, 2013b; de Waal & Yoshihara, 1983). A detailed ethogram was established to code for affiliative behaviours and aggressive behaviours of different intensities (supplementary material, tables 4 and 5). Subsequently, affiliative behaviours were identified as consolation behaviours (meeting criteria of third party initiated affiliative bodily contact). Previous studies, including the 2011 observation period of the present study (Clay & de Waal, 2013a) have demonstrated the presence of consolation by means of the post-conflict-matched control method (e.g. Clay & de Waal, 2013b; de Waal & Yoshihara, 1983), we thus here renounced the anew use of matched-control recordings.

### 2.3.5. All-occurrence aggression

Additionally, we manually recorded all observable aggressions (including aggressions occurring during PCs) using the same ethogram as for PC recordings (supplementary material, table 4) to identify aggression and victim rates throughout three observation periods (2016, 2019, 2021).

### 2.3.6. Data analysis

Analyses were conducted with generalized linear mixed models (GLMMs) in RStudio (R version 4.3.1; RStudio Core Team, 2023)); open access to our data and code (Kordon et al., 2024). We used the function glmmTMB of the equally named package (version 1.1.7; Brooks et al., 2017) for models 1 and 3. The function glmer of the package lme4 (version 1.1.30; Bates et al., 2015) was used for model 2. Datasets of all models comprised observations across several observation periods (but see appendix: supplementary material, table 2), whereby all individuals were present during at least one. As we had repeated observations of some individuals, subject ID and group per observation period were included as random intercepts in all models. Consistent with the hypothesis that empathic tendencies such as consolation are socially biased (Preston & de Waal, 2002) previous studies including from bonobo groups housed at the site of the present study have revealed that social closeness and kinship predict consolation tendencies in bonobos and chimpanzees (Brooker et al., 2024; Clay & de Waal, 2013a). Orphans do not have the same opportunities to engage in such close social relationships as they would with their kin. Consequently, all interactions between matrilinear kin (mother-offspring, maternal siblings) were removed from the analysis in order to facilitate comparisons between the two rearing categories (orphan and mother-reared). Paternities were not considered as they were only known for some of the sanctuary-born individuals. The two rearing categories differed in their age range (orphans: 3–28 years; mother-reared 3–16 years). Therefore, to ensure comparability, we only included individuals up to the maximum age of mother-reared subjects in the dataset, respectively, that s, aged up to 16 years for model 1 (affiliation tendency) and model 3 (victim tendency) and up to 14 years for model 2 (consolation tendency).

Model stabilities were assessed using a function provided by Roger Mundry (personal communication, 2022), which involved dropping one random effect at a time from the data. The resulting estimates from these subsets were then compared to the estimates obtained from models using the full dataset. *Minimum* and *maximum* values for each fixed and random effect estimate are presented in all results tables. These values show the full range of estimates obtained from the model comparisons. A relatively narrow range either above or below 0 would indicate stable significant effects. Covariate predictors were *z*-transformed to increase the likelihood of model convergence. Factor variables were dummy- coded and centred prior to their inclusion as random slopes. The R function drop1 with argument 'test' set to 'Chi$^2$' was used to test the effects of the predictor in all models. To test the overall effect of main predictors and to avoid 'cryptic multiple testing' (Forstmeier & Schielzeth, 2011), each full model was compared to an otherwise identical null model that lacked the main predictors in the fixed effects. Confidence intervals of model estimates were obtained using 1000 parametric bootstraps (function simulate of the packages glmmTMB and lme4). Collinearity was checked based on the models lacking the interaction using variance inflation factors (VIF) with the R package 'car' (Fox & Weisberg, 2019).

Inter-observer and inter-coder reliability were both assessed using Cohen's κ coefficient (Cohen, 1960). For consolation coding, a subset of 10–15% of videos across observation periods was coded by an additional independent coder trained on the ethogram to identify all social behaviours as well as the initiating party to identify the occurrence of consolation (i.e. third party initiated affiliative contact behaviours). For the identification of consolation, results indicated excellent agreement (consolation occurrence: κ>0.84; partner identity: κ>0.99). For social affiliation, observers conducted live identical scan samples in the field. For partner identity and social behaviours, results indicated excellent agreement (partner identity: κ>0.81; social behaviour: κ>0.86).

#### 2.3.6.1 Model 1: affiliation tendency

To estimate the effects of sex, age and rearing on affiliative tendency across all observation periods, we fitted a GLMM with a beta error distribution and logit-link function (Bolker, 2008; McCullagh & Nelder, 1989), which allows for the analysis of proportional data.

To test for interactions across multiple two-way combinations of our fixed effects, we included all two-way interactions between sex, age, and rearing (sex*age+rearing*age+sex*rearing), as well as all respective main effects. A full three-way interaction was not included owing to limited interpretability of such a complex parameter on a relatively small dataset. The response variable for model 1 was individual mean affiliation scores (see appendix: supplementary material, table 8 for a model overview). The initial model 1 contained all theoretically identifiable random slopes; however, to facilitate convergence and lessen the complexity of the model, we removed correlations between random intercepts and slopes. The model was not overdispersed (dispersion parameter: 0.652). Checks for collinearity revealed no collinearity issues (maximum VIF = 1.155). Stability checks revealed that all estimates for this model were relatively stable. The sample size for model 1 comprised 160 observations, across *n* = 74 individuals (female *n* = 35, male *n* = 39, orphan *n* = 55, mother-reared *n* = 19).

#### 2.3.6.2 Model 2: consolation tendency

To estimate the effects of sex, age and rearing on consolation tendency across all observation periods, we analysed data on a dyadic level using a GLMM with a binomial distribution (Baayen, 2008). Each observation row represented a bystander-victim combination per group and year, where a bystander had at least one opportunity to console a given victim. We excluded n = 6 juveniles for whom we lacked affiliation scan data (observation period 2012: LY, MAY, MAK; observation period 2019: BAR, KIT, LIK) from the analysis. The response variable for model 2 comprised a two-columns matrix using the R function 'cbind' representing the number of consolations and non-consolations per bystander- victim combination, which was thus analysed as a binomial distribution. The full model included individual characteristics of the bystander and victim (sex, age, rearing), respectively. To control for the bystander-victim relationship, we included dyadic affiliation scores calculated from social affiliation scans per dyad, group, and observation period as fixed effects. As in model 1, we proceeded with three two-way interactions as opposed to one three-way interaction to avoid overcomplexity and limited interpretability (see appendix: supplementary material, table 9 for an overview of the full model). All theoretically identifiable random slopes were included in the original model 2, however, to enable model convergence and reduce its complexity we subsequently removed the correlations among random intercepts and slopes. After the model was fitted, a Q-Q plot (quantile-quantile plot) (Field, 2005) of residuals and residuals plotted against fitted values was visually inspected to check if the assumptions of normally distributed and homogeneous residuals were met (Quinn & Keough, 2002). These indicated no deviations from these assumptions. No collinearity issues were found in collinearity checks (maximum VIF = 1.364). Stability checks revealed the model had acceptable stability. Based on a total of n = 1071 PC and PD focal follows, the model consisted of n = 1590 dyadic victim-bystander observations across n = 61 individuals (female n = 30, male n = 31, orphan n = 45, mother-reared n = 16).

#### 2.3.6.3 Model 3: victim likelihood

To investigate which factors may predict the likelihood of being aggressed across years, we conducted additional analyses based on dyadic aggressions per group and year using a GLMM (Baayen, 2008) with beta error distribution and logit-link function (Bolker, 2008; McCullagh & Nelder, 1989). The response variable was victimhood proportion, calculated as the count of being a victim within a victim-aggressor dyad and respective group and observation year, divided by the total counts of observed aggressions within the respective group and observation year. Prior to fitting the model, we transformed the response closer to 0.5 to avoid values being exactly zero or one (Smithson & Verkuilen, 2006).

As orphaned males were expected to be likelier victims of aggression and older females were expected to be more likely aggressors, we included the interactions of victim-sex * victim-rearing and aggressor-sex * aggressor-age as fixed effects. Further fixed effects were victim-age and aggressor-rearing (see appendix: supplementary material, table 10 for an overview of model 3). While several random slope components were theoretically identifiable, our data frame was too limited in size to allow for their reliable inclusion, which further led to convergence issues. To allow for model convergence and limit model overcomplexity and instability leading to unreliable estimates with greater uncertainty, we proceeded with a parsimonious modelling approach and did not include a more complex random effects structure. Random slopes of the aggressor as well as victim rearing and sex within group-year did not affect model convergence and remained in the model (excluding correlations among random intercepts and slopes). The model was overdispersed (dispersion parameter: 2.225), thus results are to be interpreted with caution. Checks for collinearity revealed no collinearity issues (maximum VIF = 1.187). Stability checks revealed that all estimates for model 3 were relatively stable. A total of $n$ = 1042 aggressions were observed across $n$ = 3 different observation periods (2016, 2019, 2021). The model included $n$ = 1853 observations with $n$ = 76 aggressors and $n$ = 62 victims (whereby individuals can be represented in both categories).

## 2.4. Results

### 2.4.1. Model 1: affiliation tendency

Overall, model 1 provided a significantly better fit than a null model lacking the predictors (full-null model comparison: $\chi^2 = 43.78$, $p < 0.001$; see appendix: supplementary material, table 11 for full model results including non-significant interactions). We further proceeded with a reduced model lacking the non-significant interactions (rearing*sex, rearing*age) to investigate the main effects of rearing (full-reduced model comparison: $\chi^2 = 4.150$, $p = 0.126$). More specifically, we found a significant interaction between sex and age on social affiliation (estimate ± s.e. = −0.265 ± 0.056, $z = -4.735$, $p < 0.001$), with females showing increased dyadic affiliation tendencies with age, and males showing decreased tendencies with age (figure 4; table 1). Furthermore, orphans showed lower affiliation tendencies than mother-reared individuals (estimate ± s.e. = −0.204 ± 0.087, $z = -2.342$, $p = 0.022$; see appendix: supplementary material, figure 2 for a model output plot).

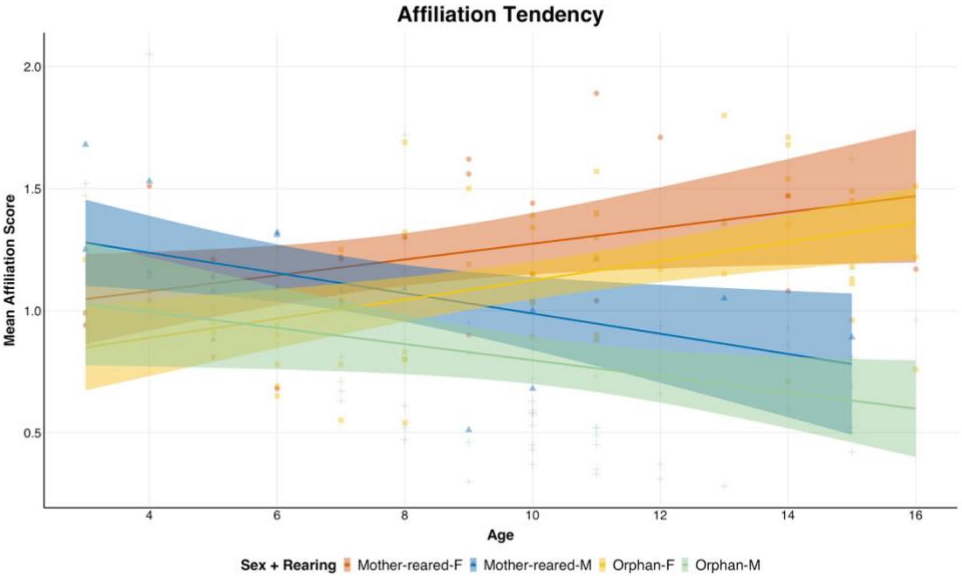
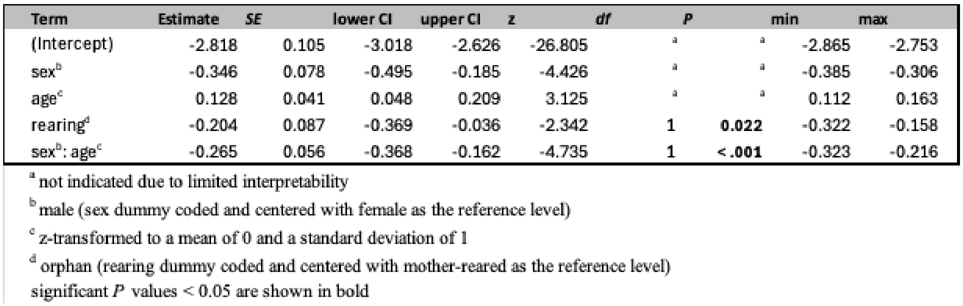


***Figure 4. Scatterplot of significant main effects of model 1:*** *investigating effects of rearing and the interaction between sex and age on affiliative tendencies. Raw data of individual mean dyadic affiliation scores controlled for group and year across age sex and rearing. Females increased their social affiliation with age, while males decreased social affiliation with age. Mother-reared showed higher affiliation scores than orphans. x-axis: age in years; y-axis: data points present individuals' mean dyadic affiliation scores, including observations of all individuals (n = 74) across the five different observation periods, only some of which are represented with repeated observations across periods, owing to demographic changes. Colours correspond to sex and rearing as indicated in the legend (F = female, M = male). Points correspond to respective individual mean dyadic affiliation scores.*



| Term | Estimate | *SE* | lower CI | upper CI | z | *df* | *P* | min | max |
|---|---|---|---|---|---|---|---|---|---|
| (Intercept) | -2.818 | 0.105 | -3.018 | -2.626 | -26.805 | [a] | [a] | -2.865 | -2.753 |
| sex[b] | -0.346 | 0.078 | -0.495 | -0.185 | -4.426 | [a] | [a] | -0.385 | -0.306 |
| age[c] | 0.128 | 0.041 | 0.048 | 0.209 | 3.125 | [a] | [a] | 0.112 | 0.163 |
| rearing[d] | -0.204 | 0.087 | -0.369 | -0.036 | -2.342 | 1 | **0.022** | -0.322 | -0.158 |
| sex[b]: age[c] | -0.265 | 0.056 | -0.368 | -0.162 | -4.735 | 1 | **< .001** | -0.323 | -0.216 |

[a] not indicated due to limited interpretability

[b] male (sex dummy coded and centered with female as the reference level)

[c] z-transformed to a mean of 0 and a standard deviation of 1

[d] orphan (rearing dummy coded and centered with mother-reared as the reference level)

significant *P* values < 0.05 are shown in bold

***Table 1*. *Results of model 1***: *reduced GLMM for affiliation tendency (estimates and standard errors, together with confidence intervals (CIs), results of likelihood ratio tests, and the range of estimates obtained when dropping levels of random effects one at a time). (Significant p-values < 0.05 are shown in bold.)*

### 2.4.2. Model 2: consolation tendency

The full model was significantly better at predicting consolation tendencies, when compared to a null model lacking its predictors (full-null model comparison: $\chi^2$= 30.828, $p < 0.001$). Although the full model resulted in non-significant interactions of sex*rearing and sex*age, we remained with the full model as it fitted significantly better than the reduced model with these interactions removed (full-reduced model comparison: $\chi^2$= 37.794, $p = 0.003$). Model estimates revealed that the interaction between bystander age and bystander rearing significantly predicted the tendency to console (estimate ± s.e.= 0.597 ± 0.16, $z = 3.725$, $p < 0.001$). As shown in figure 5 and the plotted model output (see appendix: supplementary material figure 3), mother-reared bonobos showed a decrease in consolation tendency with age while orphaned bonobos showed more consistent but lower consolation tendencies across age (only overlapping with older mother-reared bonobos). Although not under investigation, the control variable of bystander-victim dyadic affiliation tendency positively predicted consolation (estimate ± s.e. = 0.355 ± 0.059, $z = 5.995$, $p < 0.001$). See table 2 for an overview of model 2 results.

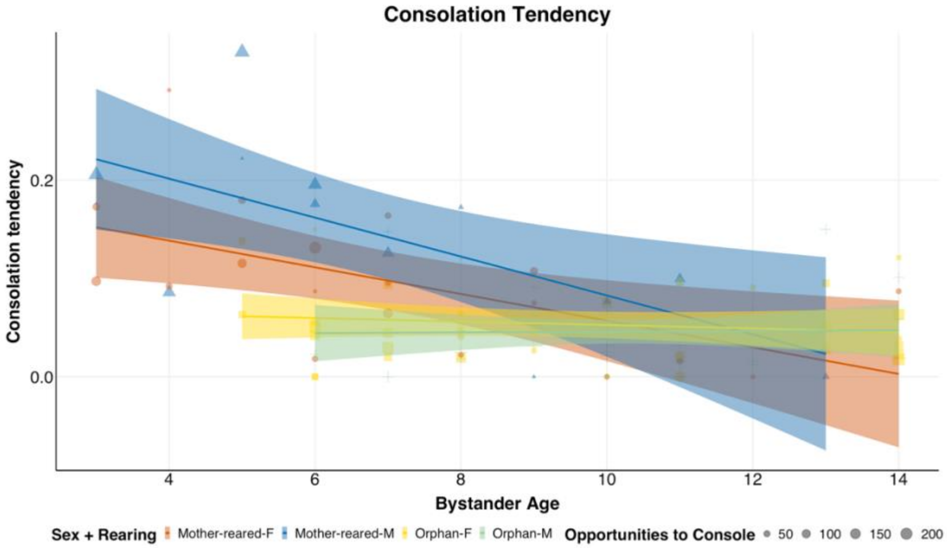
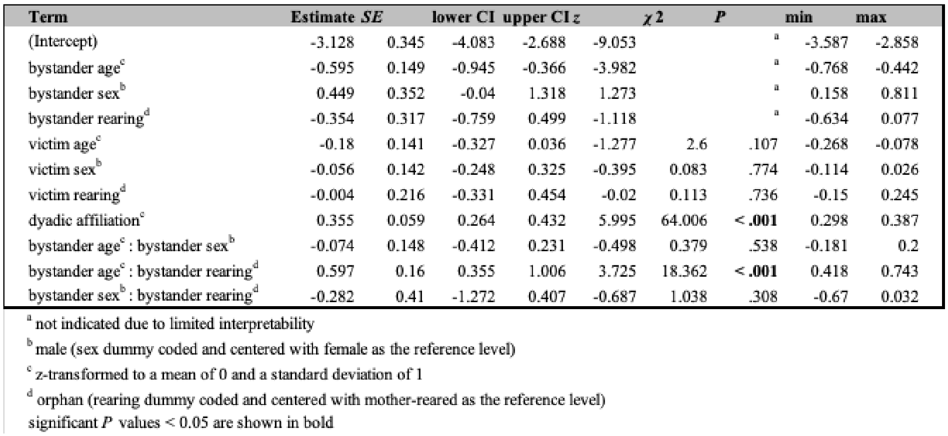


***Figure 5. Scatterplot of significant main effects of model 2:*** *investigating effects of the interaction between bystanders' age and rearing on consolation tendency. Raw data of individual mean consolation tendency per group and observation period. Mother-reared showed a developmental decline of consolation tendencies, while orphans had consistent, but lower consolation tendencies across age (within the range of older mother-reared).* x*-axis: age in years;* y*-axis: bystander mean consolation tendency per group and observation period. Data points present individual consolation tendencies of all individuals included in the model (*n *= 61) across the four different observation periods, only some of which are represented with repeated observations across periods, owing to demographic changes. Colours correspond to sex and rearing as indicated in the legend (F = female, M = male).*



| Term | Estimate | *SE* | lower CI | upper CI | *z* | $\chi 2$ | *P* | min | max |
|---|---|---|---|---|---|---|---|---|---|
| (Intercept) | -3.128 | 0.345 | -4.083 | -2.688 | -9.053 | | [a] | -3.587 | -2.858 |
| bystander age[c] | -0.595 | 0.149 | -0.945 | -0.366 | -3.982 | | [a] | -0.768 | -0.442 |
| bystander sex[b] | 0.449 | 0.352 | -0.04 | 1.318 | 1.273 | | [a] | 0.158 | 0.811 |
| bystander rearing[d] | -0.354 | 0.317 | -0.759 | 0.499 | -1.118 | | [a] | -0.634 | 0.077 |
| victim age[c] | -0.18 | 0.141 | -0.327 | 0.036 | -1.277 | 2.6 | .107 | -0.268 | -0.078 |
| victim sex[b] | -0.056 | 0.142 | -0.248 | 0.325 | -0.395 | 0.083 | .774 | -0.114 | 0.026 |
| victim rearing[d] | -0.004 | 0.216 | -0.331 | 0.454 | -0.02 | 0.113 | .736 | -0.15 | 0.245 |
| dyadic affiliation[c] | 0.355 | 0.059 | 0.264 | 0.432 | 5.995 | 64.006 | **< .001** | 0.298 | 0.387 |
| bystander age[c] : bystander sex[b] | -0.074 | 0.148 | -0.412 | 0.231 | -0.498 | 0.379 | .538 | -0.181 | 0.2 |
| bystander age[c] : bystander rearing[d] | 0.597 | 0.16 | 0.355 | 1.006 | 3.725 | 18.362 | **< .001** | 0.418 | 0.743 |
| bystander sex[b] : bystander rearing[d] | -0.282 | 0.41 | -1.272 | 0.407 | -0.687 | 1.038 | .308 | -0.67 | 0.032 |

[a] not indicated due to limited interpretability

[b] male (sex dummy coded and centered with female as the reference level)

[c] z-transformed to a mean of 0 and a standard deviation of 1

[d] orphan (rearing dummy coded and centered with mother-reared as the reference level)

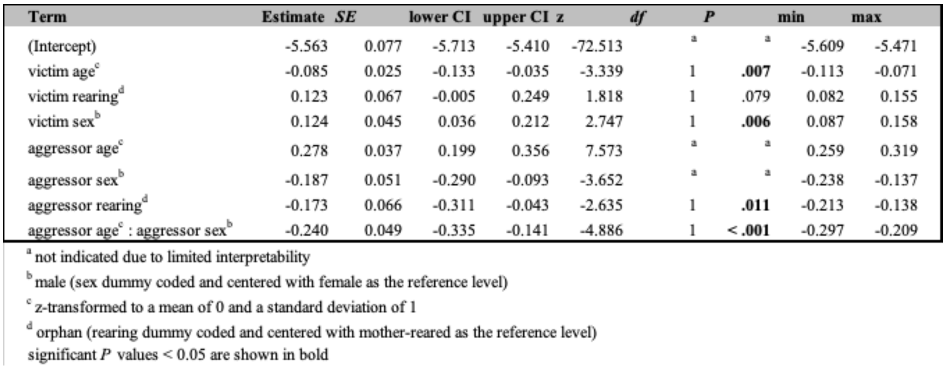
significant *P* values < 0.05 are shown in bold

***Table 2. Results of model 2:*** *Full GLMM for consolation tendency (estimates and standard errors, together with confidence intervals, results of likelihood ratio tests, and the range of estimates obtained when dropping levels of random effects one at a time). (Significant p-values < 0.05 are shown in bold.)*

### 2.4.3. Model 3: victim likelihood

Overall, the model of victim aggression tendency was significantly better at fitting the data as compared to a null model lacking main predictors (full-null model comparison: $\chi 2= 65.488$, $p < 0.001$). Results refer to a reduced model (lacking the non-significant interaction between victim rearing and victim sex) to examine the main effects (reduced-full model comparison: $\chi^2= 0.481$, $p = 0.488$).

The interaction of aggressor age and aggressor sex significantly predicted victim likelihood, that is, victims are more likely to be aggressed by older females (estimate ± s.e. = −0.240 ± 0.049, $z = -4.886$, $p < 0.001$). Mother-reared bonobos showed higher aggression than orphans (estimate ± s.e. = −0.173 ± 0.066, $z = -2.635$, $p = 0.011$). Regarding victims, young bonobos (estimate ± s.e. = −0.085 ± 0.025, $z = -3.339$, $p = 0.007$) and males (estimate ± s.e. = 0.124 ± 0.045, $z = 2.747$, $p = 0.006$) were aggressed most as opposed to older individuals and females (table 3; see appendix: supplementary material for a model output plot).



| Term | Estimate | *SE* | lower CI | upper CI | z | *df* | *P* | min | max |
|---|---|---|---|---|---|---|---|---|---|
| (Intercept) | -5.563 | 0.077 | -5.713 | -5.410 | -72.513 | [a] | [a] | -5.609 | -5.471 |
| victim age[c] | -0.085 | 0.025 | -0.133 | -0.035 | -3.339 | 1 | **.007** | -0.113 | -0.071 |
| victim rearing[d] | 0.123 | 0.067 | -0.005 | 0.249 | 1.818 | 1 | .079 | 0.082 | 0.155 |
| victim sex[b] | 0.124 | 0.045 | 0.036 | 0.212 | 2.747 | 1 | **.006** | 0.087 | 0.158 |
| aggressor age[c] | 0.278 | 0.037 | 0.199 | 0.356 | 7.573 | [a] | [a] | 0.259 | 0.319 |
| aggressor sex[b] | -0.187 | 0.051 | -0.290 | -0.093 | -3.652 | [a] | [a] | -0.238 | -0.137 |
| aggressor rearing[d] | -0.173 | 0.066 | -0.311 | -0.043 | -2.635 | 1 | **.011** | -0.213 | -0.138 |
| aggressor age[c] : aggressor sex[b] | -0.240 | 0.049 | -0.335 | -0.141 | -4.886 | 1 | **< .001** | -0.297 | -0.209 |

[a] not indicated due to limited interpretability

[b] male (sex dummy coded and centered with female as the reference level)

[c] z-transformed to a mean of 0 and a standard deviation of 1

[d] orphan (rearing dummy coded and centered with mother-reared as the reference level)

significant *P* values < 0.05 are shown in bold

***Table 3. Results of model 3:*** *reduced GLMM of the likelihood of being a victim of aggression (estimates and standard errors, together with confidence intervals, results of likelihood ratio tests, and the range of estimates obtained when dropping levels of random effects one at a time). (Significant p-values < 0.05 are shown in bold.)*

## 2.5. Discussion

Using longitudinal data collected across a decade of observations, we investigated the effects of rearing environment (specifically, early maternal loss) as well as sex and age, on the socio-emotional functioning of sanctuary-living bonobos from juvenility to adulthood. We found that, overall, orphan bonobos have lower socio-emotional tendencies than mother-reared bonobos (however, within their range). A developmental decline in consolation was found in mother-reared bonobos, while orphans had consistently lower consolation tendencies across age. Affiliation tendencies diverged between the sexes with age, and older females and mother-reared bonobos were the most aggressive. Young bonobos were at a higher risk of aggression, but contrary to expectations, victims' rearing background did not predict their aggression risk.

Our finding that females increased while males decreased their social affiliation with age is consistent with bonobo social ecology—whereby unrelated females, who typically migrate at adolescence, build strong coalitions at the core of the group (Furuichi, 1989). The developmental decline in male affiliative tendencies likewise corresponds to species-typical patterns, whereby adult males tend to stay peripheral to the group and, other than strong bonds with their mothers, show less pronounced bonding with group members with age. To enable comparisons of the two rearing backgrounds; however, we did not include kin-relationships; thus, the effect of mother-son bonds is not represented in the results. Future research is needed to test the extent to which changes in social affiliation with age reflect shifts in how selective (or not) individuals become towards certain social partners (such as mothers or other adult females).

With respect to rearing, we predicted that the effects of rearing would be less pronounced for females given their enhanced social status in bonobos and that similar to patterns observed in wild migrating females, their social integration would increase with age (Furuichi, 1989, 2011; Idani, 1991; Toda & Furuichi, 2022). By comparison, we expected that orphaned males, who lack maternal support, which has been shown to be crucial for their social integration (Surbeck et al., 2011), should continue to exhibit social deficiencies throughout their lives. Despite this, our results did not reveal interactions between rearing with either sex nor age, respectively. It is unclear why this is the case; however, we did find that overall, mother-reared bonobos had higher affiliation tendencies than orphans, as predicted. This is consistent with other evidence from rescued pet and entertainment chimpanzees that early maternal loss has long-lasting effects on social functioning, indicated by reduced affiliative behaviour and grooming activity (Crailsheim, Romani, et al., 2020; Crailsheim, Stüger, et al., 2020), or non-sustained play behaviour in orphaned chimpanzees (van Leeuwen et al., 2014) housed in a sanctuary comparable to the present study's setting. Although same-species comparisons would be preferable, the most relevant literature is available for chimpanzees. Despite the phylogenetic proximity of the two species, we are aware that direct comparisons here and henceforth need to be interpreted cautiously given some of the differences in their behavioural ecology.

We further analysed tendencies to console others in distress, considered a behavioural marker of empathy and a more general indicator of socio-emotional functioning (Clay et al., 2022). Although the underlying mechanisms remain challenging to identify, evidence that consolation is targeted towards distressed parties and effectively alleviates their distress suggests that it involves the capacity to not only recognize but appropriately respond to other's needs (as well as a capacity to distinguish self from other, to avoid becoming personally distressed in the face of another's situation) (Clay et al., 2022). We found an effect of rearing, whereby orphans showed consistently lower consolation tendencies across time than mother-reared. Interestingly, rearing also seemed to disrupt expected developmental trajectories of consolation: only in mother-reared bonobos, but not orphans, did we see the expected developmental decline in consolation over time that has been previously observed in captive apes (bonobos: (Clay & de Waal, 2013a); chimpanzees: (Webb et al., 2017); western gorillas: (Cordoni et al., 2006)) Importantly, this also meant that overall, orphan consolation tendencies remained within the range of mother-reared bonobos, even if they were initially lower during immaturity.

Although the present observational study cannot discern underlying mechanisms, the apparent developmental pattern of higher consolation tendencies during immaturity may reflect an intrinsic drive of young apes to attend to and orient towards others’ emotional states and situations. While consolation functions to relieve tension or distress in the recipient (reviewed in Romero et al., 2010), in this respect it may also confer benefits to actors, such as opportunities for immatures to learn about their social worlds and relevant social events. If affiliating with victims enhances the affiliative relationship between the victim and consoler, it may also enable immatures to expand their social networks. In chimpanzees, males initially show a social bonding strategy to affiliate with many partners, which then shifts with age to invest in fewer but stronger relationships (Rosati et al., 2020). Although this remains to be tested, it is possible that consolation efforts, too, start off initially broad but become selectively geared towards close social partners with age. Further research, examining the affiliative consequences of consolation and its selectivity with age is needed to test this.

Our results highlight that early life stress may impact species-typical developmental trajectories. Nevertheless, although orphans showed lower levels of consolation than mother-reared peers, their tendencies to console were not altogether absent, suggesting that orphans are not ambivalent to others’ states, and are sometimes able to offer appropriate prosocial responses. The fact that their consolation tendency moreover lay within the range of mother-reared, albeit at the lower end, suggests they may have sufficient skills to cope within their social groups.

A key question is whether orphans have impaired socio-emotional functioning as compared to mother-reared or are inhibited from expressing it. Young orphans, who lack the support of their mothers and have yet to establish social bonds, may behave differently than young mother-reared bonobos who may learn that they can rely on their mother’s support. Thus, avoiding socially risky situations like post-conflict periods may also be a coping strategy for traumatized young orphans lacking social support, akin to conflict-avoidance (i.e. reducing social interactions) and tension-reduction (i.e. reducing aggressive behaviours and increasing affiliative behaviours) observed in chimpanzees adapting to limited space (Videan & Fritz, 2007). Bonobos may, too, exhibit this flexibility and adaptation in certain social situations. Nevertheless, this would not clearly explain why older orphans continued to show low levels of consolation when presumably their social relationships were more established.

Regarding sex differences in consolation tendency, our results were consistent with some previous studies that found no sex differences (bonobos: Clay & de Waal, 2013a; chimpanzees: Webb et al., 2017). Nevertheless, as noted, ape studies do vary in regard to sex differences, with some finding no effects, while others finding a female and/or dominant male bias (Cordoni et al., 2006; Romero et al., 2010). This suggests that potential sex variation in consolation might be contextually dependent on a range of demographic factors, including social composition, group tolerance and social-dominance relationships, which may vary within and between groups as well as across species. Further work is needed to address this.

Finally, we also examined longitudinal trajectories of receiving as well as committing aggression, another relevant aspect of social functioning. In line with our predictions, males and young bonobos were more likely to be victims of aggression, whereas older bonobos and females were most frequently aggressors relative to young ones and males. These patterns appear to reflect the species-typical social structure of high-ranking adult females and the lower status of most males (Furuichi, 1997) and are in line with personality research on wild bonobos that found higher aggression in older individuals (Garai et al., 2016). The higher aggression in mother-reared bonobos may further reflect their higher rank and/or more central social position compared to orphans. In contrast to our prediction, victim-rearing did not significantly affect the likelihood of being aggressed, indicating that orphans are not targeted more than mother- reared despite their seemingly lower social tendencies indicated by our other results. However, a trend hints towards orphans being more likely to be aggressed, which may be explained by their lack of maternal support, especially when younger.

Taken together, our results support the overall hypothesis that although early life adversity impacts socio-emotional functioning in this ape species, orphaned bonobos still show evidence of social functioning, albeit at a reduced level. Prior to their rescue by the sanctuary, most orphans will have probably been forcibly removed from their mothers, who will have probably been killed in their presence along with other group members, as well as subsequently experiencing neglect and potentially also abuse. Yet, despite these traumatic experiences, our study suggests that their social and consolatory tendencies, an aspect of socio-emotional functioning, overlap within the lower range of mother-reared peers. Another study by Wobber & Hare (2011) experimentally showed that orphaned bonobos at this same study site were also equivalent in their cognitive and behavioural skills as mother-reared peers. While this is encouraging, it should be noted, however, that their measures, as well as our own, may not have picked up other socio-emotional factors that can be influenced by rearing. Further behavioural and physiological work is needed to pinpoint which aspects of their social functioning are impacted and the mechanisms underlying this.

Most orphans in this study arrived at the sanctuary at around 2–5 years old, thus it is also possible that the initial phase of mother-infant care they received, prior to the moment of capture, may have been a buffer for building long-term resilience. As we know from the human literature, the age and duration of deprivation are critical for informing the severity of trauma experienced (De Bellis, 2005). Rehabilitated chimpanzees, who were deprived at an earlier age, showed long-term deficits in social competence, compared to those who stayed with their mothers for longer and subsequently with peers (Reimers et al., 2007). Arriving at the sanctuary from around 2 years upwards may thus enable greater resilience. There is also evidence that being reared in a social group within a natural environment can improve social deficiencies in apes, as found in wild orphaned mountain gorillas and chimpanzees (Girard-Buttoz et al., 2020; Morrison et al., 2021). As suggested for chimpanzees (Levé et al., 2016; van Leeuwen et al., 2022), the nurturing social environment of Lola ya Bonobo sanctuary, which includes the additional surrogacy, nutritional and veterinary support offered by human carers, may compensate for early-life rearing adversities and facilitate social rehabilitation.

The rehabilitative function of great ape sanctuaries: Although our study is unable to make strong inferences regarding great ape rehabilitation, our results do indicate that the orphan bonobos are able to socially function in their groups and show social and consolatory tendencies within mother-reared range, even if to a lower degree.

As the only bonobo sanctuary in the world, Lola ya Bonobo plays an essential role in the conservation of this endangered species. Young orphaned bonobos traumatised by the illegal bushmeat and pet trades (Ortín et al., 2019) are given a second chance in a supportive sanctuary environment (by our sanctuary definition above). Importantly, mother-reared bonobos in our study represent the first generation of offspring, raised by orphan mothers. The fact that their social functioning patterns seem to be in line with the social ecology of their wild counterparts highlights the crucial role that sanctuaries like this play in rehabilitation of apes across generations.

In addition, many of these bonobos— including several subjects in the current study—are successfully being reintroduced into the wild, including orphans. Understanding their ability to function in a complex social environment is vital to these efforts. The present study may therefore aid reintroduction facilities by providing systematic information about their social functioning. In light of this objective, we recognize that our study is particularly focused on sanctuary situations. Related to these broader implications, the more naturalistic social and ecological environments afforded by sanctuary contexts, like our study, provide a unique opportunity to powerfully investigate key questions about the impacts of adversity on social development that – although a direct comparison to other contexts would be desirable – are difficult to attain in either the wild or in captivity. In the wild, for instance, amassing adequate sample sizes of surviving orphans is very difficult combined with the challenge of attaining sufficient close-up observations of social interactions, particularly those involving conflict and post-conflict interactions. In captive settings such as zoos, the social and environmental contexts vary so vastly from those in the wild, it becomes difficult to make ecologically-valid conclusions.

In this sanctuary setting our measures of socio-emotional functioning including affiliative tendencies, consolation tendencies and victim likelihood provide an established base for a general overview in the context of conflict and prosocial behaviours. Clearly, life outcomes of social functioning may be influenced by countless predictors across the life span yet, the measures used here were limited to our most systematic longitudinal dataset to build upon previous work and to enable high quality research.

Although many of these orphans cope relatively well in the social systems, investigating the occurrence of more severe aggressions would shed light on potential difficulties adult orphan males may face without maternal support. Future research should address these issues and further potential predictors, including dominance hierarchies as well as social network analysis, personality traits and physiological measures of stress (e.g. cortisol measures), maternal styles of bonobo as well as human surrogate mothers, change of group compositions and group tolerance, to complement behavioural data and to identify the challenges and strategies orphans encounter in their social integration across the lifespan.

While the direct comparison between orphans and mother-reared bonobos provides insights into their general social and emotional tendencies, more detailed longitudinal data is needed to capture the effects of their individual life histories. Although all orphans have experienced some degree of early-life trauma and adversity, there is likely to be considerable variation in individual experiences, such as the degree of trauma following capture and the age at which the maternal loss occurs. There is ample evidence from the broader literature that the relative severity of early adversity and the respective age can affect the degree of impact it shows on later-life outcomes (e.g. De Bellis, 2005; Reimers et al., 2007; Dettmer and Chusyd, 2023). As such, future work is needed to account for individual life histories and the severity and age of experienced trauma prior to their rescue. Unfortunately, detailed information about the circumstances preceding arrival at the sanctuary is often limited or unavailable, as was the case in our study. Nevertheless, expanding this research with indicators such as the estimated age at rescue could partially address this gap, as the timing of maternal loss or rescue is likely to influence later outcomes, as discussed above.

## 2.6. Conclusion

Through a much-needed longitudinal approach, our study addressed the developmental trajectories of socio-emotional functioning of sanctuary living bonobos across the lifespan. Overall, the results provide key insights into understanding the factors shaping great ape socio-emotional development and the role that sanctuaries like this play in the rehabilitation process. Future research on individual differences in predictors of life outcomes is needed to aid sanctuary management strategies in their conservation efforts of rewilding healthy bonobos. Range country great ape sanctuaries such as this, which align with high standard husbandry and welfare requirements, play a major role in protecting our endangered closest relatives from the ever-rising anthropogenic threat of extinction. With rapidly declining numbers of apes in the wild and increasing numbers of orphans overwhelming range country primate rehabilitation centres, more research should be directed at assisting these critically required conservation efforts wherever possible.

**Ethics.** This research received ethical approval from the Ethics Committee as well as the Animal Welfare Ethical Review Board (AWERB) of Durham University (ref.: PSYCH-2021-08-19T17_36_57-jlcf16) and was carried out in accordance with the guidelines and regulations at Lola ya Bonobo sanctuary and Les Amis des Bonobos du Congo (ABC) and the Ministries of Research and Environment in the Democratic Republic of the Congo (permit no. MIN. RS/SG/004/2009; MIN/RSIT/SG-RSIT/182/180/017/2021).

**Data accessibility.** Data and code can be accessed via the Figshare Digital Repository. (Kordon et al., 2024).

Supplementary material is available online (Kordon et al., 2024) and in the thesis' appendix.

**Authors' contributions.** S.K.: conceptualization, data curation, formal analysis, investigation, writing—original draft, writing—review and editing; C.E.W.:

conceptualization, funding acquisition, supervision, writing—review and editing; J.S.B.: formal analysis, writing—review and editing; F.B.M.d.W.: funding acquisition, writing—review and editing; Z.C.: conceptualization, data curation, funding acquisition, methodology, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Authors' Notes.** Prior to his tragic passing, Frans de Waal both approved and contributed to the initially submitted manuscript, therefore he remains as a co-author of the present paper.

**Conflict of interest declaration.** We declare we have no competing interests.

**Funding.** This study has been financially supported by the Templeton World Charity Foundation: Diverse Intelligences initiative (awarded to F.B.M.d.W, Z.C., C.E.W.; grant number 0309, 2018). Funding to support this work has also been received from the European Research Council Horizon 2020 Starting Grant (802979, awarded to Z.C.) and the Fürst Dietrichstein Stiftung (awarded to S.K.).

**Acknowledgements.** We thank Heritier Izansone and Pitshou Nsele Kayanga for assistance in data collection; Claudine André, Fanny Minesi, Raphaël Belais and the Ministries of Research and Environment in the Democratic Republic of the Congo (permit no. MIN. RS/SG/004/2009; MIN/RSIT/SG-RSIT/182/180/017/2021), as well as the Lola ya Bonobo staff, particularly, Stany Mokando, Jean-Claude Nzumbi for their support. We are very grateful to the Editor, Shinya Yamamoto and two anonymous reviewers for their insightful and constructive comments.

**Dedication.** With great sadness and gratitude, we would like to dedicate this paper to our co-author and mentor, the late Frans de Waal, whose groundbreaking work, generous support, and mentorship both inspired and enabled this research and has paved the way for generations to follow.

# 3. General conclusion

This thesis provides a thorough summary of the current understanding of maternal influences on primate development. The introductory review highlights the central role of maternal support in shaping not only early survival and physical health but also long-term socio-emotional functioning in primates including humans, with emphasis on our phylogenetically closest ape relatives. By drawing attention to the lasting consequences of maternal loss—ranging from physiological to psychological impairments—and by highlighting both the relevance of accredited ape sanctuaries and the lack of longitudinal behavioural research needed to better understand life outcomes in ape orphans, it frames a broader context for evaluating the developmental trajectories of orphaned bonobos. The empirical findings build on this foundation, providing one of the few longitudinal perspectives on orphaned apes in sanctuary settings. The results indicate that while orphans show reduced affiliative tendencies, their overall social behaviour falls within the range of mother-reared peers, pointing to the adaptive potential of enriched, socially complex rehabilitation environments as provided at the Lola ya Bonobo sanctuary. As anthropogenic threats continuously lead to orphaned apes at alarming rates, this work advances the scientific understanding of apes' social development and carries urgent conservation relevance. Understanding the behavioural development and social functioning of these orphans systematically is essential for supporting continuous rehabilitation and conservation efforts and calls for a further expansion of scientific work in alignment with conservation goals for this vulnerable population and their unique, yet endangered, species.

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# 5. Appendix

## 5.1. Supplementary Materials

### Methods

1) **Rescue:** Upon arrival at the sanctuary, intense veterinary care is provided to allow recovery from poor health conditions (sometimes life-threatening) of rescued orphans. At the same time, each orphan is also assigned to their human surrogate mother who provides daily care in close physical contact.

2) **Rehabilitation:** The rehabilitation process begins shortly after the initial physical recovery when orphans join the nursery, where juvenile orphans remain in peer groups in the presence of their human surrogate mothers until they become more independent, usually at an approximate age of 4 years. When ready, they are subsequently integrated into large social groups of all sex and age classes including rescued as well as sanctuary born bonobos.

3) **Reintroduction:** The final goal is to (re)introduce these groups into their natural habitat in the wild. Potential candidates for release are selected upon overall health, social integration, natural behaviours including foraging and sociability, among others.

***App. Figure 1. Box 1.:*** *The primary stages rescued bonobo orphans pass through from their arrival and rehabilitation at Lola ya Bonobo Sanctuary to their eventual transfer to the reintroduction site, Ekolo ya Bonobo.*

|  |  |  |  | 2011 [1] |  |  |  | 2012 [1] |  |  |  | 2016 [1] |  |  |  | 2019 [1] |  |  |  | 2021 [1] |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| NAME[2] | ID-Code | SEX[3] | REARING[4] | AGE[5] | GROUP[6] | SCANS[7] | PC-PD[8] | AGE[5] | GROUP[6] | SCANS[7] | PC-PD[8] | AGE[5] | GROUP[6] | SCANS[7] | PC-PD[8] | AGE[5] | GROUP[6] | SCANS[7] | PC-PD[8] | AGE[5] | GROUP[6] | SCANS[7] | PC-PD[8] |
| Api | AP | M | o |  |  |  |  | 10 | G1 | y | y | 14 | G2 | y | y |  |  |  |  |  |  |  |  |
| Balangala | BAL | M | o |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 7 | G1 | y |  |
| Baraka ya Lola $^{(Kalina)}$ | BAR | F | mr |  |  |  |  |  |  |  |  |  |  |  |  | 3 | G2 | ● | y | 5 | G2 | y |  |
| Bombo | BB | M | o |  |  |  |  |  |  |  |  | 7 | G2 | y | y | 10 | G2 | y | y | 12 | G2 | y |  |
| Bandundu | BD | F | o | 14 | G1 | y | y | 15 | G1 | y | y | 19 | G2 | y | y | 22 | G1 | y | y | 24 | G1 | y |  |
| Bikoro | BIK | M | o |  |  |  |  |  |  |  |  |  |  |  |  | 6 | G1 | y | y | 8 | G2 | y |  |
| Bili | BL | M | o | 10 | G2 | y | y | 11 | G2 | y | y | 15 | G2 | y | y |  |  |  |  |  |  |  |  |
| Boma | BM | F | o |  |  |  |  |  |  |  |  | 5 | G2 | y | y | 8 | G2 | y | y | 10 | G2 | y |  |
| Boende | BO | M | o |  |  |  |  |  |  |  |  | 17 | G3 | y | y |  |  |  |  |  |  |  |  |
| Bolingo ya Lola $^{(Kalina)}$ | BOL | M | mr |  |  |  |  |  |  |  |  | 5 | G3 | y | y | 8 | G2 | y | y | 10 | G2 | y |  |
| Bisengo ya Lola $^{(Maya)}$ | BS | M | mr | 6 | G2 | y | y | 7 | G2 | y | y | 11 | G2 | y | y |  |  |  |  |  |  |  |  |
| Chibo | CH | M | o |  |  |  |  |  |  |  |  | 11 | G3 | y | y |  |  |  |  |  |  |  |  |
| Diyoko | DIY | M | o |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 4 | G2 | y |  |
| Dilolo | DL | M | o | 10 | G1 | y | y | 11 | G1 | y | y | 15 | G1 | y | y | 18 | G2 | y | y | 20 | G2 | y |  |
| Elikya ya Lola $^{(Semendwa)}$ | EK | F | mr | 6 | G1 | y | y | 7 | G1 | y | y | 11 | G1 | y | y | 14 | G1 | y | y | 16 | G1 | y |  |
| Eleke | EL | M | o |  |  |  |  | 8 | G2 | y | y | 12 | G2 | y | y | 15 | G2 | y | y | 17 | G2 | y |  |
| Elonga ya Lola $^{(Likasi)}$ | ELO | F | mr |  |  |  |  |  |  |  |  | 4 | G3 | y | y |  |  |  |  |  |  |  |  |
| Fizi | FZ | M | o | 11 | G1 | y | y | 12 | G1 | y | y | 16 | G3 | y | y |  |  |  |  |  |  |  |  |
| Garamba | GR | M | o |  |  |  |  |  |  |  |  | 7 | G2 | y | y | 10 | G2 | y | y |  |  |  |  |
| Ilebo | IB | M | o | 10 | G2 | y | y | 11 | G2 | y | y |  |  |  |  |  |  |  |  |  |  |  |  |
| Isiro | IS | F | o | 14 | G2 | y | y |  |  |  |  | 19 | G3 | y | y |  |  |  |  |  |  |  |  |
| Kole | KE | M | o |  |  |  |  |  |  |  |  | 10 | G2 | y | y |  |  |  |  |  |  |  |  |
| Kasongo | KG | M | o | 9 | G1 | y | y | 10 | G1 | y | y | 14 | G1 | y | y |  |  |  |  |  |  |  |  |
| Kinzia | KI | F | o |  |  |  |  |  |  |  |  | 5 | G1 | y | y | 8 | G1 | y | y | 10 | G1 | y |  |
| Kinsele | KIS | M | o |  |  |  |  |  |  |  |  |  |  |  |  | 8 | G1 | y | y |  |  |  |  |
| Kitoko ya Lola $^{(Waka)}$ | KIT | M | mr |  |  |  |  |  |  |  |  |  |  |  |  | 3 | G1 | ● | y | 5 | G1 | y |  |
| Kalina | KL | F | o | 13 | G1 | y | y | 14 | G2 | y | y | 18 | G3 | y | y | 21 | G2 | y | y | 23 | G2 | y |  |
| Kimya ya Lola $^{(Salonga)}$ | KM | F | mr |  |  |  |  | 3 | G1 | y | y | 7 | G1 | y | y | 10 | G2 | y | y |  |  |  |  |
| Kinshasa | KN | F | o |  |  |  |  |  |  |  |  | 11 | G3 | y | y |  |  |  |  |  |  |  |  |
| Kodoro | KO | M | o |  |  |  |  |  |  |  |  | 9 | G1 | y | y |  |  |  |  |  |  |  |  |
| Kisantu | KS | F | o | 13 | G1 | y | y | 14 | G2 | y | y |  |  |  |  |  |  |  |  |  |  |  |  |
| Katako | KT | F | o | 7 | G1 | y | y | 8 | G1 | y | y | 12 | G1 | y | y | 15 | G1 | y | y | 17 | G1 | y |  |
| Kikwit | KW | M | o | 14 | G1 | y | y | 15 | G1 | y | y | 19 | G1 | y | y | 22 | G1 | y | y | 24 | G1 | y |  |
| Keza | KZ | M | o | 18 | G2 | y | y | 19 | G2 | y | y | 23 | G2 | y | y | 26 | G2 | y | y | 28 | G2 | y |  |
| Lalia | LAL | F | o |  |  |  |  |  |  |  |  |  |  |  |  | 6 | G1 | y | y | 8 | G2 | y |  |
| Likasi | LI | F | o | 10 | G2 | y | y | 11 | G2 | y | y | 15 | G3 | y | y |  |  |  |  |  |  |  |  |
| Likunsi ya Lola $^{(Bandundu)}$ | LIK | M | mr |  |  |  |  |  |  |  |  |  |  |  |  | 2 | G1 | ● | y | 4 | G1 | y |  |
| Lomako | LK | M | o |  |  |  |  |  |  |  |  | 9 | G3 | y | y |  |  |  |  |  |  |  |  |
| Lomami | LM | M | o | 12 | G2 | y | y | 13 | G1 | y | y | 17 | G1 | y | y |  |  |  |  |  |  |  |  |
| Lolabu | LOL | M | o |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 3 | G2 | y |  |
| Lopori | LOP | M | o |  |  |  |  |  |  |  |  |  |  |  |  | 8 | G1 | y | y | 10 | G1 | y |  |
| Lisala | LS | F | o | 10 | G1 | y | y | 11 | G1 | y | y | 15 | G2 | y | y |  |  |  |  |  |  |  |  |
| Lubi | LUB | F | o |  |  |  |  |  |  |  |  |  |  |  |  | 8 | G1 | y | y |  |  |  |  |
| Lutula | LUT | F | o |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 7 | G1 | y |  |
| Liyaka ya Lola $^{(Kisantu)}$ | LY | F | mr |  |  |  |  | 2 | G2 | ● | y | 6 | G1 | y | y | 9 | G2 | y | y |  |  |  |  |
| Matadi | MA | M | o | 10 | G1 | y | y | 11 | G1 | y | y | 15 | G1 | y | y | 18 | G1 | y | y | 20 | G1 | y |  |
| Makasi ya Lola $^{(Semendwa)}$ | MAK | M | mr |  |  |  |  | 2 | G1 |  | y |  |  |  |  |  |  |  |  |  |  |  |  |
| Mayele ya Lola $^{(Maya)}$ | MAY | M | mr |  |  |  |  | 2 | G2 | ● | y | 6 | G2 | y | y |  |  |  |  |  |  |  |  |
| Mabali | MB | M | o | 10 | G1 | y | y | 11 | G1 | y | y | 15 | G1 | y | y | 18 | G2 | y | y |  |  |  |  |
| Mbandaka | MD | M | o | 10 | G2 | y | y | 11 | G2 | y | y | 15 | G2 | y | y |  |  |  |  |  |  |  |  |
| Mongata | MG | F | o |  |  |  |  |  |  |  |  | 6 | G2 | y | y |  |  |  |  |  |  |  |  |
| Minova | MI | F | o |  |  |  |  |  |  |  |  | 6 | G2 | y | y | 9 | G2 | y | y | 11 | G2 | y |  |
| Minzoto ya Lola $^{(Tshilomba)}$ | MIN | M | mr |  |  |  |  |  |  |  |  | 3 | G3 | y | y |  |  |  |  |  |  |  |  |
| Makali | MK | M | o | 19 | G2 | y | y |  |  |  |  | 24 | G3 | y | y |  |  |  |  |  |  |  |  |
| Malaika ya Lola $^{(Kalina)}$ | ML | F | mr | 4 | G1 | y | y | 5 | G2 | y | y | 9 | G2 | y | y | 12 | G2 | y | y | 14 | G2 | y |  |
| Maniema | MM | M | o |  |  |  |  |  |  |  |  | 15 | G3 | y | y | 18 | G2 | y | y | 20 | G2 | y |  |
| Manono | MN | M | o | 17 | G1 | y | y | 18 | G1 | y | y | 22 | G1 | y | y | 25 | G1 | y | y | 27 | G1 | y |  |
| Moyi ya Lola II $^{(Tshilomba)}$ | MO | M | mr | 4 | G2 | y | y |  |  |  |  | 9 | G3 | y | y |  |  |  |  |  |  |  |  |
| Molendisi ya Lola $^{(Kinshasa)}$ | MOL | F | mr |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Moseka ya Lola $^{(Bandundu)}$ | MOS | F | mr |  |  |  |  |  |  |  |  | 4 | G2 | y | y | 7 | G1 | y | y | 9 | G1 | y |  |
| Mpongo | MPO | F | o |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 3 | G2 | y |  |
| Masisi | MS | F | o | 6 | G1 | y | y | 7 | G2 | y | y | 11 | G2 | y | y |  |  |  |  |  |  |  |  |
| Muanda | MU | F | o |  |  |  |  | 9 | G2 | y | y | 13 | G2 | y | y |  |  |  |  |  |  |  |  |
| Mvula ya Lola $^{(Muanda)}$ | MVL | F | mr |  |  |  |  |  |  |  |  | 3 | G2 | y | y |  |  |  |  |  |  |  |  |
| Max | MX | M | o | 25 | G2 | y | y | 26 | G2 | y | y |  |  |  |  |  |  |  |  |  |  |  |  |
| Maya | MY | F | o | 18 | G2 | y | y | 19 | G2 | y | y | 23 | G2 | y | y |  |  |  |  |  |  |  |  |
| Ndnjili | NDJ | F | o |  |  |  |  |  |  |  |  | 5 | G1 | y | y | 8 | G1 | y | y | 10 | G2 | y |  |
| Nyota ya Lola $^{(Lisala)}$ | NYO | F | mr |  |  |  |  |  |  |  |  | 5 | G2 | y | y | 8 | G2 | y | y | 10 | G2 | y |  |
| Omanja | OMA | M | o |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 3 | G2 | y |  |
| Opala | OP | F | o | 16 | G1 | y | y | 17 | G1 | y | y | 21 | G1 | y | y | 24 | G1 | y | y | 26 | G1 | y |  |
| Oshwe II | OS | M | o |  |  |  |  |  |  |  |  | 8 | G1 | y | y | 11 | G1 | y | y | 13 | G2 | y |  |
| Pole ya Lola $^{(Opala)}$ | PO | M | mr | 5 | G1 | y | y | 6 | G1 | y | y | 10 | G1 | y | y | 13 | G1 | y | y | 15 | G1 | y |  |
| Sandoa | SD | F | o |  |  |  |  |  |  |  |  | 10 | G3 | y | y |  |  |  |  |  |  |  |  |
| Singi | SI | M | o |  |  |  |  |  |  |  |  | 7 | G1 | y | y | 10 | G2 | y | y | 12 | G2 | y |  |
| Sake | SK | F | o | 6 | G2 | y | y | 7 | G2 | y | y |  |  |  |  |  |  |  |  |  |  |  |  |
| Salonga | SL | F | o | 14 | G1 | y | y | 15 | G1 | y | y | 19 | G1 | y | y | 22 | G1 | y | y | 24 | G1 | y |  |
| Semendwa | SW | F | o | 15 | G1 | y | y | 16 | G1 | y | y | 20 | G1 | y | y | 23 | G1 | y | y | 25 | G1 | y |  |
| Sanza ya Lola $^{(Thsilomba)}$ | SZ | F | mr |  |  |  |  |  |  |  |  | 6 | G3 | y | y |  |  |  |  | 11 | G1 | y |  |
| Tshilomba | TS | F | o | 20 | G2 | y | y |  |  |  |  | 25 | G3 | y | y |  |  |  |  |  |  |  |  |
| Tshimbulu | Tsi | M | o |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 4 | G2 | y |  |
| Waka | WK | f | o | 6 | G1 | y | y | 7 | G1 | y | y | 11 | G1 | y | y | 14 | G1 | y | y | 16 | G1 | y |  |
| Wongolo ya Lola $^{(Bandundu)}$ | WO | M | mr | 3 | G1 | y | y | 4 | G1 | y | y |  |  |  |  |  |  |  |  |  |  |  |  |
| Yolo | YL | M | o | 8 | G2 | y | y | 9 | G2 | y | y | 13 | G2 | y | y |  |  |  |  |  |  |  |  |

1 Year of observation period

2 Mother indicated in superscript and brackets

3 M = male; F = female

4 mr = mother-reared ; o = orphaned

5 Age in years in respective study period (age of orphans is estimated)

6 Group in respective study period (G3 only recorded in 2016)

7 Affiliation scans recorded in respective study period; y = yes; ● = missing scan data with available PC/PD data only

8 Post-conflict/ Post-distress (PC/PD) recorded in respective study period (no records in 2021); y = yes

***App. Table 1. Overview of the study subjects.*** *Lines comprise subject's names, sex and rearing background, as well as their age, group and type of recorded data in each observation period, respectively. N = 83 individuals (female N = 38, male N = 45, orphan N = 62, mother-reared N = 21*

Data collection

| Year (observation period) | Groups | Data | | |
|---|---|---|---|---|
| **2011** (May-August) | G1, G2 | Social affinity scan sampling (10 min intervals) | PC/PD all occurrence video focals | |
| **2012** (May-Aug.) | G1, G2 | Social affinity scan sampling (10 min intervals) | PC/PD all occurrence video focals | |
| **2016** (June-Aug.) | G1, G2, G3 | Social affinity scan sampling (20 min intervals) | PC/PD all occurrence video focals | all occurrence dyadic aggressions |
| **2019** (July-Sept.) | G1, G2 | Focal scan follows -all IDs. (10 min w. 1 min intervals) | PC/PD all occurrence video focals | all occurrence dyadic aggressions |
| **2021** (Oct.-Dec.) | G1, G2 | Social affinity scan sampling (20 min intervals) | | all occurrence dyadic aggressions |

***App. Table 2. Overview of observation periods, groups under observation and types of data collected, respectively.***

Post-conflict and post-distress observations:

Victim: The initial recipient of aggression or the individual in distress, expressing victim response behaviours (Table 3) usually accompanied by a high-pitched distress scream.

Spontaneous outburst of distress: A spontaneous distress event involving one individual (without opponent) expressing a high-pitched distress scream. Accompanying behaviours can include whimpering, pouting, self-embrace, beating the ground with hands/feet or body, twirling, rolling on the ground, front-rolls, crouching, or head shaking (adapted from (Clay & de Waal, 2013a, 2013b; Table 3).

Aggressor: An individual who directs one or more agonistic behaviours (Table 4) towards a group member resulting in 'victim behaviour' (Table 3) of the aggressee.

Aggressive behaviour: Any agonistic behaviour directed by one individual towards another group member (Table 4).

Conflicts involving contest hoots were excluded, as these generally do not lead to a clear victim of the conflict. However, rare cases of conflicts including contest hoots were added to the data set, if a clear victim behaviour was shown by one of the involved individuals. Contest hoots are acoustically distinct vocalizations produced by male bonobos and have been suggested to function to challenge group members and to assert social rank (Genty et al., 2014).

| Victim response behaviours | | |
|---|---|---|
| scream | bare teeth | ground roll |
| whimper | face-down on ground | spontaneous jump-back/avoidance |
| pout | pout-moan | self-embrace |
| self-slap | whine | |

***App. Table 3. Victim response behaviours** - based on (Clay & de Waal, 2013a, 2013b). Behaviours were used to identify the focal subject. Individual victim responses were not coded.*

| Aggressive behaviour | Code | Description |
|---|---|---|
| Threat | TH | Threat bark/grunt, threat arm wave, move body towards victim |
| Directed display | DD | During a display, the aggressor runs directly towards victim |
| Chase | CH | Aggressor runs after the victim, victim flees |
| Low contact aggression | LCO | Slightly push,-shove, poke |
| High contact aggression | HCO | Grab, hit, slap, kick |
| Multiple contact | MC | Repeat contact aggression multiple times |
| Bite | BT | Bite |

***App. Table 4. Types of aggressive behaviours** - based on (Clay & de Waal, 2013a, 2013b)*

Post-conflict/post-distress recordings and data coding:

As conflicts occurred spontaneously, we conducted all occurrence-focal sampling (Altmann, 1974) on individuals of all age classes. Comments on date, start time, identities of the aggressor and victim, type of aggression and proximities of bystanders within 1m, 5m, 10m or visible to the observer (i.e., >10m) were recorded on video and subsequently coded. Video coding was conducted with the coding software BORIS or ELAN (type of coding software differed across years of video coding) and data were transferred into an Excel spread sheet (*ELAN*, 2019; Friard & Gamba, 2016). A detailed ethogram of coded behaviours was adapted from (Clay & de Waal, 2013a, 2013b), and major operational definitions are listed below (Table 5).

Throughout a PC or PD period, all affiliative contacts that involved the victim were coded following the ethogram (Table 5). However, body contacts during conflicts over food were excluded to omit potentially food-motivated behaviours (versus consolation). These contacts were expected to occur while food is taken away from the other rather than in a manner of offering comforting contact to the victim.

Per PC or PD period, the occurrence of affiliative contact was coded for each bystander. Start and end time, initiator (i.e., approaching individual) and recipient of the contact, type of contact (see Table 5), and the recipient's response (engage, passive, avoidance) was coded. A new contact bout started when the type of contact changed. Further, the latency of occurring contact was coded from the latest aggression towards the victim. This can include further aggressions following the initial conflict such as secondary aggression, renewed aggression or intervention in support of the aggressor (i.e., aggression towards the victim). In case of PDs, latencies of affiliative contacts related to the onset of latest signs of distress (Table 4) by the victim. This included renewed spontaneous distress without preceding received aggression.

Affiliation Scans

| Code | Behaviour and description |
|---|---|
| em | Embrace: Place one/both arms around the recipient's body while facing the partner or in lateral position (includes clinging to the back of another individual) |
| gg | Genito-genital contact:  Swing hips laterally while keeping vulvae in contact; usually while embracing ventro-ventrally, female-female partners |
| mo | Mount: Positioned behind recipient in lateral contact including genital contact, thrust pelvis onto recipient's behind/back |
| gt | Genital touch: Touch recipient's genitals using any other body part than genitals (e.g., using hand/foot to touch recipient's genitals) |
| co* | Copulation: Penile intromission and hip thrusting with male or female partner |
| to | Touching: Any instantaneous soft touch of the recipient's body, other than their genitals; actor uses any body part other than their genitals |
| gr | Grooming: Directed cleaning/touching/visual inspection of the recipient's hair/skin |
| cs | Contact sitting: Sit/rest in physical contact with the recipient |
| hd | Hold: Grasp/hold onto recipient's body with one or both hands. Generally, when recipient is walking or standing |
| pt | Pat: Pronounced tapping/patting contact onto recipient's body using flat hand |
| in | Inspect: Visual and contact inspection of the recipient's wound/injured body part, after a conflict |
| pl | Play: wrestle/run/jump/chase/tickle in physical contact accompanied by play face and/or laughter |

***App. Table 5. Types of affiliative bystander contacts.*** **In case of doubt of copulation's occurrence (i.e.: unclear if intromission occurred), this behaviour was coded as 'mount' instead. Based on (Clay & de Waal, 2013a, 2013b).*

| Behaviour | Code | Description |
|---|---|---|
| Grooming | GR | Directed cleaning/touching/visual inspection of the recipient's hair/skin |
| Sex | SX | Mount, copulation, genito-genital contact, genital-touch |
| Contact | CS | Any physical contact other than genital contact: touch, contact sit, embrace, cling onto other's back, peer with contact |
| Play | PL | Wrestle/run/jump/chase/tickle accompanied by play face and/or laughing |
| Arm's reach | AR | Dyadic proximity within 1 meter/within arm's reach |

***App. Table 6. Ethogram of social behaviour including bodily contact applied during scan sampling in addition to dyadic proximity within 1 meter.*** *Based on (Clay & de Waal, 2013a, 2013b).*

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|  | Group 1 | Group 2 | Group 3 |  |
|---|---|---|---|---|
| Year | N (scans) | N (scans) | N (scans) | Total (N scans) |
| 2011 | 794 | 411 |  | 1205 |
| 2012 | 789 | 785 |  | 1574 |
| 2016 | 478 | 440 | 223 | 1141 |
| 2019 | 706 | 587 |  | 1293 |
| 2021 | 585 | 539 |  | 1124 |
|  |  |  |  | 6337 |

***App. Table 7. Tally of scan data per group and observation year.***

## Data analysis

| **GLMM for Affiliation Tendencies** |  |
|---|---|
| **Variable** | **Description** |
| *Response:* |  |
| Affiliation tendency | Individual mean dyadic affiliation score with all group members per observation period |
| *Fixed effects:* |  |
| sex * age + sex * rearing + age * rearing | Subject's sex (m = male; f = female)<br>Subject's age (continuous age in years per observation period)<br>Subject's rearing (m = mother-reared, o = orphaned) |
| *Random effects:* |  |
| Individual | Subject's ID |
| Group-year | Group per observation period |

***App. Table 8. Model 1 - GLMM for affiliation tendency;*** *all observations refer to non-kin interactions.*

| **GLMM for Consolation Tendencies** | |
|---|---|
| **Variable** | **Description** |
| *Response:* | |
| Consolation tendency (per observation period) | Binomial matrix:<br>1 number of consolation offered<br>2 number of bystander opportunities |
| *Fixed effects:* | |
| sex * age + sex * rearing + age * rearing | Bystander's sex (m = male; f = female)<br>Bystander's age (continuous age in years per observation period)<br>Bystander's rearing (m = mother-reared, o = orphaned) |
| Dyadic affiliation | Dyadic victim-bystander affiliation score per observation period |
| *Random effects:* | |
| Individual | Bystander ID |
| Group | Bystander's group per observation period |

***App. Table 9. Model 2 - GLMM for consolation tendency;*** *all observations refer to non-kin interactions.*

| **GLMM for Victim Likelihood** | |
|---|---|
| **Variable** | **Description** |
| *Response:* | |
| Victim proportion | N of being a victim within a dyad/total N of observed aggressions within respective group and year |
| *Fixed effects:* | |
| v.rearing * v.sex + v.age + a.sex * a.age + a.rearing<br>(v = victim, a = aggressor) | Victim's and aggressor's sex (m = male; f = female)<br>Victim's and aggressor's age (continuous age in years)<br>Victim's and aggressor's rearing (m = mother-reared, o = orphaned) |
| *Random effects:* | |
| Individual | Aggressor ID, victim ID |
| Group per year | Group per observation period |

***App. Table 10. Model 3 - GLMM for victim likelihood;*** *all observations refer to non-kin interactions.*

## Results

### Model 1

Table 11 shows results of the original full Model 1, where only the interaction between sex*age was significant. A full-null model comparison showed non-significant interactions of age*rearing and sex*rearing. To investigate the effect of rearing, a reduced model was fit with the significant interaction of sex*age and rearing as fixed effects (see results in main text). A model output plot of the full Model 1 is shown in Figure 2 below.

| Term | Estimate | *SE* | lower CI | upper CI | z | *df* | *P* | min | max |
|---|---|---|---|---|---|---|---|---|---|
| (Intercept) | -2.942 | 0.126 | -3.181 | -2.703 | -23.423 | [a] | [a] | -3.001 | -2.888 |
| sex[b] | -0.167 | 0.148 | -0.435 | 0.121 | -1.129 | [a] | [a] | -0.228 | -0.114 |
| age[c] | 0.061 | 0.057 | -0.052 | 0.179 | 1.073 | [a] | [a] | 0.02 | 0.089 |
| rearing[d] | -0.051 | 0.121 | -0.275 | 0.182 | -0.419 | [a] | [a] | -0.114 | 0.006 |
| sex[b]: age[c] | -0.236 | 0.058 | -0.348 | -0.130 | -4.098 | 1 | **< .001** | -0.293 | -0.134 |
| age[c]: rearing[d] | 0.082 | 0.060 | -0.028 | 0.194 | 1.375 | 1 | .175 | 0.042 | 0.169 |
| sex[b]: rearing[d] | -0.243 | 0.168 | -0.572 | 0.081 | -1.450 | 1 | .147 | -0.373 | -0.18 |

[a] not indicated due to limited interpretability

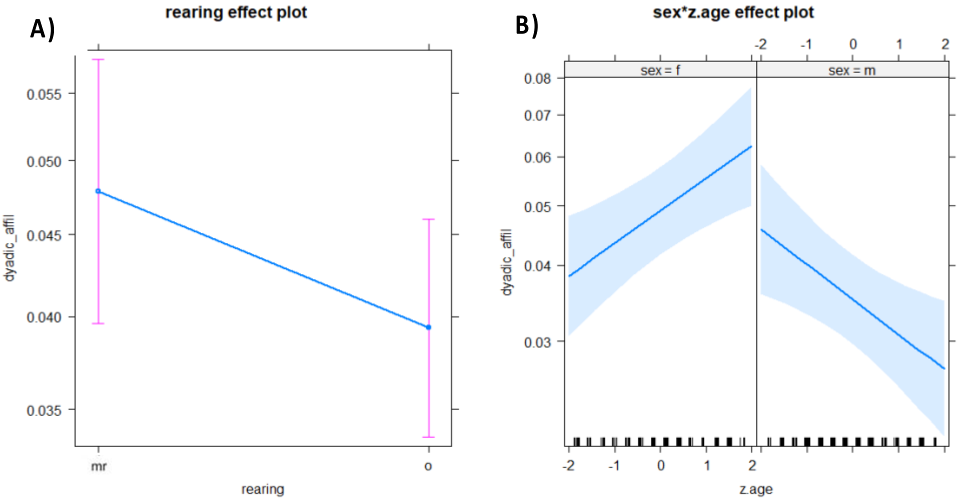
[b] dummy coded and centered with female as the reference level

[c] z-transformed to a mean of 0 and a standard deviation of 1

[d] dummy coded and centered with mother-reared as the reference level

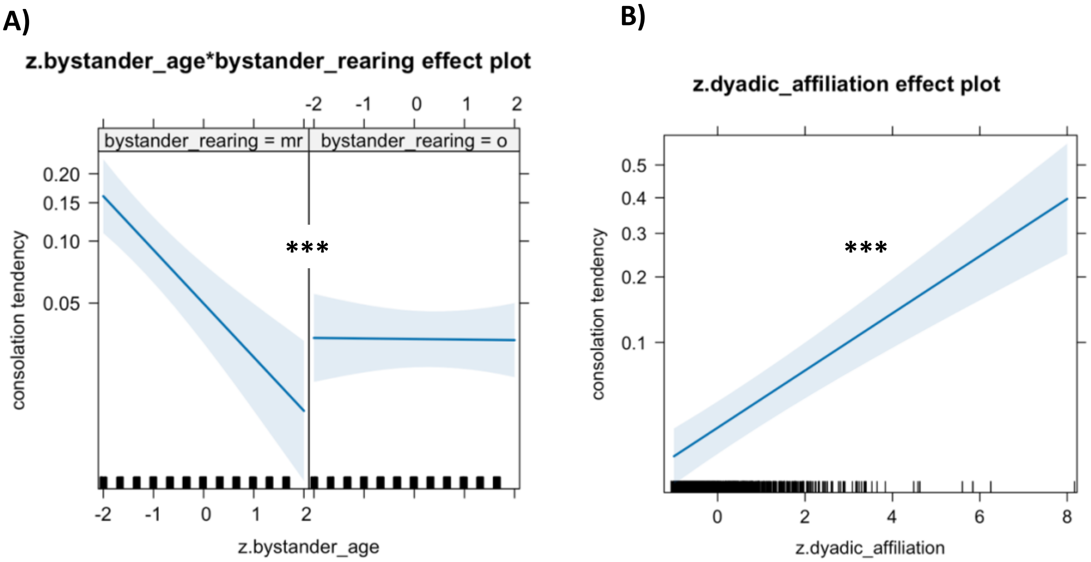
significant P values < 0.05 are shown in bold

***App. Table 11. Full Model 1 results:*** *Affiliation tendency including non-significant interactions as fixed effects. A subsequent reduced model is shown in the main results.*



***App. Figure 2. Reduced Model 1 results:*** *Affiliation tendency with significant fixed effects of A) rearing B) sex*age interaction. Y-axis: mean dyadic affiliation score, x-axis: respective fixed effects: A) mr = mother-reared, o = orphaned; B) z-transformed age, sex: f = female, m = male.*

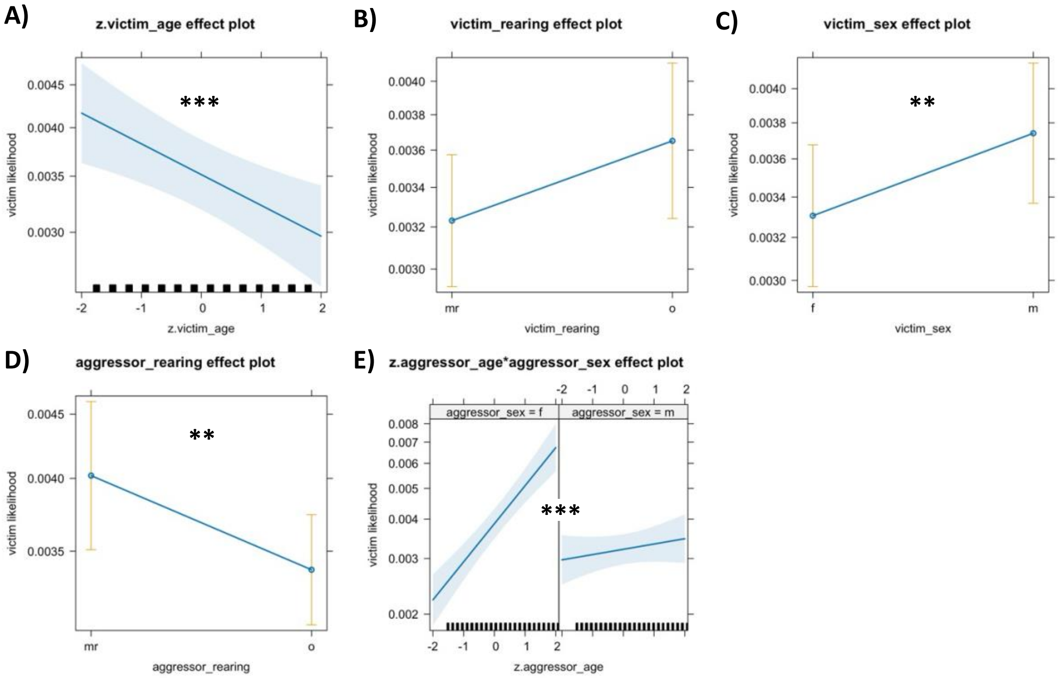
The below plot shows the model results output of the singificant fixed effects of Model 2 as presented in the main text results section.



***App. Figure 3. Model 2 - Plotted model output (full model) of significant effects on consolation behaviour:*** *A) Interaction between bystander age*bystander rearing (mr = mother-reared, o = orphaned): x-axis= z-transformed bystander age in years, y-axis = dyadic bystander consolation tendency. asterisks indicate predictors' significant p-values (*** P < .001). For detailed model results see main text Table 5.*

Model 3

Figure 4 shows the model output plot of Model 3 with its main predictors of the likelihood of being a victim of aggression as described in the results of the main text.



***App. Figure 4. Model 3 - Plotted model output of predictors of victim likelihood.*** *Tested predictors in reduced model (lacking non-significant interaction): A) victim age (age in years z-transformed), B) victim rearing (mr = mother-reared; o = orphaned), C) victim sex (f = female, m = male), D) aggressor rearing (mr = mother-reared; o = orphaned), E) aggressor age * aggressor sex (f = female, m = male); asterisks indicate predictors' significant p-values (*P < .05; ** P < .01; *** P < .001). See main text Tab.6 for detailed results.*