Personality and Wellbeing in Gorillas: Captive-Wild Comparisons and Implications for Zoos

Picture 1 *Gorilla Group at Apenheul Primate Park, the Netherlands*

A thesis submitted for the degree of Doctor of Philosophy

by

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Except for instances clearly stated in the text, everything in this dissertation is the product of my own work and does not represent the results of work completed in collaboration.

The present dissertation has not been, nor will it be, presented for the purpose of obtaining a degree, diploma, or any other qualification at any other academic institution.

This thesis does not exceed 88,000 words.

Yvonne Pohlner

Abstract

The One Plan Approach integrates in situ and ex situ strategies for wildlife conservation, emphasizing biodiversity preservation through cross-sector collaboration. Zoos are crucial in this approach, engaging in activities such as ex situ breeding and translocation programs, thus contributing to the conservation of endangered species and promoting individual animal welfare. Understanding personality in animals can significantly enhance these conservation and welfare efforts. This study investigates the personality of Western lowland gorillas (WLGs) using the Hominoid Personality Questionnaire (HPQ) across both ex situ (eWLGs) and in situ (iWLGs) populations. Data were collected from 203 eWLGs (678 ratings, 94 raters, 30 zoos) and 198 iWLGs (501 ratings, 25 raters, 5 African field sites). Key findings reveal distinct personality structures: eWLGs exhibited six factors (Dominance, Openness, Conscientiousness, Agreeableness, Neuroticism, Extraversion) while iWLGs displayed four (Neuroticism, Sociability, Dominance, Self-Control/Tolerance). Demographic variables such as sex and age influenced personality differences in both populations. Comparative analysis with previously published data on Virunga mountain gorillas (iVMGs) highlights the impact of socio-ecological factors like habitat, diet, social structure, and life history on personality development. These differences demonstrate the complex interaction between environmental dynamics, adaptability, and the evolution of personality. Additionally, personality is linked to subjective wellbeing (SWB) and social engagement in gorillas. SWB ratings were analysed for 189 eWLGs (607 ratings, 84 raters, 30 zoos) and 189 iWLGs (499 ratings, 25 raters, 5 field sites), with validation through observed behaviour in 124 iWLGs. Strong correlations between SWB, mood, emotions, and personality factors were found in a subset of 24 eWLGs. The integration of positive welfare and SWB concepts with personality insights offers a novel perspective within the One Plan Approach. This research advocates for a holistic One Welfare Plan to optimize conservation, management, and wellbeing of gorillas, enhancing their overall welfare by fostering positive emotions and social interactions.

Acknowledgements

"The love for all living creatures is the most noble attribute of humanity." - Charles Darwin

To my beloved children, Amelie and Timmy, and in homage to the incredible beings that have fuelled my unwavering commitment to conservation.

Writing a thesis is a journey, and I have been fortunate to be accompanied by a multitude of incredible people and wonderful gorillas. This work would not have been possible without their unwavering support, guidance, and inspiration.

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The gorillas themselves have been the silent yet profound contributors to this thesis. You, the gentle giants of the forests, have etched a profound mark on my heart and my journey as a researcher and conservationist. Your presence in this world, resilient and magnificent, has illuminated my path and kindled a flame of dedication within me. I extend my deepest appreciation for allowing me into your world, in ex and- and in situ. Studying your individual behaviours' and your social-ecology differences has been an unforgettable experience. The lessons you've taught me about family, community, and the enduring importance of compassion are immeasurable.

This thesis, dedicated to your welfare and the preservation of your natural habitats, is an embodiment of my deepest love and respect for your kind. My ultimate aspiration is that it contributes to a world where your existence is safeguarded, your homes are secure, and your lives are enriched.

Finally, to all the silent moments and sleepless nights, to the piles of research papers and the endless revisions—thank you. You have been the crucible in which this thesis was forged.

As I present this work, I carry with me the hope that my efforts may, in some small way, contribute to the protection and prosperity of species. My adapted One Plan Approach - the One Welfare Plan, underpinned by collaboration and the principle of collective wellbeing, holds the promise of a brighter future for you, the remarkable gorillas.

We share a moral obligation to protect and safeguard all living beings and their natural environments. The positive psychology approach inherent in this work is designed to contribute to the fulfilment of the One Plan Approach's objectives for species survival. Together, we aspire to create a world where humans and animals coexist harmoniously, guided by compassion, empathy, and a commitment to the welfare of all.

With my deepest love for the creatures who inspire my every step, and with my children as a guiding light, I pledge to work relentlessly for a world where the well-being of all animals is cherished. This is a tribute to your beauty, resilience, and the profound impact you have on our lives, the lives of generations to come, and the better world we aspire to create.

Thank you all for being a part of this incredible journey. With profound reverence and optimism for a better future of all living beings.

Yvonne Pohlner

"In the heart of a gorilla, a person feels the magic and mystery of the jungle." - Dian Fossey

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List of Abbreviations

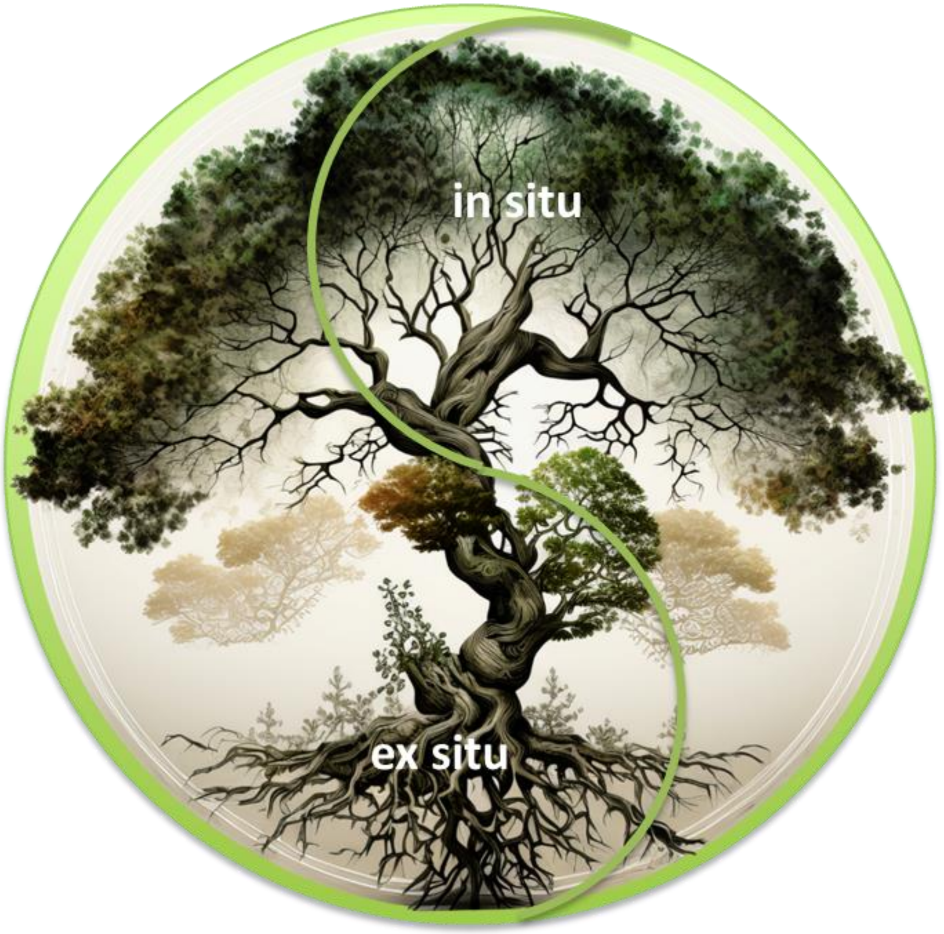
ACH	Achievement
ACT	Active
Agg	Aggressive
AGR	Agreeableness
ALT	Altruism
ANX	Anxiety
ASAB	Association for the Study of Animal Behaviour
BB	Blackbacks
BIAZA	British and Irish Association of Zoos and Aquariums
BMG	Bwindi Mountain Gorilla
BPG	Best Practice Guideline
CBD	Convention on Biological Biodiversity
Cnf	Confidence
Con	Conscientiousness
CPSG	Conservation Planning Specialist Group
CREA	Creativity
CRG	Cross River Gorilla
DEFRA	Department of the Environment Food and Rural Affairs
Dom	Dominance
DRC	Democratic Republic of the Congo
DSPA	Dzanga-Sangha Protected Areas
EAZA	European Association of Zoos and Aquaria
EEP	EAZA Ex situ Programm
EFA	Exploratory Factor Analysis
EG	Eastern Gorilla
ELG	Eastern Lowland Gorilla
EMO	Emotional Stability
EV	Eigenvalue
eWLG	Ex situ Western Lowland Gorilla
Ext	Extraversion
FA	Factor Analysis
Fef	Fearful
FFM	Five Factor Model
GBF	Global Biodiversity Framework
GBI	Gorilla Behavioural Index
GI	Generalised weighted least squares
GPQ	Gorilla Personality Questionnaire
HPQ	Human Personality Questionnaire
ICAP	International Collection Assessment and Planning
INT	Intelligence
IBI	Inter Birth Interval
IUCN	International Union for Conservation of Nature

iVMG	In situ Virunga Mountain Gorilla
iWLG	In situ Western Lowland Gorilla
KRC	Karisoke Research Centre
LRS	Lifetime Reproductive Success
LTMP	Long Term Management Plan
MAP	Minimum Average Partial
MG	Mountain Gorilla
MGNP	Mgahinga Gorilla National Park
MinChi	Minimum Chi Square
MinRes	Minimum Residual
ML	Maximum Likelihood
MLE	Maximum Likelihood Estimation
MMRG	Multi-Male Reproductive Group
NegAff	Negative Affect
Neu	Neuroticism
NRG	Non-Reproductive Groups/Bachelor Groups
OPA	One Plan Approach
OPN	Openness
OWA	One Welfare Approach
OWP	One Welfare Plan
PAF	Principal Axis Factoring
PCA	Principal Component Analysis
PNVi	Parc National de Virunga in the Democratic Republic of the Congo
RCP	Regional Collection Plan
RDB	Rwanda Development Board
REFA	Regularized Exploratory Factor Analysis
SB	Silverback
s-dbr	State-Dependent Behaviour Response
SDGs	Sustainable Development Goals
SMRG	Single-Make Reproductive Group
SOC	Sociability
SS	Solitary Silverback
SSC	Species Survival Commission
SSP	Species Survival Plan
SUP	Supportive
SWB	Subjective Wellbeing
TAG	Taxon Advisory Group
THV	Terrestrial Herbaceous Vegetation
T/SC	Tolerance/ Self-Control
TNS	Sangha Tri-National Protected Area complex
UN	United Nations
UND	Understanding
UNEP	United Nations Environment Programme
VMG	Virunga Mountain Gorilla
VNP	Volcanoes National Park
WAZA	World Association of Zoos and Aquaria

WG	Western Gorilla
WLG	Western Lowland Gorilla
WLS	Weighted Least Squares

Chapter 1

General Introduction and Aims



Picture 2 *One Plan Approach*

“Putting an end to the seemingly intractable controversies between animal protectionists and wildlife managers and integrating their conflicting ethical frameworks will require the development of a bifocal view in which zoo animals are seen simultaneously as individuals in need of specific care and as members of a species in need of protection.” Jozef Keulartz (2023, Page 1).

1.1 Introduction

The global demographics and evolution of animal species are being impacted by the changing environmental circumstances caused by human activity. To mitigate this human-induced 6th mass extinction of species and the loss of biodiversity (Ceballos et al., 2015), it is imperative to enhance human capacity to reestablish natural habitats and populations. Zoos have undergone significant changes from their origins as collections of exotic animals intended to display wealth and social status (Bostock, 1993), as many modern zoos have evolved into conservation facilities that contribute towards the achievement of various goals and targets outlined in the Global Biodiversity Framework (UN, 2015; DEFRA, 2018; UNEP and IUCN 2021a,b; CBD, 2011, 2022).

Critical milestones in the change of zoos to conservation facilities

The focus of zoos shifted towards the protection of endangered animals and wildlife throughout the 1970s and 1980s. In 1992, at The Earth Summit in Rio de Janeiro, The Convention on Biodiversity was signed, which was a significant turning point in history, encompassing a holistic strategy that involves effective management of species within their native habitats (**in situ)** at the level of the Conservation Strategy, Action Plan, and Recovery Plan, as well as through specific breeding and release programs (**ex situ**) at the level of the Zoo Species Program Goals and Masterplan (Conde et al., 2013; Gilbert & Soorae, 2017; Traylor-Holzer et al., 2019). The One Plan Approach (OPA) was a foundational concept in the 2015 World Zoo and Aquarium Conservation Strategy (Barongi et al., 2015). Since 2016, the Integrated Collection Assessment and Planning (ICAP), developed by the Conservation Planning Specialist group (CPSG), is a continuously updated procedure designed to achieve the integrated in situ and ex situ goals of the OPA. The 2020 update prioritises collaborative conservation planning as one of its three key aspects in the Species Conservation Cycle: Assess to Plan (A2P)-Act (2020). The latest framework includes core principles at its foundation and planning steps (rooted within roots of a planning tree, and planning steps in the form of leaves CPSG, 2021 (see **Figure 1**, Byers et al., 2022). Early integration of this framework into species management projects has the potential to reverse the decline of threatened species Additionally, the approach is integrated into Regional Collection Plans (RCPs) and Taxon Advisory Groups (TAGs) globally (Traylor-Holzer et al., 2019).

At the level of the species-target planning (Bolam et al., 2023), the OPA considers all pertinent factors and involves all relevant stakeholders such as zoos and aquariums, sanctuaries, museums, wildlife managers, landowners & local community representatives, government officials, academics, non-governmental organisations, Species360 (Species360, 2018 applied in e.g., Ginal et al., 2023), International Union for Conservation of Nature (IUCN) Species Survival Commission (SSC) Specialist Groups (e.g., Primate Specialist Group), IUCN Reverse the Red (e.g., IUCN 2020), Conservation Planning Specialist Groups (CPSG) (Byers et al., 2013), ICAPs (Traylor-Holzer et al., 2019) and other organisations like European Association of Zoos and Aquaria (EAZA), British and Irish Association of Zoos and Aquaria (BIAZA), World Association of Zoos and Aquaria (WAZA) and more. It also considers international laws and the involvement of communities in protected areas, while efficiently utilizing available resources. This approach offers a better delineation of the functions of zoo and aquarium ex situ programmes, leading to the development of more tailored and effective processes that significantly contribute to species conservation. The primary objective of conservation management is to ensure the protection of species, their wellbeing, both in situ and ex situ populations, and their respective habitats within natural environments, all with the overarching aim of promoting species survival and supporting overall ecosystem health (Byers et al., 2013, 2022; Traylor-Holzer et al., 2019). Furthermore, the OPA aligns with the broader goal of landscape-level conservation and the maintenance of ecological integrity, while also fostering efficient resource utilization among various stakeholders (Byers et al., 2013).

To summarize, the OPA is a “joint development of management strategies and conservation actions for all populations of a species by all responsible parties to produce a single, comprehensive conservation plan” (Byers et al., 2013, Page 4). This shift in priorities signifies a transition from the conventional "ark" paradigm in zoos, where the focus was on self-sustainability as genetic reservoirs (Soulé et al., 1986) to the OPA paradigm (Traylor-Holzer et al., 2019). Recent findings indicate that 57% of endangered species' extinction risks can only be reduced through targeted recovery activities, including ex situ conservation, reintroductions, and species-specific procedures (Bolam et al., 2023). The Convention on Biological Diversity (CBD) states we need to “Ensure active management actions to enable the recovery and conservation of species and the genetic diversity of in situ and domesticated species, including through ex situ conservation, and effectively manage human–wildlife interactions to avoid or reduce human–wildlife conflict”

(CBD, 2021b, page 6). The OPA is particularly significant for zoos and aquariums, making them pivotal stakeholders in this endeavour (Traylor-Holzer et al., 2019).

However, the OPA has not come without challenges, as there is no “one size fits all” method to be applied to all species (de Man et al., 2016), nor is it easy to combine both directions – the in situ and ex situ. Conservation efforts must be adapted to the unique needs of the taxonomic group with diverse habitat requirements, demography, and life histories (see Chapter 2 for information on gorilla biology). Therefore, species-specific TAGs develop RCPs to fulfil their crucial role in the overall implementation of the OPA.

Within the following section, special attention is given to the following statements, which provide insights leading towards the understanding of **Figure 1**, below.

Conservation and welfare management of endangered species – a continuum between in and ex situ (Veasey, 2017), and a “bifocal view, one, on the welfare of the individual in need of specific care and, second, as a member of a species in need of protection” (Keulartz, 2023, p. 2):

Reciprocal transfer

An important element advocated within the OPA is the **reciprocal transfer** of animals between in- and ex situ populations. This movement of animals in both directions holds the potential to enhance the resilience and long-term viability of both populations. Ex situ populations may serve to replenish regions facing declining numbers or reintroduce species where populations have gone extinct, and the introduction of genetic founders from in situ populations has the potential to enhance the demographic and genetic sustainability of ex situ populations (Byers et al., 2013). This approach aims to protect the genetic and demographic viability of ex situ and in situ populations (Sauve et al., 2022) while preserving the natural habitats and animals within it (Traylor-Holzer et al., 2019).

Continuum between in situ and ex situ

It is also of utmost importance to understand that a continuum exists between in situ and ex situ environments, which encompasses various levels of naturalness (in situ) and confinement experienced by animals (Veasey, 2017). This recognition emphasizes the complexity of evaluating animal wellbeing, particularly for animals living in ex situ settings.

The spectrum of animals' living conditions, from untouched natural habitats to highly controlled environments, highlights the complexity of assessing their wellbeing, especially those living ex situ. The recognition is made that the categorization of in situ and ex situ is not strictly dichotomous, but rather comprises a spectrum of situations and varying levels of liberty. Taking this into account promotes their general subjective wellbeing and harmonises ethical concerns and conservation goals. Therefore, zoological institutions are prioritising the provision of enhanced habitats, expansive enclosures that closely resemble natural settings, and teaching initiatives that underscore the need of wildlife preservation. The ongoing discourse regarding the ethical implications and advantages of supporting animals inside zoological institutions persists, promoting the need for zoos to constantly adapt and emphasise the wellbeing of animals, conservation efforts, and educational endeavours as essential tenets of their purpose.

Optimised welfare strategies

Zoological institutions also supply a vital function in the conservation and advocacy of the **wellbeing** of animals in their care and are integral to the ecosystem by providing habitats and populations with essential resources. The primary objective to optimised welfare strategies (Veasey, 2017) is, to stimulate “meaningful”, natural behaviours that go beyond basic survival needs. Promoting mental stimulation, emotional engagement, and positive affect will lead to increased subjective experiences (Brando & Buchanan-Smith, 2018; Mellor et al., 2020; Veasey, 2017). Understanding animals’ subjective preferences, likes, and needs, can guide the design of enriched environments that cater to an individual's psychological and emotional needs (Bovenkerk & Keulartz, 2018; Brando & Buchanan-Smith, 2018; Veasey, 2017). Fundamentally, settings that foster positive wellbeing are characterised by complexity and novelty, choice and control, and their correlation with predictability (Buchanan-Smith, 2011). The promotion of good wellbeing also facilitates the generation of ecologically valid study results pertaining to the health of animals (Buchanan-Smith et al., 2001). Hence, the promotion of optimal animal welfare is essential not only for the wellbeing of individual animals, but also for the attainment of elevated benchmarks in effective conservation of in situ populations.

Balancing Animal welfare and species conservation

Striking a **balance between animal welfare of both populations** remains a challenge. To help achieve this balance, the approach of my thesis investigates how the knowledge on individual differences can be used as an additional strategy to link conservation (in situ) and ex situ with the overall goal to ensure survival by optimising welfare (for ex- and in situ populations) within the OPA (Bovenkerk & Keulartz, 2018).

Figure 1, below, will be used throughout the thesis as a road map to explain the connection and contribution of each of the chapters to the overarching goal of my thesis. The subjective wellbeing and continuum between in situ-and ex situ concepts of Veasey (2017) and that of Keulartz's bifocal view (2023), based on individual subjective wellbeing contributing towards optimal wellbeing in the ex situ and in situ population are the keys to reaching the goals of the OPA. My goal is to increase the recognition of the role of personality within the OPA, as a connecting tool within the ex situ (Chapter 3) and in situ (Chapter 4) population. In addition, I wish to show how understanding personality promotes positive subjective wellbeing and happiness (Chapter 5) in ex and in situ populations, its relevance to sociability, environmental conditions, conservation and social wellbeing by comparing ex situ and in situ personality findings. Studying personality in the in situ population within their natural habitat contributes to a more comprehensive understanding of how individual differences influence ecological processes, population dynamics, and responses to environmental changes and emphasizes the importance of considering the subjective experiences and wellbeing of the ex situ gorilla population.

Picture 2/ **Figure 1** visualizes the OPA in this study, with the tree of life in the middle, the ex situ and in situ population within the circle of life. The balance between the ex situ and in situ and the resilience of the species is represented in the Yin and Yang symbol. The tree is a combination of the WAZA Animal Welfare Strategy (2015) in respect to Maslow's hierarchy of wellness and wellbeing and the SSC's Species Conservation Planning Principles and Steps represented within the tree (Byers et al., 2022). In Chapter 6, I integrate the 5 Domains Model of Mellor (Mellor, 2016; Mellor et al., 2020), and extend the WAZA Animal Welfare Strategy of Maslow's Hierarchy of Needs (2015) within the OPA model and interconnect the 24/7 across lifespan framework of Brando & Buchanan-Smith (2018), and integrate it into the One Welfare Plan.

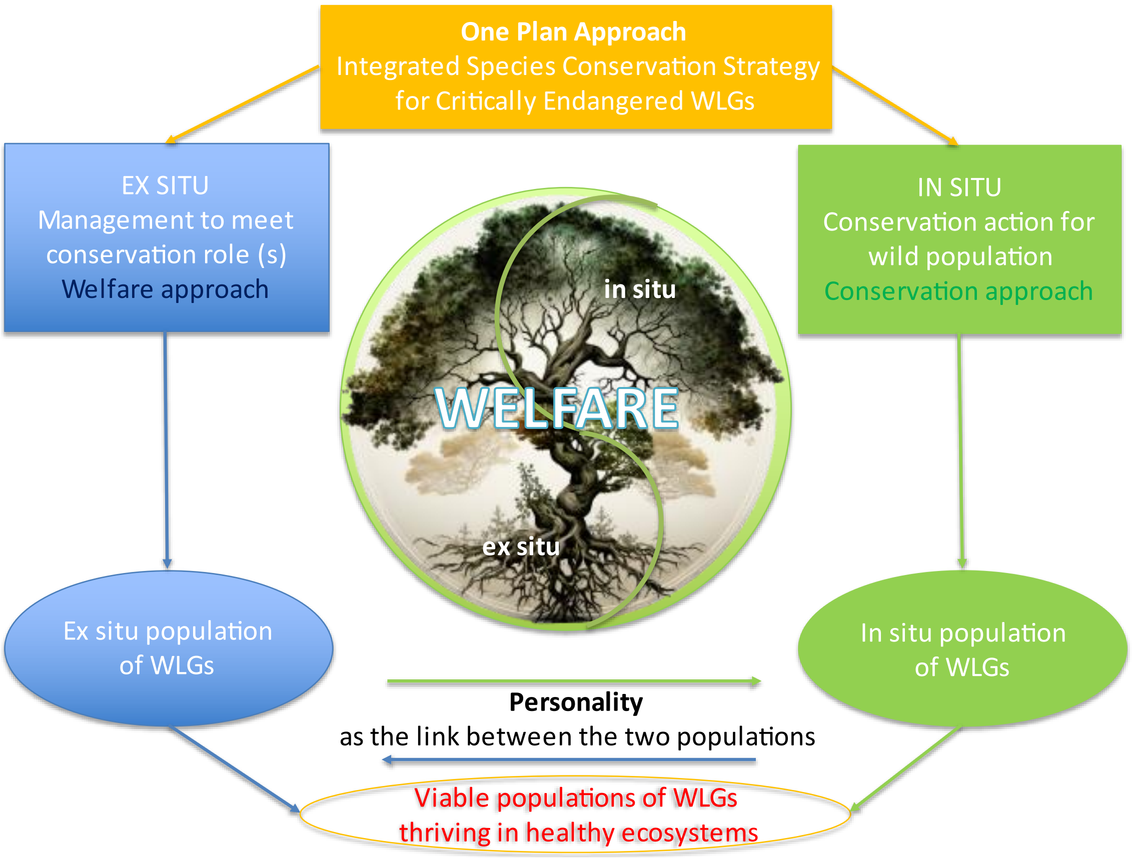


Figure 1 *Personality as an extended conservation tool kit and the link between in situ and ex situ Conservation and Welfare within the OPA*

Note

WLGs = Western lowland gorillas.
Left: blue path: includes the ex situ population of WLGs.
Right: green path: includes the in situ population of WLGs.
Middle: upper part: OPA, integrated strategy, middle: visual representation of the OPA, including the tree of life within the circle of life and the Yin and Yang, denoting the reciprocal transfer between ex-and in situ, the continuum between in situ and ex situ (Veasey, 2017), and the balance (Bovenkerk & Keulartz, 2018; Keulartz, 2023), which needs to be reached between the populations. Lower middle: a proposed tool kit: Personality as the link between ex situ and in situ (see arrows), used in my study.
Bottom: goal to reach visible population of WLGs thriving in healthy ecosystems.

Within the following section, I introduce the tool kit: Personality and its contribution to the OPA.

Within the extensive literature on how to define and classify personality in animals, the terms personality, temperament, behavioural types and behavioural syndromes have been used more or less interchangeably. The perception of personality indicates that behavioural differences in individuals are **consistent over time** and **across diverse behavioural conditions** (e.g. in anti-predator and foraging behaviour) and **ecological circumstances** (Powell and Garnter, 2011; Sih et al., 2000; Weiss and Adams, 2011; Gosling, 2001; Sih et al., 2004). However, there is also

plasticity within individual **behaviour responses** via **state-dependent feedback loops** (Sih et al., 2015). Overall, the term "personality" in this thesis describes the phenomenon by which **individuals differ systematically** in their **emotional, cognitive,** and **behavioural tendencies** (Weiss & Adams, 2010; Wolf & Weissing, 2010).

Personality research has been applied to animals and have been found in a broad range of taxa from small insects such as fruit flies (Kain et al., 2012), to large mammals such as elephants (Lee & Moss, 2012, Williams et al., 2019), including a growing number of nonhuman primate species (Chotard, 2019). Zoos have begun to realize the implications of personality differences with respect to managing ex situ animals' welfare, breeding, conservation success, and reintroduction in zoological facilities and in situ conservation (Carlstead & Shepherdson, 1994; Gartner & Powell, 2012; Gartner & Weiss, 2013; Gold & Maple, 1994; Powell & Gartner, 2011; Watters & Meehan, 2007; Watters & Powell, 2012; Weiss, King, et al., 2011; Wielebnowski, 1999). By analysing personality traits, conservationists can tailor management and reintroduction strategies to minimize stress and maximize adaptation for different individuals (Merrick & Koprowski, 2017; West et al., 2019). Behavioural monitoring and management can also be improved by considering individual personalities in reintroduction success (Allard et al., 2019; L. Baker et al., 2016; Biro & Stamps, 2008; Bremner-Harrison et al., 2004; Haage, Angerbjörn, et al., 2017; Haage, Maran, et al., 2017; Mittelbach et al., 2014). Personality traits can provide insights into human-wildlife conflict, such as hunting (Nogueira et al., 2017) and climate change, as well as human mitigation strategies (Arroyo et al., 2017; Heinen-Kay et al., 2016; Merrick & Koprowski, 2017). Ex situ management and wellbeing can be improved by creating enriched environments catering to individual needs, especially in the selection of social partners (Gartner & Weiss, 2018). Incorporating personality traits into breeding programs and population biology can help maintain or select desirable traits (Castanheira et al., 2016; Griffiths & Dos Santos, 2012; Martin-Wintle et al., 2017). The knowledge of individual variations can be meaningful for the longer-term viability and longevity of individuals, populations, and species (Watters & Meehan, 2007) as well as for entire ecosystems both at environmental (social and developmental) and evolutionary time scales (Sih et al., 2004, 2015; Wolf & Weissing, 2012). Personality differences are therefore a crucial, yet largely neglected aspect of biodiversity, influencing the stability, resilience, and persistence of populations, communities, and entire ecosystems at both ecological and evolutionary timescales (Wolf & Weissing, 2012). Furthermore, the integration of knowledge of animals' emotional sensitivity and, thus, their personality, can be a meaningful tool to improve ex situ confinement and increase the subjective wellbeing of animals (Gartner et al., 2016; Robinson & Weiss, 2023; Weiss & Robinson, 2020). Therefore, personality traits play a crucial role in species within in situ conservation and ex situ management (Bremner-Harrison et al., 2018; Caro, 2007; Gartner & Weiss, 2018; Greggor et al., 2016; MacKinlay & Shaw, 2023; McDougall et al., 2006; Wielebnowski, 1999).

By integrating personality research into the conservation strategies listed within this thesis, the OPA can become even more comprehensive and effective. It acknowledges the individuality of animals within a population and harnesses this knowledge to create tailored, adaptive, and successful conservation efforts to preserve the species.

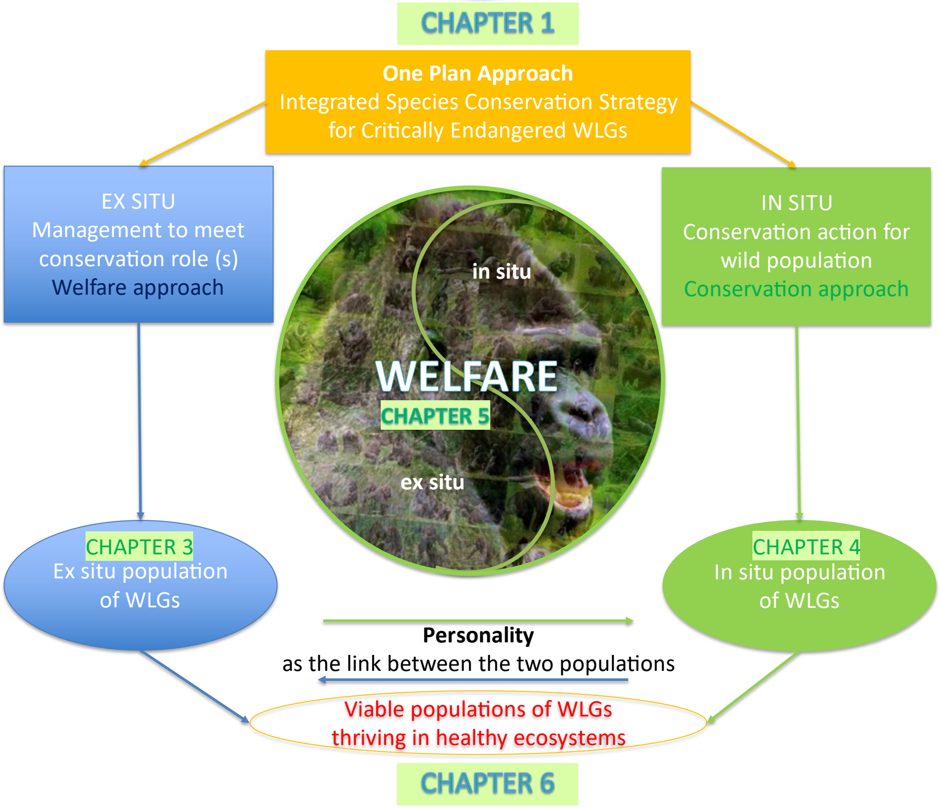
Within the following sections, I review personality research and how it is interlinked within my thesis:

The evolution and measurement of personality

Many different approaches have endeavoured to explain the fundamental basis of animal personality. Phylogenetically related cross-species comparisons on personality similarities have highlighted strong relationships within personality dimensions (Adams et al., 2015; Weiss, Adams, Widdig, et al., 2011). For example, a cross-species comparison of macaques showed sociality as a key factor in the emergence and maintenance of personality structures (Adams et al., 2015). Another method is to use a phenotypic selection approach (Brodie et al., 1995; Lande & Arnold, 1983) to explain evolutionary mechanisms based on natural and sexual selection (Réale et al., 2010). A more recent model integrates state-dependent feedback loops (Sih et al., 2015). According to Sih and colleagues, personality is inherently dynamic, shaped by a complex interplay between internal states, such as mood, physiology, and motivation, and external feedback from social interactions and environmental cues. This interaction forms intricate feedback loops, where alterations in one aspect lead to reciprocal changes in the other, creating a continuous cycle of influence. Within this framework, personality is examined through both proximate and ultimate lenses, encompassing immediate causes and evolutionary explanations. By integrating genetic, neurobiological, and environmental factors, this model provides a holistic understanding of how personality traits emerge and evolve over time (Sih et al., 2015). Therefore, this model allows for the **variability (plasticity) and stability (consistency) of within-and between-individual differences** on the **proximate (individual)** and **ultimate (population)** level of personality, as personality strongly influences the structuring of animals’ social inter-relationships within-and between-individuals, populations, and species (Bergmüller & Taborsky, 2010; Bolnick et al., 2003; Dingemanse et al., 2002; Koski, 2011; Koski & Burkart, 2015; Sih & Watters, 2005; Wolf & Weissing, 2012).

1.2 Aims of the Thesis Chapters

In my thesis, I endeavour to illustrate the valuable application of personality research in optimizing the management and conservation of both in situ and ex situ populations of Western lowland gorillas (WLGs) within the overarching framework of the OPA. I discuss why and how evolutionary causes (selective pressure, like natural, sexual, and artificial selection; adaptation) shaped differences in WLGs personalities on the level of the population (**ultimate causes:** on the personality structure, Chapter 3) and the individual (**proximate causes:** subjective wellbeing, Chapter 5). Integrated within an extended state-dependent feedback loop model (based on Sih et al., 2015), I explain how sociability impacts personality and happiness (Chapter 5). The OPA is further developed into the One Welfare Plan, Chapter 6.



CHAPTER 1

One Plan Approach
Integrated Species Conservation Strategy
for Critically Endangered WLGs

EX SITU
Management to meet
conservation role (s)
Welfare approach

IN SITU
Conservation action for
wild population
Conservation approach

in situ

WELFARE

CHAPTER 5

ex situ

CHAPTER 3
Ex situ population
of WLGs

CHAPTER 4
In situ population
of WLGs

Personality
as the link between the two populations

Viable populations of WLGs
thriving in healthy ecosystems

CHAPTER 6

Figure 2 *Road map for a better understanding of operating chapters within the thesis*

Note.
Chapter 1: Introduction to the **One Plan Approach (OPA,** image on top), integration of personality as a new tool within the OPA and aims of the thesis.
Chapter 2: Gorilla biology.
Chapter 3: Evaluating the **ex situ personality structure** and cross-great ape comparison.
Chapter 4: Identifying the **in situ personality structure**, facilitating a cross-genus *Gorilla* comparison on the personality structures (in situ: WLG vs. Virunga mountain gorillas & ex situ – in situ WLGs) on the level of a **social-ecological approach.** Generation of shared social-gorilla constructs in their personality.
Chapter 5: Multi-dimensional Welfare Approach. Extend the personality framework, based on Sih and colleagues (2015) model on state-dependent feedback loops and include sociability as key to personality and subjective wellbeing.
Chapter 6: Discussion of findings in respect to welfare improvements of in situ and ex situ WLG populations. Extending the One Plan Approach to the **One Welfare Plan,** Chapter 6 (image on bottom).

Overview thesis structure:

Chapter 2: I encompass a detailed exposition of the taxonomy and biology of gorilla sub-species, elucidating socio-ecological differences and the distinctions in the life cycles of WLGs (in situ vs ex situ) in comparison to Virunga mountain gorillas (VMGs).

Chapter 3: On the **ultimate level**, the personality structure of the ex situ WLG population will be generated and compared to a previous study on ex situ WLGs in which four factors were found using a shorter personality inventory (Gorilla Behavioural Index (GBI), by Gold & Maple, 1994) to see if the results are aligned using different methods. Further comparison to great ape species and humans on the higher-order factors and on lower-order trait constructs was compared to examine phylogenetic relationship between the species.

Chapter 4: A cross-genus *Gorilla* comparison on the level of the personality structure of in situ WLGs' to the previously published personality structure of in situ Virunga mountain gorillas (Eckardt et al., 2015), and to ex situ WLGs (see Chapter 3) is conducted to shed light into the stability or dynamic of the personality on the **ultimate level**. A detailed social-ecological comparison on the three populations was addressed to explain personality differences within the sub-species. I also generated shared sociability constructs across the genus *Gorilla* to underpin that Sociability is key to personality. The impact on sex and age differences on the in situ personality structure was also assessed.

Chapter 5: General methodologies to measure positive welfare on different timescales **are** introduced, such as how to measure pleasurable short-term experiences, such as emotions, longer term mood states, zoo records, and measures of personality and **Subjective Wellbeing (SWB)**, which are consistent over time and across different behavioural contexts and ecological situations. Further, a detailed description of the various involvements of **social aspects on diverse levels of personality** and **SWB** and the complex interaction between all facets, within the **extended framework of the state-dependent feedback loop model are** assessed**,** as it is assumed that social relationships play a pivotal role. They function not only as conduits for external feedback but also as the backdrop against which behaviour unfolds. I show that the quality of social connections is intricately linked to subjective wellbeing, thereby exerting a profound impact on the development and expression of personality traits. Conversely, I show that adverse social interactions hold the potential to instigate alterations in personality or wellbeing over time.

Chapter 6: The concluding chapter serves as a comprehensive synthesis and discussion of the thesis's overarching findings, elucidating how they effectively address the various hypotheses outlined in earlier chapters. This chapter acts as a bridge connecting the ex situ and in situ perspectives, presenting recommendations for both contexts within the OPA. It underscores the pivotal role of personality and SWB as a valuable tool for assessing in situ and ex situ animal welfare, underscoring their significance within the broader framework of animal ethics and within the overall achievement of the OPA.

Moreover, the chapter ventures beyond the WAZA Animal welfare strategy (WAZA 2015) and the "Five domains" welfare model, to exploring an expanded welfare model (**One Welfare Plan (OWP),** Chapter 6) that transcends the traditional boundaries, encompassing both in situ and ex situ perspectives. This holistic approach considers the in situ framework as a blueprint for guiding ex situ management practices. The chapter culminates in the proposal of the OPA tailored specifically for gorillas, offering a comprehensive framework for the enhancement of their welfare and wellbeing across diverse settings (in situ and ex situ).

A nuanced understanding of personality differences among individuals can yield reciprocal advantages by offering novel avenues to enhance management practices by increasing positive wellbeing and happiness, consequently bolstering the conservation efforts for critically endangered animals, in this case the WLG. This study serves as an example of the potential advantages that can be derived from the integration of personality knowledge into ex situ management, thus augmenting their efficacy as well as on the level of the species survival in respect to conservation efforts.

Chapter 2

Gorilla Biology

Picture 3 *Gorillas group living*

“Only if we understand, will we care. Only if we care, will we help. Only if we help, shall all be saved.” (Goodall, 1999)

2.1 General Introduction

Among African apes, gorillas supply a rare chance to reconsider existing evolutionary theories in which ecology, demographic differences, diet, life history, social group structures, dispersal patterns, and behaviours shape population dynamics. Gorilla habitats and their spatiotemporal resource availability can vary between subspecies and even between populations within a subspecies (Parnell, 2002; Watts, 1984, 1991, 1996; Williamson et al., 1990). The interaction between these factors plays a significant role in shaping socio-ecological differences among gorilla subspecies. Significant variations have been established among gorilla subspecies with regards to various socio-ecological, cultural, and behavioural aspects (M. Robbins & Robbins, 2018). They supply themselves as intriguing subjects for the examination of the differences due to the prevalence of philopatry, natal dispersion, and secondary dispersal within the subspecies. The prevalence of philopatry in both sexes, which occurs in humans and gorillas, and that gorillas are more closely related to humans than they are chimpanzees (Koop et al., 1989) highlight the close evolutionary relatedness between us and gorillas and thus, studying gorillas can help understand multiple aspects of human evolution.

Within this chapter, I provide background information on gorilla taxonomy, morphology, distribution, as well as the conservation status of the genus *Gorilla*. I provide a comparative overview of gorillas' behavioural ecology, their dynamic social structures, and complex social relationships. Differences in life history patterns, behaviour, and reproduction strategies are compared across in situ Western lowland gorillas (iWLG), in situ Virunga Mountain gorillas (iVMG), and the ex situ population of Western lowland gorillas (eWLGs). Understanding these social-ecological differences, presumed to be due to adaptations to their diverse environments, this cross-gorilla comparison holds significant importance for conservation, reintroduction, and management. Therefore, understanding between-subspecies and environmental differences will help to interpret personality differences among gorilla subspecies and their environments (Chapter 4) and identify implications and recommendations in the context of a One Plan Approach (OPA) for positive welfare specifically for ex situ gorilla care (Chapter 5) and more general for gorilla conservation strategies (Chapter 6).

2.2 Taxonomy & Morphology

2.2.1 Taxonomy

Gorillas (genus *Gorilla*) once belonged to the Pongidae family with *Pongo* (orangutans) and *Pan* (chimpanzees and bonobos) - the *Hominidae* family was restricted to *Homo* (humans) (Groves, 2001). Recent molecular techniques have provided new insights in the evolution of these four genera. Gorillas are more closely related to humans (genus *Homo*, with 1.6% nuclear DNA; and 10.3% mitochondrial DNA difference) than chimpanzees (genus *Pan*, with 1.8 % nuclear DNA, and 10.6% mitochondrial DNA difference, Hayasaka et al., 1988; Koop et al., 1989). Much of the human genome is, however, closest to the chimpanzee genome on average. A significant minority, 15 percent, is closer to the gorilla, and another 15 percent is where gorilla and chimpanzee are closer to each other (Scally et al., 2012). According to the genetically close relationship, Groves (2001) included these African apes (*Gorilla* and *Pan*) plus humans into a subfamily called *Homininae*. Genetically closest are chimpanzees (*Pan*) and humans (*Homo*), who differ 1.2 % in the nuclear DNA, and 8.8 % in the mitochondrial DNA (Koop et al., 1989). Today, all four of the genera (*Homo, Pan, Gorilla and Pongo)* comprise the *Hominidae* family, also known as the great apes, and within the *Hominoidae* superfamily. Great apes differ from the *Hylobatidae* (*Hylobates*, gibbons) being heavier with larger bodies and brains (Groves, 2001).

2.2.2 The Genus *Gorilla*

Groves' first comprehensive study on gorilla taxonomy was released in 1970, and he included three subspecies of gorillas into the genus *Gorilla*: *Gorilla gorilla gorilla* (Western lowland gzorilla = WLG), *Gorilla gorilla beringei* (the mountain gorilla = MG), and *Gorilla gorilla graueri* (the Eastern lowland gorilla = ELG). Genetic research (Garner & Ryder, 1996; Groves, 2001; Ruvolo et al., 1994) adjusted this earlier taxonomy and reclassified the genus into two species, the Eastern (*Gorilla beringei* = EG) and Western gorillas (*Gorilla gorilla* = WG) (see **Figure 3**). The two Eastern subspecies (*G.b. graueri* and *G.b. beringei*) are separated by approximately 1,000 km, and it is believed that these subspecies diverged around 1.2 – 3 million years ago (M. Robbins et al., 2016; Yamagiwa et al., 2003). The classification of the species was justified by a variety of physical traits but also by genetic separation (Garner & Ryder, 1996). According to (Butynski, 2001), the genetic divergence between EG and WG is greater than that identified between chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). There are four distinct subspecies recognized in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (2013): two subspecies of EGs - the ELG and MG; and two subspecies of WGs - the WLGs and the Cross River gorilla (CRG = *Gorilla gorilla diehli*), which separated approximately 18,000 years ago (Prado-Martinez et al., 2013; Thalmann et al., 2011).

2.2.3 Morphology

Gorillas are among the world's largest primates, and they share many features with humans and other primates (Gregory, 1950; Groves, 1986). Their hands and feet more closely resemble those of humans than those of any other ape, which is a genetic adaptation to their way of locomotion and greater territoriality (Ruff et al., 2021). The short distance between their big toe and other toes makes them better walkers on their knuckles than other primates (Tuttle, 1985).

Multiple external features separate the species (Meder & Groves, 2012). WGs have a noticeably wider jaw compared to EGs. Adult WG males have a silvery back that goes all the way down to their hips and upper thighs. Both male and female WGs may have hair with a grey or brownish tinge, in contrast to the typically dark black hair of the EG (apart from the silvery back of the males). On average, adult male ELGs are the largest of all gorilla subspecies, characterized by longer limbs and a slimmer body compared to MG (Rutt et al., 2021). The differences seem to result from locomotor gradience. As an adaptation to the colder mountain habitat and territoriality, MG have short limbs and are more robust build as well as longer, shaggy hair (Harper et al., 2021). Western LG being the smallest of all subspecies, with shorter limbs and have more compact bodies, adapted to their arboreality with greater joint mobility with ELG being intermediate between WLGs and MG due to the transition towards arboreality (like WLGs) (Harper et al., 2021; Knigge et al., 2015). The CRG show adaptions to their forested habitat in terms of long bone proportions, shorter hands and feet and smaller dentitions, palates, and cranial vaults (Sarmiento & Oates, 2000; Stumpf et al., 2002).

Due to the silvery colouration of their back hair, adult males are referred to as silverbacks. Additional secondary sexual characteristics seen in males are the long arm hair, long canines, and a sagittal crest (Breuer et al., 2009; Dixson, 1981), which is responsible for the mitre-shaped head (Schultz, 1969). Long, strong chewing muscles coming from the mandible attach to the sagittal crest (Gregory, 1950). The head of a mature male is crowned by a large pad of skin, and a fibrous, fatty deposit mass at the back of the head (Dixson, 1998). Except for the very large and pointed canines of mature males, their teeth are strikingly like ours (Abelló et al., 2017). Those canines are used as weapons in fights, the strong chewing muscles and therefore a strong bite also when protecting against predators or in fights. They also have a sizable colon and caecum, perhaps with symbiotic microbes (Collet, 1984; Tutin et al., 1991) allowing gorillas to digest their large amounts of almost exclusively vegetarian material, including plant items, such as fruits, leaves, flowers, roots, stems, pith, and bark.

WLGs weigh an average of 140–160 kg, a MG male weighs 150–160 kg, and ELG males weigh 160–180 kg, but rarely more than 200 kg. CRG are said to weigh up to 200kg as well. Females typically weigh 70-110 kg with extensive individual and subspecies variation, with males being twice the size of females (Caillaud et al., 2008; Harcourt & Stewart, 2007). Size and external body features of adult males and females exhibit a strong sexual dimorphism, in size and colouration (Breuer et al., 2007; Caillaud et al., 2008). EWLG (Ex Situ WLG) males can weigh up to 200kg and females show extremely developed head crests in comparison to in situ conditions (Caillaud et al., 2008).

2.3 Distribution and Conservation Status

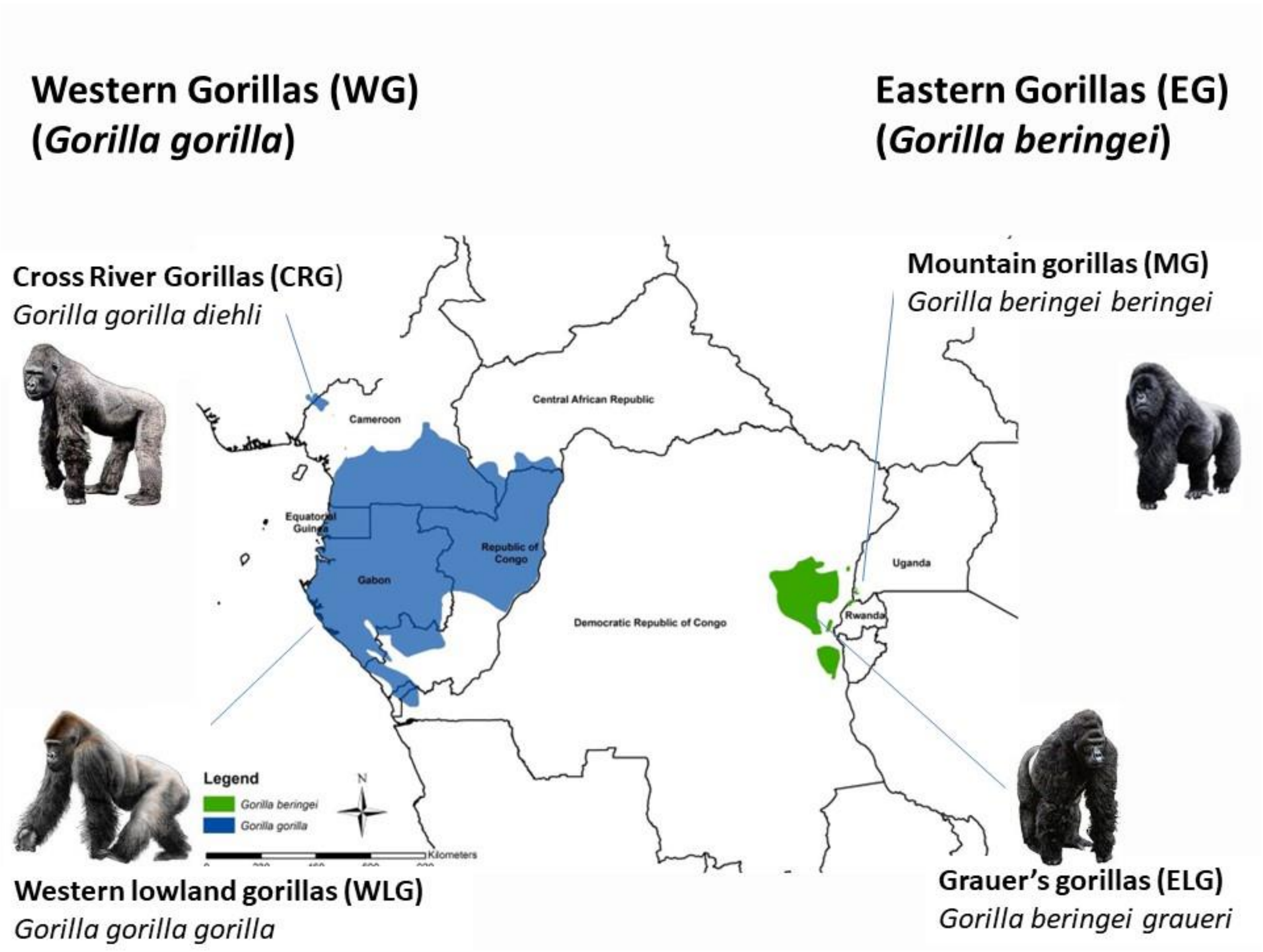


Figure 3 *Distribution of gorilla subspecies across Africa*

Note.
Graphic is (M. Robbins et al., 2016), Fig 3, (M. Robbins et al., 2016), blue area = iWLGs, green area= iVMGs.
Graphic of the images of the gorilla subspecies (© *https://gorillafoundation.nl/species/*)
EG= divided into MG and ELG, WG= divided into CRG and WL.

According to IUCN criteria A (A4bcd), ELGs are Critically Endangered (IUCN, 2018a). They can only be found in multiple isolated populations in the Democratic Republic of the Congo. Recent studies indicate that the population has declined to a low of 6,800 individuals from an estimated 16,900 in 1994-1996 in only one generation, a decline of 60%, and with a bleak forecast (Plumptre et al., 2021). Poaching for bushmeat connected with mining and commercial trade as well as ongoing civil conflicts had a devastating effect on ELGs over the last 20 years (Plumptre et al., 2016, 2021). The largest population is found in Kahuzi-Biega National Park (Yamagiwa et al., 2012).

The MGs are the only great ape taxon that has seen their in situ numbers rise (Gray et al., 2013). There were as few as 273 in 1973 (Gray et al., 2013), but their status is still endangered because of their low numbers. According to a survey conducted in 2015-2016, the Virunga population has expanded to over 600 MGs, bringing the total population (VMGs and the Bwindi gorillas = BMGs) to almost 1,000 in 2018 (Hickey et al., 2019). MGs are located within the Greater Virunga Landscape, which consists of 11 protected areas spanning Uganda, Rwanda, and the Democratic Republic of the Congo (Plumptre et al., 2007). Mgahinga Gorilla National Park (MGNP) in Uganda, the Mikeno sector of the Parc National de Virunga in the Democratic Republic of the Congo (PNVi, DRC), and Volcanoes National Park (VNP) in Rwanda all contribute to about 450 km^{2}in total. The geological area pertaining to the Albertine Rift counts as one of the most species- and endemic- rich landscapes in Africa (Plumptre et al., 2003) however, it is also surrounded by one of the most populated local communities.

The VMGs inhabit the highest elevational range of all gorilla populations (> 2,500 m). The BMGs, the second population, live in southwestern Uganda at the Bwindi Impenetrable National Park (< 40 kilometres apart from the Virunga massif) and in the Sarambwe in DRC at lower altitudes of 1,400 – 2,500m (McNeilage et al., 2006; A. Robbins et al., 2011; M. Robbins & McNeilage, 2003). A protected area of 165 km^2 which is situated in the VNP in the Rwandan component, between the latitudes of 1°21' and 1°35' south and the meridian lines 29°22' and 29°44' east (Plumptre et al., 2004) contains the VMGs. This is where the data for the personality study was collected by Winnie Eckhart which were compared to the WLG's personality in this thesis.

The distribution of WGLs includes Equatorial Guinea, Gabon, Nigeria, Cameroon, the Central African Republic, Central Republic of Congo, and Angola. Habitat types range from coastal scrub, primary forest, thicket, undisturbed secondary vegetation, to swampy forests covering over 700,000km^2. As of 2013, a global population of about 361,919 iWLGs (in situ Western lowland gorilla) was estimated by Strindberg and Colleagues (2018). Further estimates from IUCN state the number of WLGs at 316,000 in 2018 (IUCN, 2018b). Results of a survey across the entire range of the iWLG revealed a 19.4% decline between 2005 and 2013, corresponding to an annual loss of ~2.7% (Strindberg et al., 2018). Over three generations (i.e., 66 years, 2005-2071), the population is expected to decrease by more than 80% at a conservative rate of decline (2.7% per year rather than 4%, calculated from Walsh et al. 2003). The widespread clearing of iWLG habitat for industrial agriculture, an increase in poaching with the development of new pathways into forests, and the disease risk posed by the Zaire Ebolavirus contributed to being classified as Critically Endangered (Walsh et al., 2005).

The second WG subspecies, the CRG, is notably less well-known and the rarest of all gorillas (Groves, 2001). Less than 300 individuals are thought to exist (IUCN, 2018b; Oates, 2007), and their range is confined to about 12,000 km^2 of woodland region between Nigeria and Cameroon (Bergl & Vigilant, 2006). Sub-populations are dispersed and surrounded by some of Africa's most populated local communities (Bergl & Vigilant, 2006). Thus, the CRGs are also classified as Critically Endangered according to criteria A (IUCN, 2018b).

2.4 Ecological Comparison of Gorilla Subspecies – an In situ-Ex Situ Comparison

In this section, I provide an overview of the ecological distinctions between two in situ subspecies: the iWLG and iVMGs (**Table 1**). I elucidate these variances to differentiate them from eWLGs, laying the groundwork for discussing in Chapter 5 how socio-ecological factors might influence the disparities in personality structures among these populations. I start with ecological variability, such as habitat variations, resource availability, activity patterns, foraging strategies, and diet.

2.4.1 Ecology in iWLG

IWLGs live in deep primary forest, swamp forest, thicket, undisturbed secondary vegetation, exploited forest, and coastal scrub (Tutin & Fernandez, 1984). Although WG is classified as a folivore-frugivore (A. Robbins et al., 2011), this subspecies favours fruit. Foraging for fruit requires a comprehensive grasp of the environment, including familiarity with a broad home range. IWLGs demonstrate a knack for optimizing their travel patterns in pursuit of this necessity (Salmi et al., 2020). Space use (travel distances, range, and revisitation patterns) and therefore increased effort to reach fruit depends on the availability of fruits. In times of low availability, costs for foraging in terms of long-distance travels are higher (Salmi et al., 2020; Seiler & Robbins, 2020). Nishihara (1995) noted that the WLGs at Nouabalé-Ndoki National Park eat 20-40% fruit during the non-fruiting season (October to May), but up to 80% during the fruiting season (April to September). However, during the dry season when fruit is sparse, other non-reproductive “fall-back foods”, such as terrestrial herbaceous vegetation (THV) of which leaves, bark, and piths are ingested at high rates (Doran et al., 2002; Doran-Sheehy et al., 2009; Masi et al., 2009; Rogers et al., 2004). This seems to hold in other areas as well (Salmi et al., 2020; Seiler & Robbins, 2020). Invertebrates are also eaten regularly (Doran-Sheehy et al., 2009; Tutin & Fernandez, 1985, 1992; Williamson et al., 1990). Even though diet composition varies throughout different locations where WLGs live, the nutritional content of main food items is comparable, indicating that WLGs eat similar foods to suit their dietary demands (M. Robbins et al., 2022). Therefore, the nutritional flexibility of the widely distributed WLGs, may help explain life cycle variance and inform conservation management approaches.

IWLG ranging and activity patterns are affected by the seasonal availability and clumped distribution of fruit (Masi et al., 2009; Salmi et al., 2020; Seiler & Robbins, 2020, Doran & McNeilage, 2001). A group's daily travel distance range varies between 1.5–2 km but may expand during fruiting seasons (Bermejo, 2004; Doran-Sheehy et al., 2004; Goldsmith, 1999; Remis, 1997). Home ranges vary in size from 11 km^2 in Lossi, Republic of Congo (Bermejo, 2004) to 22.9 km^2 at Bai Hokou, Central African Republic (Remis, 1997). Inter-site habitat, seasonality, individual preferences, and resource availability may explain this variance (Seiler & Robbins, 2020). Home ranges are overlapping between different groups, intergroup encounters are low, and competition is more about mates than food (Kuroda et al., 1996; Remis, 1994; Tutin, 1996).

2.4.2 Ecology in iVMG

The VMGs of the VNP in Rwanda have been studied extensively since 1967. Therefore, most of what we know about gorilla behaviour stems from this study population monitored by researchers and other field staff of the Dian Fossey Gorilla Fund’s Karisoke Research Center, the world longest running gorilla research program. Today’s study groups are descended from groups the initially habituated by Dian Fossey resulting in over 55 years of long-term data on demography, behaviour, ranging patterns, and health. VMGs have the most folivorous diet of all gorilla populations, and their habitat provides rich and high-quality herbaceous vegetation throughout the year (McNeilage, 2001; Watts, 1984). Between group size and home-range form a quadratic relationship (Grueter et al., 2018). Larger groups show lower travel distances and higher energy intake rates, improved foraging efficiency, and lower home range overlaps with other groups, due to group avoidance in terms of male mating competition. Intermediate-sized groups had the lowest foraging efficiency, indicating non-linear relationships between group size and foraging efficiency in primates (Grueter et al., 2018).

About 60% of groups in the Virunga massif population are habituated and monitored daily by different field teams. Protecting, monitoring, and studying habituated populations is a top priority for the Karisoke Research Centre (KRC) and the government through the Rwanda Development Board (RDB).The presence of researchers and protection of the groups seem to be one of the driving forces for population growth (Granjon et al., 2020). IVMG can be identified by their unique nose prints, facial markings, and scars, as well as by their bodily characteristics, such as their size, hair colour, and the degree of syndactyly of their toes, as well as from individual differences in terms of their personalities (Eckardt et al., 2015).

Table 1 *Intra-specific and inter-specific variation in the ecology of iWLG and iVMG*

	In situ WLGs (by location)	**Literature iWLGs**	**In situ VMG (by location)**	**Literature iVMGs**
Home range size in km^2	[a]Mondika: 15.4 [b]Bai Hokou, 15.9 (13.1-18.1) [a]Loango NP: 14 (12.3-15.3)	[a]Seiler et al., 2018 [b]Arandjelovic et al., 2010	[c]iVMG: 8.1 (3.2-23.6) [d]Bwindi Imperial National Park (BINP): 10.0 (4.1-22.9)	[c]Caillaud et al., 2014 [d]Seiler et al., 2018
Daily travel distances	[a]Mondika: 2.0 (0.1–4.9) [e]Bai Hokou, 1.5 (0.3–3.0) [a]Loango NP: 2.6 (0.4–7.6)	[e]Cipolletta, 2003	[c]iVMG: 0.8 [d]BINP: 1.0 (0.1–6.5)	
Herb density per m^2	[f]Mondika: 0.78 [g]Bai Hokou, 1.11 [a]Loango NP: 0.22	[f]Doran-Sheehy et al., 2004 [g]Wright, 2015	[h]iVMG: 8.8 [i]BINP: 4.4–10.6	[h]Ganas et al., 2004 [i]Watts, 1984
Gorilla density per km2	[j]Mondika: 4.48 [g]Bai Hokou, .90 [b]Loango NP: 0.82–1.06	[j]Head et al., 2011	[i]iVMG: 1.0 [i]BINP: 1.0	[i]M. Robbins & Robbins, 2018
Habitat type[d]	Forest: subtropical/ tropical moist lowland, swamp and montane		Forest: subtropical / tropical moist lowland, swamp and montane	
Temperature	23–27 C	[j]Head et al., 2011	Temperature: being a function of elevation, little seasonal variation Increase approx..2.1 C/ year leading to lower seasonality and longer dry periods. iVMG: T: 21.4 +/-1.2 BINP: 22.8 +/- 1.2	Eckardt et al., 2019 Nsubuga & Rautenbach, 2018 Wright et al., 2022
Influence of climate change	Warmer climate, thus climate change may lead to higher disease risks	Gurven et al., 2016		
Rainfall			Bimodal rainfall distribution (March- May: heavy rain; September-November: lighter rains iVMG: 36.4mm +/- 31.8 BINP: 32.0mm +/- 31.6	Eckardt et al., 2019 Wright et al., 2022
Elevation			iVMG: > 2,500m BINP: 1,400 – 2,500m	M. Robbins & McNeilage, 2003 McNeilage et al., 2006 A. Robbins et al., 2011
Seasonal fluctuation of food[d]	high	Doran-Sheehy et al., 2009; Salmi et al., 2020; Seiler & Robbins, 2020	iVMG: absent to low BINP: higher space use	[d]Seiler et al., 2018
Diet/ drinking			Food comprises 60-90 % of water	Grueter & Stoinski, 2016
Diet/ energy [b,f,i]	[k]frugivorous (30–35%) which might limit group size 10-70% fruits, 20 % leaves, stems, and other matters, 1 – 2 % small animal matters	[k]Yamagiwa et al., 2003 Doran-Sheehy et al., 2009; Masi et al., 2009; M. Robbins et al., 2022	folivorours[d] 70-80% leaves, buds, shoots, stems, vines, 20 – 30 % other plant matters, 0.5 – 2 % small animal items, fruits (<1%)Watts (Bwindi: fruits 10-15%)	[d]Seiler et al., 2018 [k]Yamagiwa et al., 2003 [k]Watts, 1984
Time spend in feeding[i]	67%, females and immatures spend more time 12%	[i]Masi et al., 2009 [k]Yamagiwa et al., 2003	55%, males spend more time feeding	
Time spend travelling[i,d]	21%, females and immatures spend less time		6.5% 34%, may be due to fermentation of fibers	
Time spend resting[i]	0.5%			
Time spend in social activities[i] and others[i]	more often seen as in iVMGs, still rare		3.6%, may be possible due to longer resting times	
tool use[10,11,12]			rare, due to diet	
Difference in energy intake	Fruit consumption may lead to temporal changes	Wright, 2015	No difference between season	Grueter et al., 2014
Predation risk	Presence of leopards	Klailova et al., 2013	No longer available	Klailova et al., 2013

2.4.3 Ecology in eWLG

The EAZA Best Practice Guidelines (BPG) for Gorillas from 2017 (Abelló et al., 2017) provides the background for the social and ecological information on the ex situ gorilla population. I use these guidelines to discuss the potential differences in the personality structure between the ex situ and in situ population of WLGs. In addition, I argue that the integration of knowledge on personality in future Best Practice Guidelines may be useful for the individual's welfare levels, as well as for breeding and housing management. Furthermore, such an integration could help build a healthy ex situ population for in situ conservation. (Abelló et al., 2017).

Feeding ecology

To flourish, zoo gorillas require diets closely modelled on those of in situ gorillas (Abelló et al., 2017, p.58). However, the composition of in situ fruits and cultivated fruits fed to zoo-kept gorillas can differ (Allen & Oftedal, 1996; Schwitzer & Kaumanns, 2003).

Zoo gorillas may have dietary adaptations to their digestive systems (Chivers & Hladik, 1984; Popovich et al., 1997) and adaptations in feeding behaviour that not only permit the digestion of nutrition particularly rich in fibre but may even require it. Research on the dietary preferences of eWLG has shown that these great apes gravitate towards food that is rich in calories but low in dietary fibre and protein, as well as those that have a high sugar-to-fibre ratio (Abelló et al., 2017). It is believed that gorillas can tolerate significant quantities of tannins because their taste inhibition threshold for tannins is high, and this threshold rises with sugar concentration (Remis & Kerr, 2002). Zoo housed gorillas may like sweet fruits and "regard" those with moderate tannin levels as tasty (Abelló et al., 2017). It is possible that iWLGs have a similar preference for high-calorie foods but lack consistent access to their favourite fruits in situ. According to Less et al. (2014), this preference for sugar-rich diets in zoo gorillas causes obesity and dental issues. Fat and carbohydrate levels of both ex situ-and in situ diets are comparable, but the fibre and protein content are quite different (Abelló et al., 2017; Hampe, 1999). A major consideration in the development and improvement of zoo gorilla diets is to add more foods high in fibre and protein (Abelló et al., 2017).

The EAZA BPG (Abelló et al., 2017) for gorillas specifies: a quantity equivalent to 4.5% of the gorilla body mass and a composition of 70% vegetables, 15% browse, and a maximum of 15% dry high-fibre primate biscuits. The length of time for search, manipulation, processing, and feeding should be maximised, with the help of four daily feeding times as a minimum. Monopolisation of multiple food items by one or few gorillas should be prevented, such as by feeding whole items and prolonging the feeding procedure.

2.5 Social Comparison of Gorilla Subspecies – an In Situ-Ex Situ Comparison

Similar to other non-human primates, the social organization of gorillas, for example the group size, the composition, their relationship, life history, intergroup-interplay and competition is shaped by a multi-faceted cultural interplay of ecological factors, habitat saturation, predation, and infanticide avoidance (Isbell & Young, 2002; Kappeler & Schaik, 2002; M. Robbins et al., 2023; Sterck et al., 1997; Wrangham, 1980). Environmental variety also results in significant behavioural changes (Masi et al., 2009; Tutin, 1996), and cultural traits have been described between the subspecies of iMGs and iWLGs (M. Robbins et al., 2016) as caused by socio-ecological factors.

Within the following section, I highlight differences in the social structure, relationships, and life history patterns between iWLGs, iVMGs and eWLGs. For Intra-specific and inter-specific variations in the socio-ecology of the two in situ populations (iWLG and iVMG), see **Table 2**.

Longitudinal research on gorillas has shown that their social structure is based on four social units: (1) **single-male reproductive groups** (harem groups) and (2) **multi-male reproductive groups**, (3) **non-reproductive groups** (mainly all-male, but can include non-reproductive adult females, Robbins, 1995), and (4) **solitary silverbacks** (M. Robbins, 1995).

2.5.1 Social Units

2.5.1.1 Reproductive Groups

A reproductive group is established when a fertile female joins an adult Silverbacks (SB) (M. Robbins, 1995).

2.5.1.1.1 Single-male Reproductive Groups (SMRG)

Most (~95%) of iWLGs' social structure consists of a single male, a small number of adult breeding females, and their offspring (Breuer et al., 2010; Gatti et al., 2004; Parnell, 2002), whereas 60 % of iVMGs are single male groups (Robbins et al., 2016).

2.5.1.1.2 Multi-male Reproductive Groups (MMRG)

Groups containing more than one adult SB are rare among iWLGs (5%), but common in iVMGs (40%, Kalpers et al., 2003; McNeilage et al., 2006). The majority of MMRGs, which are characterised by the presence of several adult SB males and at least one breeding female, typically consist of just two adult males, several adult females and their offspring. However, in exceptional cases, these groups may include as many as nine adult SBs in iVMGs (Rosenbaum et al., 2011).

Male iVMG's remain in their natal group or disperse, resulting in the development of a social structure typified by the coexistence of groups consisting of either a single male or multiple males. The occurrence of this combination is a rare phenomenon within the primate hierarchy, hence enhancing the unique characteristics of iVMGs.

2.5.1.2 Non-Reproductive Groups/ Bachelor Groups (NRG)

Non-reproductive groups exist for in situ MG and WG (Gatti et al., 2004; M. Robbins et al., 2004). They are also common in groups of eWLGs which may have up to 20 individuals.

2.5.1.3 Solitary Silverback (SS)

In iWLGs, a period of solitary travel is required by all young SB prior to reproduction, until they successfully attract a female from another male to create their own harem (M. Robbins et al., 2004; Stokes et al., 2003), typically no earlier than 18 years of age (Breuer et al., 2009). According to Manguette (2022, pers. comm.), it usually takes between 2 and 10 years to become a reproductive male and form a group. Adult SS rarely join or gain control of an established breeding group.

2.5.2 Social Systems in Gorilla Subspecies

The life cycle of female and male Western lowland gorillas (WLGs) encompasses several distinct stages and behaviours, each playing a crucial role in their development, reproduction, and survival.

Reproduction

There is no specific mating period in gorillas, thus births and mating occur all year around. The female gorilla enters oestrus in the middle of her cycle. When females attain sexual maturity, they generate a hormone cycle (akin to the human menstrual cycle) that lasts between 26 and 32 days (Abelló et al., 2017). Females approach males (occasionally young males and even females) to instigate reproduction, whereas other gorillas attempt to increase contact with the fertile female, too. As in humans, if the egg is not fertilised, the uterine mucous membrane is expelled out of the body with monthly menstruation. The duration of bleeding is two to three days and is significantly lower than in humans.

2.5.2.1 Life Cycle and Maturation in iWLGs

Weaning and maturation

During birth, both males and females have a weight just over 2 kg and undergo similar rates of growth until around seven years old. For weaning and maturation period, infant gorillas typically remain within their natal groups. Notably, WLGs exhibit an extended suckling period of approximately 4.6 years, resulting in older infants after weaning in comparison to iVMGs (Breuer et al., 2009). Weaned but not yet puberty, juveniles are between the ages of four and seven ½. Subadults are those who are between the ages of seven ½ and ten (females) or eleven (males), or between puberty and fertility. Male and female developmental trajectories differ at this point (Watts and Pusey, 1993). Females mature around the age of ten, males turn into blackbacks (BB) between the age of eleven and fourteen, whereas the young male begin to develop secondary sexual characteristics by the age of 9 years. They continue to grow musculature, their BB turns silvery, and their sagittal crest turns reddish. This is part of maturing and lasts until 18 years of age. More information on developmental stages, see above in part Morphology. In general, iWLGs face lower survival chances (50%, in contrast to iVMGs with 73%, Breuer et al., 2010). Although infant mortality tends to be higher in the first few years of life, there are no discernible differences between sexes in infant survival (Breuer et al., 2010).

Dispersals of matured females and male iWLGs

Female dispersal

Adult females invariably leave their natal groups around the age of 12.2 years (Robbins et al., 2013), with the earliest known emigration occurring at 10 years, primarily to avoid inbreeding (Manguette, Breuer, et al., 2020). On average, females give birth to their first offspring at the age of 12 years (typically between 11-13 years**,** Manguette, Breuer, et al., 2020). It was also observed that nulliparous females, irrespective of their relationship with the dominant male, disperse before their first pregnancy (Manguette, Breuer, et al., 2020). These transfers usually involve moving to another group or forming a bond with a solitary SB. Female WLGs typically do not range on their own (Harcourt & Stewart, 1987).

Secondary dispersal: In contrast to iVMGs, females of iWLGs have developed strategies to enhance their reproductive success by employing counterstrategies to minimize the costs of sexual coercion. Therefore, secondary dispersal by female iWLGs is considered a mate selection strategy to mitigate the risk of infanticide, reduce feeding competition, and increase mate choice, a behaviour observed more frequently in gorillas compared to other primates (Manguette, Breuer, et al., 2020). Such dispersal, while not without costs (e.g., reproductive costs, exposure to predators, lower habitat quality), offers numerous benefits (e.g., long-term reproductive success, increased protection from predators, better habitat quality, more resources, and superior males) (Manguette, Breuer, et al., 2020; Manguette et al., 2019; Manguette, Robbins, et al., 2020). Secondary transfers by individual female gorillas have been noticed in 20 years of observation (Manguette pers. communication, 2022) but varied widely. Some females remained in a group for 20 years, others left after a few weeks, and again others might never transfer. The phenomenon of secondary dispersal is categorized into two types: voluntary and involuntary.

Voluntary secondary transfer**:** Voluntary secondary dispersals have a significant impact on the reproductive group's lifespan, with females transferring from an adult solitary SB to a reproductive single-male group, or another solitary SB based on their choice (Manguette, Robbins, et al., 2020). Transfer rates tend to be higher when the group size is larger (Stokes et al., 2003; Tutin, 1996, Manguette, Breuer, et al., 2020), indicating the influence of intra-group foraging competition or the avoidance of outsider males and predators. Female iWLGs are more likely to stay with younger males at the beginning of their tenure rather than relocate, and the tenure length plays a role in their decisions. Age also plays a significant role in females' decisions, as they prefer younger males. Female iWLGs who transfer before the last five years of the leading SB's tenure experience a higher infant survival rate (approximately 60%) compared to those who stay with the older SB in his last five years (20%). As a result, transferring after a five-year inter-birth gap can be challenging, as females have only a few months between weaning and conceiving a new infant. Transferring multiple times can lead to longer inter-birth intervals and reduced birth rates (Manguette et al., 2019; Manguette, Breuer, et al., 2020; A. Robbins & Robbins, 2015; Sterck et al., 2005). Additionally, transferring does come with a cost, as it increases the length of the interbirth-intervals after transfer for approximately 5 months, and negatively affects the birth rates after transferring multiple times (Manguette et al., 2019). Results show that zero transfers end in one surviving infant every 7 years, whereas e.g., 4 transfers end in one surviving infant every 17 years (Manguette, Breuer, et al., 2020; Manguette et al., 2019). Findings indicate that pregnant iWLGs females have the potential to relocate to a different group without experiencing infanticide from a male, provided that this relocation occurs before the midpoint of the gestation period. These results underscore the adaptable behaviour exhibited by these females in reaction to male sexual coercion (Manguette, Robbins, et al., 2020). Species, whose females depend on within-group kinship and the capacity to create and sustain social relationships over long time spans, such as philopatric species, or multimale species (iVMG), stay in contrast to the secondary transferal strategy in iWLGs (Manguette, Robbins, et al., 2020). The transfer of females is some sort of intersexual power of females in contrast to the sexual coercion by males, (Manguette, Robbins, et al., 2020).

Females choose males capable of protecting them and exhibiting competitive abilities, further increasing their chances of reproductive success (Manguette, Breuer, et al., 2020). The dynamics of dispersal decisions are complex (earlier infant loss; group age; group size, and therefore intra-group feeding competition; male competitive ability; attractiveness towards males or predator outside the group), and are influenced by multiple factors, making it challenging to discern the individual effects of each factor **(**Baudouin and al., 2019; Breuer et al., 2012; Manguette, Robbins et al., 2020; Stokes et al., 2003). It has also been shown that male phenotypic features such as crest size **or** higher-quality males, as supported by evidence that groups with larger SBs have more female gorillas and lower infant mortality rates (Caillaud et al., 2008, Breuer et al., 2010). According to Doran-Sheehy et al. (2009), when multiple females are attracted to the same male, as often happens early in the tenure of a SB, increased competition for mating opportunities and intra-group feeding rivalry or avoidance of extra-group males and predators may occur**.** Therefore, female iWLGs face a trade-off between staying in their group and transferring. They should transfer to young protective males to improve their reproductive success, reduce the risk of infanticide, and minimize the risk of predation if the male has low competitive ability near the end of his tenure (Manguette et al., 2019).

Involuntary secondary transfer by group disintegration

Following the death of the SB, female involuntary dispersal occurs when females are forced to join an extra-group male or a group. This situation poses a high risk of infanticide (Manguette, Breuer, et al., 2020; A. Robbins et al., 2013; Stokes et al., 2003; Watts, 1989). Under normal circumstances, females do not transfer voluntarily when they have dependent offspring due to the risk of the offspring's death (A. Robbins & Robbins, 2015).

Risk of infanticide

Infanticide is a potential risk if the infant transfers with its mother and is under four years old, as the new silverback may likely kill the infant (M. Robbins & Robbins, 2018; Watts, 1989). Infanticide rates following group disintegration are around 12% (Breuer et al., 2010). However, some studies have documented females' dispersals with unweaned infants to new silverback males without any negative consequences for their offspring (Stokes et al., 2003; Yamagiwa & Kahekwa, 2001). This contrasts with the behaviour of iVMGs and may be attributed to variations in male competitiveness, protectiveness, familiarity between males from different groups, or their personality (further research is needed).

If the infant is older than four years, it is likely that the infant alone joins a non-breeding group and has a higher chance of survival, there. In case of a young iWLG, the female matures then in the non-breeding group after disintegration and transfers for a second time out of the “survival group” to become a breeding iWLG female to a breeding group or a single silverback. Non-fertile females sometimes also join a non-breeding group for safety reasons. In the case of a young male infant gorillas older than 4 years of age, they may also independently join non-breeding groups. These non-breeding groups are highly flexible in terms of composition, accommodating both sexes.

Male dispersal

Solitary phase and development in male gorillas

Around 15 years of age (between 14-21 years), when males become young SBs, all iWLG males experience natal emigration (Breuer et al., 2009). The mechanism behind the dispersal of maturing males from their social group, whether it is due to the influence of an adult SB or a voluntary decision, remains incompletely comprehended. Nevertheless, observations have indicated that these young SBs progressively occupy more peripheral positions within the group prior to their eventual transition to a solitary state (Parnell, 2002; M. Robbins et al., 2004). A later age of maturation than the physical development may partially explain why iWLG populations lack multi-male groups, as a male's tenure may not last long enough for his male progeny to attain maturity (Breuer et al., 2009).

However, the transition from the natal group is a significant phase in the life cycle of male gorillas, which involves a period of solitary existence before attaining reproductive status. This phase is essential for developing the skills necessary to become a leading male and, thereby preparing them for intra-sexual competition for access to limited resources, females, or food. Simultaneously, it serves to mitigate the risks of inbreeding and reproductive competition (Breuer, 2008; Greenwood, 1980; Perrin & Mazalov, 2000). Adolescent males during this phase must grapple with trade-offs as they face potential survival challenges. While ranging alone, they become more vulnerable to predation (Alberts & Altmann, 1995). However, they also acquire vital knowledge about the accessibility and dispersion of food resources within their habitat and enhance their competitive capabilities. This period of solitude contributes to decreasing uncertainty regarding their competitive abilities and is an invaluable source of experience (Fawcett & Johnstone, 2010; Sachser et al., 2013; van Schaik & Burkart, 2011). It is noteworthy that this dispersal primarily occurs within a limited geographical range relative to the original group (Bradley et al., 2004). The analysis of genetic relationships among WLG males from several groups revealed compelling evidence indicating that the harem leader tends to exhibit genetic relatedness with one or more neighbouring males. As a result, males belonging to the same family may establish overlaps of territories and meet each other. It has also been observed that there are also still playful behaviours happening between peripheral young and maturing SBs. This solitary phase can last up to 10 years (2-10 years), although the duration varies among individuals (Breuer et al., 2009). It is noteworthy that transitions occur in both directions (single male or bachelor groups), allowing males to shift between non-breeding and solitary SB statuses. However, direct transitions to a reproductive group are typically less common before the age of 18-25, when solitary SB may successfully acquire females and establish a single-male reproductive group (Breuer et al., 2009; M. Robbins et al., 2004; Stokes et al., 2003). A solitary SB will rarely join or take over a pre-existing breeding group and group takeovers have been observed by a son of a reproductive SB (Marie Manguette, Nov. 2022 personal communication).

Breeding males

A breeding group starts when a single male successfully acquires females. This leading reproductive single-male gorillas, often referred to as harem leaders, play pivotal roles in protecting females and their young from predators and providing stability, leadership, and safeguarding against infanticidal males (Fossey, 1983; M. Robbins et al., 2007). These leaders typically maintain their tenure for over 20 years, with age and male aggressiveness acting as key predictors of their competition strategies. Harem leaders and solitary SBs tend to exhibit lower levels of aggression towards kin or individuals with whom they are familiar. Phenotypic traits are responsible for higher reproductive success and larger harems, such as being larger or having a bigger crest (Breuer et al., 2010, 2012, 2021; Caillaud et al., 2008).

Transition between non-breeding and solitary silverback status

Between the age of 30-40 breeding males start losing their females. However, males that have lost their females can acquire new females, thus a change between solitary and reproductive groups happens in both directions.

Life history summary

IWLGs usually have one infant every five years and have slower physical growth and higher mortality compared to iVMGs (Manguette, Breuer, et al., 2020).

2.5.2.2 Life Cycle and Maturation in iVMGs

Weaning and Maturation

In situ VMGs exhibit earlier weaning, with a mean weaning age of 3 years and 7 months compared to iWLGs with a mean of 4 years and 9 months (Breuer et al., 2009). This difference may be attributed to ecological factors, including abundant and uniformly distributed foliage, which is a characteristic feature of the iVMG habitat (Fossey & Harcourt, 1977; Mcneilage, 1995; Vedder, 1984; Watts, 1984). Variations in milk quality have been considered a factor contributing to differences in weaning age. Therefore, iVMGs may produce higher-quality milk, which, in turn, could lead to faster growth rates and earlier developmental milestones. However, it is essential to note that there exists significant variation in weaning age within MG populations (Eckardt et al., 2015). Juveniles who have been weaned but have not yet reached puberty are typically between the ages of three ½ and six. Subadults are classified between the age of six to eight (Breuer et al., 2009). In social MG groups with multiple gorilla males, interactions depend on personalities and histories, creating a tension that escalates as younger males reach adulthood (young SB, between, 12-15 years). Immature males closely associate with the dominant SB (older than 15 years), grooming him, but as they become BB (between the age of 8-12), they spend less time near the older male and face increasing aggression from him (Harcourt, 1979, Watts & Pusey, 1993). Males older than 11-12 years typically have tense relationships, coexisting through avoidance or tolerance (Harcourt, 1979; Watts & Pusey, 1993).

Ovulation in female MGs may begin as early as age eight, but often doesn't occur until the tenth year of life. According to research by Robbins et al. (2009), the average age at first conception in female MGs is about 10 years of age, whereas the average tenure of a dominant male is around 14 years. Robbins et al. (2006) have identified age and parity as significant factors influencing female reproductive success in MG, wherein the youngest and oldest females exhibit relatively low fertility. The study revealed that MG mothers who gave birth for the first time experienced a 50% increase in offspring mortality and a 20% longer interbirth interval (IBI) compared to mothers who had previously given birth.

Dispersals of matured females and male iVMGs

Female dispersal

In situ VMGs groups exhibit specific behavioural characteristics, including philopatry in multi-male groups, natal dispersion from multi-male groups, and dispersal from one-male groups. This adaptability is evident in the flexible dispersal patterns of iVMG females between groups with varying compositions, involving transitions between polygynandrous and polygynous mating systems. (M. Robbins et al., 2023). Research suggests that multi-male iVMG groups exhibit a considerable variability in their mating systems. It is also worth noting that the variable of rank appears to exhibit a higher degree of predictability in female partner selection when compared to the variable of paternity. It seems that iVMGs, in the opposition to iWLGs, show hierarchical relationships between males and females.

Natal transfer

In situ VMGs females can either stay in their natal group when they mature or leave their natal group (54 %, A. Robbins et al., 2009). In the study conducted on a sample of 44 nulliparous female iVMGs, it was found that 46% gave birth within their natal group (A. Robbins et al., 2009). The dispersal pattern contributes to a unique social structure within gorilla groups, where breeding females are largely unrelated, thereby impacting the genetic diversity and dynamics of the groups (Harcourt et al., 2008). Intriguingly, the reproductive success of female gorillas in the Virunga region doesn't seem to decline even as group sizes expand to 3-5 times larger than average, suggesting that there are no clear socio-ecological limitations on group size (M. Robbins et al., 2007). Group size has minimal influence on factors such as average inter-birth intervals and infant survival, despite higher infant mortality in one-male groups due to infanticide following group disintegration (M. Robbins et al., 2007).

A substantial correlation between the likelihood of dispersion among natal nulliparous female MGs and the composition of the social group, with a higher tendency to disperse seen in one-male compared to multi-male groups was shown by Robbins and colleagues (2009a). It has been observed that nulliparous females are more likely to disperse and may choose to depart from single-male groups to prevent infanticide, whereas mothers with suckling infants are less likely to leave. This behaviour might account for the elevated proportion of females who have already given birth within these groups. According to Waser et al., (1986), it is anticipated that the costs associated with inbreeding would be more pronounced for females compared to males in a multi-male group if the female remains in the group. In addition, Robbinson and colleagues (2009a) could demonstrate that iVMG females have the capacity to adapt their copulation patterns in a variable manner, considering factors like age, stages of reproduction, and the composition (multi-male or single-male) of the group. For instance, in single-male groups, females seem to engage in sexual activity with the highest frequency seen over the course of their pregnancy, especially in their first trimester. The frequency is lower, however, occurrences are nevertheless possible when females have already dependent infants. Age-related declines in reproduction in VMGs may have behavioural causes, as shown by the fact that older females copulate less often and with fewer partners.

Initially encountering single-male units, dispersing females showed a preference for smaller newly formed units. In the case of exclusively multi-male group encounters, dispersal patterns showed mixed results, emphasising the dynamic nature of the behaviour (M. Robbins et al., 2009). While most females transfer once or twice after leaving their natal group, some individuals exhibit greater mobility, transferring up to five times during their adulthood (Watts, 1996). Female dispersal remains a subject of intrigue due to the suddenness and unpredictability of the behaviour, with females often making the transition between males during interunit encounters, taking just a matter of minutes (Harcourt, 1978a; Sicotte, 1993). This complex behaviour highlights the intricate interplay between reproductive strategies and social dynamics in gorilla societies (Harcourt et al., 2008; Robbins et al., 2007; Robbins et al., 2009c). In situ VMG females from non-breeding “survival” group will leave this groups or will be taken over by a single SB or by a multi-male reproductive group when reaching fertility.

Risk of infanticide

In single-male groups, females with offspring under a year old tend to spend more time near the dominant male and develop stronger bonds with him to prevent infanticide, unlike females without young offspring. In multi-male breeding groups, where the risk of infanticide and the level of confidence about paternity are reduced, mothers with young offspring (<1 year), exhibited a relative increase in their proximity to males with whom they had previously maintained little contact, as opposed to males they had previously favoured. This behaviour may be interpreted as an attempt to foster confusion over paternity and discourage aggressive behaviour. Offspring (89%, older than 2-3 years) imitate their mothers' choices of male social partners, and spent most of their time near that specific male throughout their first year of life (Rosenbaum, Hirwa, et al., 2016).

Infants under the age of four that transfer with the mother is most likely to be killed from the new SB (M. Robbins & Robbins, 2018; Watts, 1989). Most instances of infanticide are seen after the death of the dominant SB in single-male breeding groups. During the process of group disintegration, it has been observed that all females, even those who have not yet weaned their offspring, disperse either to other groups or to solitary males (Harcourt, 1978; Harcourt & Stewart, 1987; Stokes et al., 2003; Watts, 1989). In this case, also collective migration, meaning that multi-female transfer occurs (Harcourt, 1978; Harcourt & Stewart, 1987; Stokes et al., 2003; Watts, 1989). The patterns of co-dispersal of relatives in certain populations underscore the significance of kin relationships in this behaviour (Bradley et al., 2005; Yamagiwa & Kahekwa, 2001). Therefore, during the period of dispersal, the new SB engage in the infanticide that are not biologically related to them to enhance their reproductive opportunities with the arriving female. When there is still a SB alive, females rarely lose their infant during interunit encounters (Watts, 1989). Infanticide has been identified as a major factor contributing to the death of the infants within the iVMG population, constituting more than one-third of infant fatalities
In recent years, the rise in the number of iVMGs has resulted in increased group density, leading to the splitting of groups into smaller ones (ranging from 3 to 11) within the same restricted area.

Consequently, incidents of inter-group aggression tripled, causing a significant increase in stress levels, thereby impacting rates of infanticide and resulting in the death of seven males. This decline in welfare has restricted population growth in densely populated mountain regions (Caillaud et al., 2020). Moreover, the presence of surplus males in iVMG groups may exacerbate this trend by potentially reducing the risk of infanticide within these groups.

Male dispersal

Male iVMG's remain in their natal group or disperse resulting in the development of a social structure typified by the coexistence of either a single- or multi-male groups. The occurrence of this combination is a rare phenomenon within the primate hierarchy further contributes to the distinctive nature of iVMGs vs. iWLGs.

The iVMG male reaches adulthood at 13 years (~13 (14-21 years), **~5 years earlier than iWLGs.** It has been shown that juvenile males tend to remain within their natal groups for a significant portion of their developmental period, accounting for over 50% of their lifetime. During this period they undergo maturation and eventually assume the role of the dominant SB. Young SB males who exhibit philopatry tend to have a higher average lifetime reproductive success in comparison to those who emigrate (A. Robbins & Robbins, 2005). This study ultimately determined that dominant males do not experience any negative repercussions on their reproductive success because of permitting younger males to remain within their social group.

Multi-male groups are common (~40 %). Male emigration is only ~45 % in VMGs (M. Robbins et al., 2009). Males have the capacity to establish a single-male reproductive system. This occurs when a mature solitary male acquires females from other groups through group fission. Alternatively, they may join a non-breeding group or bachelor group, enter a solitary breeding period, or directly integrate into a reproductive group. For instance, in the event of their father's demise, they may assume control of the group as a solitary breeding male (A. Robbins & Robbins, 2005; M. Robbins, 1995; Watts, 2000). Take over by sons or outsider males is common. Tenure is shorter than that of iWLGs. The dominant SB male in the multi-male group can father around 90% of the infants with females that are not genetically related to him. In general, males who disperse to attempt to build new groups have a lower success of obtaining reproductive opportunities (M. Robbins, 1995; Watts, 2000). Other advantages of a multi-male group seem to be that ageing males will not be evicted from the group (M. Robbins, 1995), protection against predation; and resources, and care for group members is increased (M. Robbins et al., 2001).

When the dominant SB in a multi-male group dies, the composition of the new unit depends on the number of remaining SBs and any maturing males from the previous unit. Multi-male MG groups often include numerous offspring who have reached SB status. Consequently, upon the death of the dominant SB, the group usually maintains cohesion, as one of the SB offspring may assume the role of the new leading SB male. However, if no successor is apparent, the loss of the dominant SB may prompt the group to transition into a single-male group, especially if there were only two adult SBs. Alternatively, it may retain its multi-male status or split into smaller male groups if there were multiple SB males.

A notable difference exists between VMG and WLG groups: in the case of WLGs, the death of the dominant SB leads to group disintegration, prompting females to seek new affiliations with either alternative breeding groups or a single SB.

If the group was previously led by a single male, a maturing male might either join a non-breeding or bachelor group, enter a solitary period, or take over his natal group, maintaining its reproductive status. However, if the male is immature, he might be killed by the succeeding leading silverback who assumes control of the group. If the mother transfers, there's a risk of him being killed by the leading males/male of the new group. If he is four years or older, he might independently join a non-breeding group, with higher survival chances in VMG (73%) compared to WLG (50%), increasing the likelihood of the male infant surviving the death of his single male father.

Single males or males who have lost their breeding group can acquire new females and establish a new breeding group. The duration of being a solitary SB is uncertain, but during this time, they may acquire females or take them over from another reproductive group. Only a few males never achieve living in a breeding group, highlighting the highly dynamic life cycle of males.

Non-breeding groups typically consist of 2-8 gorilla males, although their size may occasionally exceed 20 members. Additionally, the composition of non-breeding groups undergoes more frequent alterations compared to breeding groups.

Most group competitions primarily revolve upon male endeavours to acquire or maintain mates and safeguard their offspring, rather than competing for food resources (Harcourt, 1978; Sicotte, 1993; Watts, 1994c; Doran and McNeilage, 1998). Cooperative behaviour like grooming and coalitions between males within the same group is rare, except during times of external threats or predator defence. Nonetheless, close relatives like fathers and sons exhibit more tolerance and occasionally support each other during aggressive encounters (Harcourt & Stewart, 1981; M. Robbins, 1996; Watts, 1997). Most conflicts between males are mild, involving displays, cough grunts, or lunges without physical contact. For instance, Robbins (1996) documented many instances of mild aggression among SBs, with only a few involving physical contact. Resident adult males establish dominance relationships primarily based on age, with older and fully mature males commonly outranking younger ones. Rank reversals between ageing and younger males occur over time.

2.5.2.3 Life Cycle and Maturation in eWLGs

The primary objective of the international breeding book and the associated Gorilla SSP is, to ensure the maintenance of a robust and genetically diversified collection of WLG within zoological institutions across globe, with a focus on their overall health and long-term sustainability. One objective of the Gorilla SSP is to maintain the presence of gorillas in groupings that align with their species' characteristics. These groupings include a troop, which encompasses a SB male leading the group, several females, and their dependent offspring.

Weaning and maturation

As there are variations in energetic costs across ex-situ and situ population, in situ populations are expected to have somewhat greater costs compared to ex situ gorillas due to their increased engagement in locomotion, thermoregulation, and digestion of a more fibrous diet (Stoinski et al., 2013; Breuer 2009, Nowell and Fletcher, 2008, Robbins et al.,2023, Eckardt et al., 2016). Therefore, comparable life history patterns across the two populations showed significant variations in weaning age (eWLGs: 3.8 years vs. iWLGs: 4.7 years) and IBI (eWLGs: 4.3 years vs iWLGs: 5.2 years) (Stoinski et al., 2013). Ex situ WLGs and iVMGs show accelerated developmental life histories compared to iWLGs. Specifically, eWLGs wean their offspring roughly one year sooner, resulting in a corresponding reduction in IBI by one year (Stoinski et la., 2013). The life history characteristics by different gorilla populations are likely influenced by an intricate combination of many ecological factors (energy costs), which act via genetic adaptations and phenotypic plasticity (Stoinski et al., 2013; Robbins et al., 2023). However, also individual differences play a role in rearing and development of the infants (Stoinski et al., 2013; Eckardt et al., 2016).

Dispersals of matured females and male iWLGs

Female dispersal

Typically, eWLGs reach sexual maturity earlier than their in situ counterparts, with some achieving this status as early as six years, but more typically between the ages of 6 and 8 (Meder, 1993). Ex situ WLG females may have their first offspring between the ages of 7 and 8. This is much earlier than in situ conditions, where iWLG females usually have their first offspring when they are between 11 and 13 years of age. The youngest recorded birth of a eWLG occurred with 5 years. There are other documented cases in the Studbook of females having offspring before the age of seven. Research suggests that maternal proficiency tends to improve with increasing experience (Nadler, 1974; Stewart, 1977). Gorilla females who were first-time mothering and lacked prior experience in observing infant rearing are fully capable of successfully raising their own offspring (Abelló et al., 2017). Various social factors can impact maternal behaviour, such as the composition of the group, and their personality, the availability of skilled family gorillas, infant's sex, those who care for them (caretaker) and notably, an experienced female mother. The maternal aptitude of a female is impacted by her upbringing, whether it was through maternal-rearing or hand-rearing, as well as her level of exposure to social groups that provide the opportunity to observe maternal behaviour in other females (Meder, 1989, Abelló et al., 2017). However, factors such as the physical environment and the physical condition of the mother can play a role for the survival of the infant.

Additional differences

A big difference to the in situ conditions is, that in eWLGs females often remain in their natal group. The reason for that is multifactorial: e.g., if the male dies, or is transferred to another facility, he will be replaced. The main reason given for the transfer is that his genes are already overrepresented in the eWLG population. Therefore, female eWLGs remain in their former facility and a new breeding male is introduced.

Male dispersal

Usually, young males that are high on the mean-kinship list and/or chosen for breeding are supposed to stay within their natal group until the ages of 9 to 11 (Abelló et al., 2017). The studbook keeper decides, based on genetic inbreeding avoidance, which male will be chosen for breeding. Only in rare cases will the males have the chance to undergo a solitary period before he takes over a reproductive group (see above 2a). The transition from natal to breeding group happens sometimes even at a very young age (around 12 years). Thus, in ex situ circumstances, males do not transit to the solitary period and the age at attending breeding male is much younger in comparison to iWLGs. The breeding period ends when the male is no longer of value for the breeding program and tends to be much shorter as in the wild. Selected males for non-breeding situations can be taken out of their natal group at the age between 5 to 9 years of age (EAZA BPG (Abelló et al., 2017), p. 72). Rarely do males change between solitary SB, non-breeding group and reproductive group. In captivity, SB has been transferred up to 9 times. One of the primary obstacles encountered in the implementation of an effective eWLG breeding initiative concerning the appropriate handling and management of male individuals that exceed the population's requirements.

Bachelor groups, which is a social arrangement consisting only of male gorillas, are common due to the surplus of male gorillas in the harem setting. Additionally, the Gorilla Species Survival Plan (SSP) initiated the establishment of bachelor groups during the latter part of the 1980s (in the US) with the intention of replicating natural occurrences. Throughout this process, valuable insights have been accumulated on the factors contributing to the efficacy of these bachelor groups within a zoo environment.

2.5.3 Social Relationships

2.5.3.1 Male-Male Relationships

2.5.3.1.1 Breeding Group

In social groups with multiple gorilla males, their interactions depend on personalities and histories, creating a tension that escalates as younger males reach adulthood. Immature males closely associate with the dominant SB, grooming him, but as they become blackbacks (BB), they spend less time near the older male and face increasing aggression from him (Harcourt, 1979) (Watts & Pusey, 1993). Males older than 11-12 years typically have tense relationships, coexisting through avoidance or tolerance (Harcourt, 1979; Watts & Pusey, 1993).

Cooperative behaviour like grooming and coalitions between males within the same group is rare, except during times of external threats or predator defence. Nonetheless, close relatives like fathers and sons exhibit more tolerance and occasionally support each other during aggressive encounters (Harcourt & Stewart, 1981; M. Robbins, 1996; Watts, 1997).

Most conflicts between males are mild, involving displays, cough grunts, or lunges without physical contact. For instance, Robbins (1996) documented numerous instances of mild aggression among SB, with only a few involving physical contact. Resident adult males establish dominance relationships primarily based on age, with older and fully mature males commonly outranking younger ones. Rank reversals between ageing and younger males occur over time.

2.5.3.1.2 Non-breeding Groups

The understanding of male social behaviour in non-breeding gorilla groups primarily stems from bachelor groups of mountain gorillas (M. Robbins, 1996; Yamagiwa, 1987). Similar multi-male groups are also observed in WG populations (Levréro et al., 2006). Within bachelor groups, including SBs, males display greater friendliness compared to those in breeding groups. They spend more time together during rest and feeding and engaging in frequent play. In some cases, such as one bachelor group, this increased camaraderie even led to homosexual behaviours, where a younger male imitated female courtship and copulatory actions (Yamagiwa, 1987).

Despite kinship, as shown in Robbins' study (1996), social interactions among bachelor males were not influenced by kinship, even though some were half-siblings. Dominance still prevailed, with older males typically dominating younger ones. However, discerning rank differences among males of similar age proved more challenging, as bachelor males were less competitive than those in breeding groups.

The reasons for the relaxed relationships among bachelors become evident with the introduction of adult females, introducing competition. In an example from the study on VMGs, when multiple females joined a non-breeding-male group, two SBs that had coexisted peacefully for six years began intense fighting. After a week of escalating aggression, the group split into two: the dominant SB and females going one way, while the subordinate SB and younger males went another way (Watts, 2001).

2.5.3.1.3 Inter-Group Encounter

Interactions between different groups of gorillas have the potential to lead to competition for reproduction among male individuals (Breuer et al., 2010; Parnell, 2002; A. Robbins et al., 2011; Stokes et al., 2003).

Nevertheless, the reactions of the SB towards males from other units exhibit considerable variability. It’s not fully understood why certain individuals exhibit a high level of tolerance towards the presence and behaviours of other males, whereas other male gorillas display high levels of aggression or avoidance (Bermejo, 2004; Harcourt, 1978; Magliocca & Gautier-Hion, 2004; Schaller, 1963; Sicotte, 1993).

2.5.3.2 Male-Female Relationships

The attractiveness of the male group leader to females is often credited for the high level of group cohesion (Yamagiwa et al., 2003). Relationships between mature males and adult females are considered the "core" of a social community; they vary based on kinship, tenure, and reproductive status (Manguette, Robbins, et al., 2020). Male aggression towards females is prevalent and is frequently characterised as "courtship aggression." It is increased when the female is in oestrus; typically, females act submissively (Bradley et al., 2005).

2.5.3.3 Male-Infant Relationships

Infants in their third year develop an attachment to the mature male, preferring his company over other adults except their mother or occasionally a closely related female. Males, particularly the SB, exhibit tolerance and protective behaviour toward immature gorillas, especially orphans. When mothers of infants and young juveniles die or emigrate, these young ones increase their association with the male, sometimes sharing his night nest for safety (Stewart, 2001; Watts & Pusey, 1993). Many immature males and females establish grooming relationships with the dominant SB, which offers them benefits such as intervention in aggressive encounters with older gorillas. Such advantages might persist into adulthood, with certain SBs supporting their adult offspring more in fights compared to unrelated adults (Watts, 1992).

2.5.3.4 Female-Female Relationships

The ecological variables have a significant impact on females, primarily due to the substantial investment required for parental care and their comparatively slower rates of reproduction when compared to the males. Consequently, the geographic dispersion of females is frequently constrained by the availability of food within the confines of their environment. In contrast, males with lower parental expense ratios tend to be more affected by the geographic dispersion of females in their environment rather than the availability of food (Clutton-Brock, 1989; Trivers, 1972).

In iVMGs: Unrelated female gorillas in social groups tend to tolerate each other without much interaction, often displaying mild threats (Harcourt, 1979; Watts, 1994). In contrast, close relatives like mothers and daughters engage in frequent grooming and mutual support (Harcourt & Stewart, 1989; Watts, 2001). Paternal relatives, such as half-sisters from the same male, exhibit intermediate levels of friendliness and antagonism between unrelated and maternal relatives (Watts, 1994). Determining dominance relationships among female gorillas can be challenging due to sporadic interactions (Harcourt & Stewart, 1989). Nonetheless, certain pairs consistently display non-aggressive supplants indicating stable dominance (Harcourt & Stewart, 1987, 1989;

Watts, 1994). Recent research by Robbins et al. (2005) analysed long-term data from 51 females in six groups, revealing stable rank differences among most females. Dominant females often maintained their status over time, with rank positively correlated with age and group tenure, except when tenure differences exceeded seven years (Harcourt & Stewart, 1987; Watts, 1985).

In contrast to some species like baboons and macaques, female iWLG do not rigidly follow social status rules (Cheney 1977; Seyfarth and Cheney 1984; Sterck et al. 1997; Thierry 2007). Aggressive interactions among females lead to unpredictable outcomes, with responses varying from ignoring to retaliation (Harcourt, 1979; Watts, 1994). Notably, female gorillas lack reconciliation behaviour post-aggression (Watts, 1995). While rare in small groups, fights between females become more frequent in larger groups, occasionally escalating to physical conflict (Watts, 1994, 1997). These conflicts often arise during feeding or near mature males (Watts, 1994).

2.5.3.5 Female-Infant Relationships – Mothers Matter

In species with maternal care, reduced mother-offspring contact as offspring age is common (Harcourt & Stewart, 1981; Nicolson, 1986). Gorilla infants maintain fulltime contact with mothers until about the 5th month, with slight variations (Eckardt et al., 2016). Mother-infant contact offers protection from predators, infanticidal males, and environmental factors. In captivity, these threats are minimal, leading to earlier contact breaks. WLGs exhibit more prolonged mother-offspring contact than MGs, especially between 15-27 months and 33-36 months of age (Stoinski et al., 2013). Factors like differences in habitat might influence these patterns (Parnell, 2002).

Summary:

Table 2 *Intra-specific and inter-specific variation in the sociobiology of iWLG and iVMG*

	iWLGs	Literature for iWLGs	iVMG	Literature for iVMGs
Group size	~ 10 (2-20 individuals)	Parnell, 2002	12.5 ± 9.1	Granjon et al., 2020
	3.6 +/- 1.5 adult females			
	group sizes are slightly smaller (mean 8-9 individuals)	Oates et al., 2003		
	8.4 ± 4.3			
Social cohesiveness	Lower, i.e., larger average interindividual distance	Yamagiwa et al., 2003	Higher	Yamagiwa et al., 2003
Single-male group	95%	Robbins et al., 2016	60%	Robbins et al., 2016
Fission of groups	during feeding	Robbins et al., 2013		
Sub-grouping		Yamagiwa et al., 2003		
Life expectancy at birth	14.5 years in Mbeli Bai	Colchero et al., 2021	19.2 years in iVMGs	Colchero et al., 2021
			19.9 years in Bwindi MGs	
Female philopatry	Stronger	Yamagiwa et al., 2003	Lower	
		Doran and McNeilage, 2001		
Female maturation age	7 and 8	M. Robbins et al., 2023	7 and 8	M. Robbins et al., 2023
Female natal dispersal	100%	Manguette et al., 2020	50%	Robbins, Stoinski, et al., 2009
				Robbins, Gray, et al., 2009
Age at transfer	8.6 years	M. Robbins et al., 2023	8.3 years	M. Robbins et al., 2023
Female 2nd dispersal	100 %		?	
Reproduction	higher cost as longer periods of maternal	Robbins et al., 2013 Sicotte 1993	lower costs, shorter birth interval for surviving infants	
Age at first birth	12.2	Robbins et al., 2023	10.1	Robbins et al., 2023
Age at weaning	long suckling period and late weaning age > 6 years	Breuer et al., 2009	3.3 years	Eckardt et al., 2016
	Mbeli Bai: suckling till 4.6 years	Nowell & Fletcher, 2007		
Infant survival	55 % (48-62 %),	Breuer et al. 2010	73%	
	No differences between females and males infants		(Bwindi 74 %)	
	till age of 4: Mother’s experience seem to influence infant survival	Manguette et al 2020		
Interbirth intervals, IBI	longer	Yamagiwa et al., 2003	4.2 in iVMGs	Eckardt et al., 2016
	5.4 in Mbeli Bai	Robbins, Stoinski, et al., 2009	4.1 in iVMGs	Stoinski et al., 2013
	5.7 (4.25-8.80 years)	Robbins et al., 2006	5.1 in Bwindi MGs	Robbins et al., 2006 (the age related)
	5.2	Stoinski et al., 2013		
		Nowell & Fletcher, 2007		
Life history	slower	Breuer et al., 2009	age related	Robbins et al., 2006
		M. M. Robbins et al., 2009		
		Stoinski et al., 2013)		
Male philopatry	Rare	M. Robbins et al., 2017	common	M. Robbins et al., 2017
Male dispersal	100%	Breuer et al., 2012	50%	Stoinski et al., 2009
Age at becoming SB	18-19 (14–18)	Breuer et al., 2009)	12-14 (Bwindi 14-15 years)	Breuer et al., 2009)
Age of male emigration	14-21years	M. Robbins et al., 2016	15.3	M. Robbins et al., 2016
Male 1 sire	18-25 years	A. Robbins et al., 2013	15.3	A. Robbins et al., 2013
Male tenure length (years)			15.7	A. Robbins et al., 2013

				M. Robbins & Robbins, 2004
Disintegrations per group year	0.08–0.11	Arandjelovic et al., 2014 Hagemann et al., 2018	0.05	M. Robbins & Robbins, 2004
Infanticide	rare cases, might be due to larger group dispersal and less hostility in intergroup encounters		known cases, 37% infant mortality in one-male groups- the risk may be lower in multi-male groups	Bradley et al., 2005 Robbins et al., 2007; Watts, 1989
Behavioural variations, cultural differences	not observed in situ	Robbins and Robbins, 2015		
Communication	greater, may be due to coordination of the groups	Masi et al., 2009	less well studied	
food competition (fc)	low, but expected to be higher gorilla females may avoid intragroup competition by temporarily subgrouping to feed in fruiting trees	Bermejo, 2004; Remis, 1994; Tutin, 1996		
	males monopolise highly preferred foodi spread widely to forage, differentiated relationships.	Masi et al., 2009		
inter-group competition	usually peaceful however, during fruiting season increased intergroup encountersg	Doran & McNeilage, 2001 Tutin, 1996	low, more egalitarian (Bwindi: high)	

Chapter 3

Personality of Ex Situ Western lowland gorillas

Picture 4 *Gorillas in Captivity*

“Every individual matters. Every individual has a role to play. Every individual makes a difference.” Jane Goodall.

3.1 Abstract

Recent research has described personality structures in a wide range of non-human primate species and ultimate explanations have addressed the personality of humankind from an evolutionary perspective. Phylogenetic comparisons explore the emergence and maintenance of personality dimensions across species, yet the comparability of personality structures characterized in ex situ Western Lowland Gorillas (eWLGs) with those of other non-human primates remains uncertain due to methodological constraints. This study addresses this gap by evaluating the personality structure of 203 eWLGs, rated by 94 raters using a variant of the Hominoid Personality Questionnaire (HPQ), a well-established tool in primate personality research (Weiss et al., 2009). Six personality factors were identified: Dominance (Dom$_{\text{eWLG}}$), Openness (Opn$_{\text{eWLG}}$), Conscientiousness (Con$_{\text{eWLG}}$), Agreeableness/ Sociability (Agr$_{\text{eWLG}}$), Neuroticism (Neu$_{\text{eWLG}}$), and Extraversion (Ext$_{\text{eWLG}}$), thereby replicating and extending previous findings on the personality structure in this species in ex situ conditions. The study's validity was further supported by correlations between personality scores and social state-dependent behaviour responses (s-dbr) in two social eWLG groups (N=24), affirming convergent validity for all personality factors. The robust and reliable dataset enabled a comparison of upper-order dimensions (factor level) with those of other ex situ great ape species (bonobos, orangutans, and chimpanzees), as well as humans. The personality dimensions of eWLGs showed significant similarities with those described in ex situ orangutans and bonobos, and humans. Additionally, a comparative analysis of lower-order facets (correlated trait constructs) among these closely related great ape species provided insights into species-specific similarities and differences, informed by phylogenetic relatedness. I also show that demographic variables, such as sex or age influence personality differences. Demographic variables, including sex and age, were found to significantly influence personality traits. Specifically, sex negatively impacted on Dom$_{\text{eWLG}}$ and Con$_{\text{eWLG,}}$, and positively impacted Agr$_{\text{eWLG.}}$. Age affected all factors except for Dom$_{\text{eWLG,}}$ with negative effects on Opn$_{\text{eWLG,}}$ Neu$_{\text{eWLG}}$, and Ext$_{\text{eWLG}}$, and positively effects on Agr$_{\text{eWLG}}$. The interaction between of sex and age negatively influenced Dom$_{\text{eWLG}}$, Agr$_{\text{eWLG}}$ and Neu$_{\text{eWLG}}$. This research highlights the critical importance of accounting for demographic variables in primate personality studies and underscores the potential for cross-species comparisons to deepen our understanding of the evolutionary roots of personality traits. Demographic variables, including sex and age, were found

to significantly influence personality traits. Specifically, sex impacted on Dom$_{eWLG}$ and Con$_{eWLG}$, negatively, and positively on Agr$_{eWLG}$.. Age affected all factors except for Dom$_{eWLG}$, with negative effects on Opn$_{eWLG}$, Agr$_{eWLG}$, Neu$_{eWLG}$, and Ext$_{eWLG}$, and positively effects on Con$_{eWLG}$. The interaction between of sex and age negatively influenced Dom$_{eWLG}$, Agr$_{eWLG}$ and Neu$_{eWLG}$. This research highlights the critical importance of accounting for demographic variables in primate personality studies and underscores the potential for cross-species comparisons to deepen our understanding of the evolutionary roots of personality traits.

3.2 Introduction

Based on the existing body of research, the incorporation of personality variations offers a unique and beneficial framework for the management of ex and-in situ animals and the realisation of the One Plan Approach by increasing welfare and conservation initiatives (e.g., Arcese et al., 2004; B. Steel & Hogg, 2003). It has been shown that disparities in personality traits can significantly influence individual or population survival (Biro & Stamps, 2008; Weiss et al., 2013), reproduction (e.g., mate choice, Bergmüller & Taborsky, 2010; Seyfarth et al., 2012; Weiss et al., 2023; Wolf et al., 2008), fitness success (Réale et al., 2009: Smith and Blumstein, 2008), and are associated with distinct life-history strategies (Réale et al., 2009; Stamps, 2007; Wolf et al., 2007). The emphasis here is to ensure that knowledge on personality should be taken into consideration as it affects and interacts with ex situ-and in situ populations, simultaneously.

Personality impacts on animals in ex situ settings

The process of domesticating animals stands as a pivotal event in the annals of human civilization, originating from the lasting bond established between hunter-gatherer societies and wolves around 40,000 to 15,000 years ago (e.g., see Serpell, 2021). A diverse array of animals, including but not limited to sheep, goats, cattle, pigs, poultry, horses, and dogs, have become indispensable components of human civilization. The diverse range of characteristics shown by different domesticated animals has furnished successive generations of scientists with a vital foundation for understanding evolution. The personality structure of individuals in ex situ settings may undergo enduring changes due to unintentional effects or artefacts of confinement. Alterations to the structure of an individual's personality can arise as a result of human interventions, such as the implementation of selective ex situ breeding techniques like hand-rearing, the influence of social learning, and various other factors that facilitate developmental modifications (Drent et al., 2003; Marliave et al., 1993; Trut, 1999). These interventions ultimately contribute to the enhancement of specific genetic and phenotypic characteristics (Arnold, 1995; Carlstead, 1996; Gilligan & Frankham, 2003). Thus, various socio-ecological factors, including the absence of predators, consistent food supply, and low or no risk of infanticide, along with social dynamics such as group composition, rank, age structure, dispersal, and life history patterns, collectively and human handling can shape the personality structure of gorillas in confinement.

Personality impacts on translocation success

These dynamics, in turn, can have implications for the success of translocation and reintroduction initiatives, thus influencing conservation activities (Bell et al., 2009; Santos et al., 2009). Diverse behavioural patterns relevant to conservation efforts, such as anti-predator responses, tolerance responses, exploration patterns, and foraging behaviours, can be influenced by variations in personality (Coleman & Wilson, 1998; Coss & Biardi, 1997; Dingemanse et al., 2003; Drent et al., 2003; D. Fraser, 2001; Godin & Davis, 1995). Therefore, animals with specific personalities may have a higher likelihood of survival (Bremner-Harrison et al., 2004; Carere & Locurto, 2011), establishment, and reproduction in new environments. Considering personality traits when selecting individuals for reintroduction and planning post-release monitoring strategies can enhance the effectiveness of reintroduction programs.

The influence of personality on in situ populations and the achievement of conservation goals

Numerous studies have shown that intra-species changes may have notable impacts on several phenomena. The factors under consideration encompass local adaptation (Riechert, 1993; Storfer & Sih, 1998), the proliferation of invasive species (Cote et al., 2010; Fogarty et al., 2011), interspecies interactions (Griffen et al., 2012; Toscano & Griffen, 2014), the conservation of biodiversity (Crutsinger et al., 2006, 2009), and even the peril of extinction (Pruitt, 2013). Additionally, the impacts of intra-specific variation may intersect and even surpass those associated with variation within species (Pruitt et al., 2012; Pruitt & Ferrari, 2011).

Several studies on in situ animals operate on the bold-shy axis to address personality differences (Brooker et al., 2016; Merrick & Koprowski, 2017; Mittelbach et al., 2014; Wolf & Weissing, 2012). They present empirical evidence indicating that animals exhibiting bolder behavioural traits exhibit higher vulnerability to traps in comparison to their shyer counterparts. A recent study on in situ bottlenose dolphins pertains to the significant contribution of this phenomena. López (2020) suggests that dolphins who are bolder play a significant role in enhancing group cohesion, stability, and the transmission of information within the social network. This underscores the potential influence of certain social personalities on overall fitness. A recent study on in situ Gombe chimpanzees provides evidence for the functional significance of personality traits, particularly Dominance, in relation to social rank, reproductive success and how these variations in personality can therefore impact fitness-related outcomes (Weiss et al., 2003). However, the observed adaptive variation in personality among male chimpanzees in their natural habitat did not demonstrate long-term persistence. This lack of persistence may be attributed to the association of alternative phenotypes with reproductive strategies at different stages of life, as suggested by Wolf et al., (2007).

The Gorilla Personality Questionnaire (GPQ)

The dominant theory of personality in humans is trait theory, which predicts that an individual's behaviour should exhibit some degree of consistency over time because personality remains stable from situation to situation (Pervin, 1980). The Five-Factor Model (FFM) of human personality has become the most widely accepted model to use to get complete maps of personality in humans (John, 1990). This model includes five bipolar factors (Neuroticism (Neu), Agreeableness (Agr), Extraversion (Ext), Openness (Opn), and Conscientiousness(Con)) that can be used to describe most human behaviour patterns and they encompass a larger number of even more specific traits (Digman, 1990).

This section provides insight into how personality and subjective wellbeing (SWB, Chapter 5.3.4) is measured in gorillas and why a rating procedure was chosen instead of behavioural coding to measure personality. The same GPQ was used in the Chapter 4 to assess the structure of in situ Western lowland gorillas and to build the basis to improve welfare of ex situ and in situ WLGs as the overall goal of the OPA (Chapter 5).

Evaluation of personality. There are three broad approaches to personality assessment in animals: (1) behavioural observations, such as controlled behaviour/ experimental tasks (e.g. open field test, dark-light test), (2) systematic analysis of behaviours according to an ethogram of a focal individual, and (3) rating forms via coding (Weiss et al., 2009). With rating forms, the scorer uses a questionnaire to rate an individual's propensity to display a trait or item. This can either be done using a top-down approach (fixed number of comparable traits across species as used in the Human Personality Questionnaire (HPQ; Weiss et al., 2009) or a bottom-up approach, rating species-specific behavioural based traits (Gosling, 2001; King & Figueredo, 1997; Koski, 2011).

Comparing personality structure across species based on different behavioural and rating methods is challenging because personality structure can differ depending on the diversity of behaviours evaluated (Gosling, 2008; Uher, 2008b; Uher & Asendorpf, 2008). Rating scales have an advantage over behavioural measures in terms of enabling much larger sample sizes, and being quick and easy to assess the incorporation of traits that are difficult to validate using behaviour measurements (Freeman & Gosling, 2010; Gold & Maple, 1994).

Freeman & Gosling (2010) examined primate personality research – which encompassed several methodologies such as behaviour observation and trait rating – and revealed that Sociability (Soc), Fearfulness (Fef), Playfulness, and a composite dimension of Confidence (Con)/Aggressiveness (Agg) emerged as the most frequently reported dimensions in primate personality descriptions. Clear species differences have been found in these identified traits and in how they are grouped into facets and higher order dimensions (Budaev, 2000; Freeman & Gosling, 2010). The ability to directly compare personality traits across different species is frequently hindered by inconsistencies in the assessment of personality and the varied methodologies employed to extract personality structures (Adams et al., 2015; Budaev, 2000; Freeman & Gosling, 2010; Morton, Lee, Buchanan-Smith, et al., 2013; Weiss et al., 2009).

A widely used rating form for cross-species comparison is the HPQ (Weiss et al., 2009), which is a cumulative rating scale with a fixed number of predefined personality traits (Adams et al., 2015; Freeman & Gosling, 2010; Weiss, Adams, Widdig, et al., 2011). The HPQ is based on traits like those found in the Five-Factor Model (FFM) of personality in humans (Goldberg, 1990; John & Srivastava, 1999; McCrae & Costa, 1991, 1997; Weiss, 2022; Weiss & Adams, 2013) which includes five bipolar dimensions: Neuroticism (Neu), Agreeableness (Agr), Extraversion (Ext), Openness (Opn) and Conscientiousness (Con). These dimensions, also called higher-order factors or domains, are hierarchical and encompass a high number of human behavioural traits (Digman, 1990), consisting of several lower-level facets (dispositional trait correlations), and they subsume specific traits with similar meanings (Costa & McCrae, 1992; Goldberg, 1990). This approach is also called trait psychology or, more recently, physics of personality (McCrae, 2009).

King & Figueredo (1997) were the first to use the FFM (Digman, 1990; Goldberg, 1990; McCrae & John, 1992) as a basis to create a rating scale for chimpanzees (CPQ). To achieve this, they selected adjectives from as many of the clusters or facets that defined each of the five human personality domains. King and colleagues (King & Figueredo, 1997; King and Landau, 2003) also ensured that traits measured characteristics and not just behavioural differences among chimpanzees, including differences in emotional responses and consistency, reactions with members of the same species, and cognitive domains like self-control and curiosity. Thus, additional chimpanzee-related adjectives have been added (King et al., 2005; personal communication with King). These authors were therefore able to identify five factors that were strikingly like the five human factors. Another further factor was identified, and its composition of trait markers from several domains indicated that it was associated with a dominant or competitive prowess which led them to label this factor "dominance". More notably, they discovered that the reliability of the raters was comparable to that seen in human personality studies (Costa & McCrae, 1992; King & Figueredo, 1997; McCrae & Costa, 1987, 1989).

Different personality dimensions have been identified in other non-human primate species using variations of the HPQ, allowing phylogenetic relationships to be examined using direct cross-species comparisons (chimpanzees: King et al. (2005); Weiss et al. (2007); orangutans: Weiss et al. (2006); rhesus macaques: Weiss et al. (2011); barbary macaques: Konečná et al. (2012); capuchin monkeys: Morton et al. (2013); gorillas: Schaefer & Steklis, (2014), iVMG: Eckardt et al. (2015)). Furthermore, several studies suggest that the HPQ is a good predictor of behaviours and life fitness outcomes, and a useful tool to compare across human and non-human primate species (Eckardt et al., 2015; Konečná et al., 2008, 2012; Morton, Lee, Buchanan-Smith, et al., 2013; Weiss et al., 2013). In addition, low-level dispositional trait correlation within a dimension (facets, also called patterns or behavioural syndromes) has been used to explain the persistence of traits in evolutionary closely related species (Weiss, Adams, Widdig, et al., 2011). For example, in rhesus macaques, sociability and altruism create the "blended" friendliness dimension, whereas sociability and activity are combined to form the higher-order Extraversion dimension in chimpanzees. Within humans, the facets of altruism and dominance are combined in the Agreeableness dimension but for other primates, Dominance commonly emerges as an independent dimension (Eckardt et al., 2015; King et al., 2005; Weiss, Adams, Widdig, et al., 2011; Weiss et al., 2015, 2016). In the ex situ orangutan population, those traits associated with Conscientiousness and Openness in other species are combined as facets into an Intellect dimension (Weiss et al., 2006).

Human raters who know an animal are able to assess non-human ex situ primate personalities with high levels of reliability for a range of animal species (Freeman & Gosling, 2010; King & Landau, 2003; Weiss et al., 2006, 2009; Weiss, Adams, Widdig, et al., 2011; Weiss, King, et al., 2011; Weiss, 2017a) and this is independent of different social cultures (habitat or rater/observer) or rearing strategies (King et al., 2005; Weiss et al., 2007, 2009). Primate personality dimensions based on ratings have demonstrated convergent validity by identifying correlations with related behaviors (Konečná et al., 2008, 2012; Kuhar et al., 2006; Morton, Lee, Buchanan-Smith, et al., 2013; Pederson et al., 2005; Weiss & Adams, 2013), welfare, and happiness in ex situ housed primates (King & Landau, 2003; Robinson, Morton, et al., 2016; Robinson, Waran, et al., 2016; Weiss et al., 2006; Weiss, King, et al., 2011). Genetic and neural correlates have also been identified in primates (Latzman et al., 2014, 2015; Robinson, Waran, et al., 2016; Weiss et al., 2000, 2002; Wilson et al., 2017). Findings obtained using the HPQ are broadly convergent with those identified using bottom-up rating or behavioural approaches to personality assessment, (e.g., in chimpanzees, Dutton, 2008; Freeman et al., 2013).

To investigate the personality of gorillas, I used the HPQ and adapted it to gorillas (therefore renamed as GPQ) and included additional questions on the online version. The HPQ variant enables the revelation of the evolutionary origins of WLG structures, facilitating comparisons across various great ape species and humans in a cross-species analysis. The comparative analysis of the personality structure of ex situ and in situ gorilla populations allow me to elucidate social-ecological variances within the framework of personality models. An additional study aim is to compare sociability among great apes and the gorilla subspecies to extract a crucial component of their overall social personality, and to investigate the relationship between subjective wellbeing and the social-ecological approach to shed light on happiness and wellbeing. Below is an overview of how I assessed personality and SWB and the statistical analyses carried out to ensure reliable and valid measurements of happiness and individual differences.

In this chapter, the foundation for comparing the ex situ Western lowland gorilla population (eWLG) with ex situ great apes and humans is established. This comparison extends to the genus Gorilla in Chapter 5. Additionally, it encompasses the personality structure of in situ Western lowland gorillas and Virunga mountain gorillas (iVMGs) to serve as a basis for the OPA and enhance welfare on both ultimate and proximate levels. Here, we delve into the personality of eWLGs.

The ultimate level

I undertook the following:

a. Generating the personality structure of the eWLGs population (N=203) and testing for robustness.

b. The personality structure of eWLG is compared to the results of earlier studies conducted on eWLG in the United States, in which four factors were identified using a shorter personality inventory (Gorilla Behavioural Index (GBI) by Gold & Maple (1994)), to determine if the results obtained from the two methods are comparable.

c. Using the GPQ, a variant of the HPQ, to identify the personality structure of eWLG enables me to examine phylogenetic relationships through direct cross-species comparisons of personality dimension of other primates in ex situ settings (Freeman & Gosling, 2010; King et al., 2005; Konečná et al., 2008, 2012; Morton, Lee, Buchanan-Smith, et al., 2013; Robinson, Morton, et al., 2016; Schaefer & Steklis, 2014; Weiss et al., 2006, 2007, 2009; Weiss, King, et al., 2011; Weiss et al., 2015). Thus, the extracted personality structure was compared across a range of ex situ non-human great ape species, as well as humans (Weiss, 2022). Examining personality traits in non-human primates, which are the most closely related species to humans (Goodman et al., 1998; Stauffer et al., 2001) significantly enhance our comprehension of the evolutionary origins of human personality (Buss, 1988), and the similarities or discrepancies facilitating the identification of selective pressures, which may have contributed to the development of certain personality traits, also in ourselves (Buss, 1988; Nettle, 2006). This direct comparison allows us to argue that the FFM is an appropriate personality model for comparing higher-order trait constructs (dimensions) and lower-order trait facets (correlated trait constructs) in the personality structure of humans and other great apes. This strategy informs the evolutionary link between several ex situ non-human primate species and humans at the most fundamental level.

d. Using a regression model, the effects of gender and age, as well as the interaction between the two factors was examined.

The proximate level:

On the proximate level, the personality structure was validated with observed behaviours. They also serve for the level of the state-dependent feedback loop on the proximate level of **Figure 21**, Chapter 5 (green).

3.3 Methods and materials

3.3.1 Personality Questionnaire (GPQ)

As a tool to assess personality for ex and in situ WLG populations, I used the **Gorilla Personality Questionnaire (GPQ),** which included small adaptations to the original HPQ (Weiss et al., 2009, full description on the development, see Weiss et al., 2017). For instance, I replaced “subject” with “gorilla,” and I included additional questions (See Sample GPQ, **TableAPP 1**) into the original HPQ (Weiss et al., 2009). The HPQ has been widely utilised in other non-human primate personality studies both in captivity (Altschul et al., 2018; Konečná et al., 2008, 2012; Morton et al., 2013; Robinson, Morton, et al., 2016; Schaefer & Steklis, 2014; Weiss, Adams, & King, 2011; Weiss et al., 2006, 2007, 2009, 2015, etc.) and in situ (Eckardt et al., 2015; Wilson et al., 2017), and it has been translated in to several languages (Weiss et al., 2015).

As with the HPQ, the GPQ presents raters with a list of personality trait items and their descriptors and asks raters to score how strongly the given individual gorilla displays each trait. The GPQ consists of 54 traits that can be rated using a 7-point Likert scale (where 1 = either total absence or negligible amounts of the trait displayed and 7 = extremely large amounts). Each trait consists of an adjective followed by a one to three sentence descriptor. For example, “sociable: Gorilla seeks and enjoys the company of other individuals and engages in amicable, affable interactions with them."

In addition to the questionnaires filled out in by hand, I created an online GPQ, which was accessible via the University of Stirling homepage to allow easier access for the raters. A screenshot of the online version of the GPQ can be found in the Appendix (**TableAPP 1**). The online GPQ was especially created for the in situ population, to receive additional information, such as demographic information, group composition and social rank of the gorilla in his/her current group, as for the ex situ population, those information were accessible from the International Studbook (e.g., Wilms & Bender, 2017).

Additional questionnaire: As I was interested in the rater’s personal perception of a trait and how their age or gender might influence how they complete the GPQ, I added an additional questionnaire into the online questionnaire. The rater was asked, in addition to filling the GPQ, to rethink whether the scored trait is of negative, neutral, or positive importance for a gorilla living in their social group. For example: "*Is being sociable of positive, negative or neutral importance for being a gorilla?*"

3.3.2 Study Sites and Subjects

Data on the GPQ was collected on 203 eWLGs, 115 females and 88 males, categorised by age and sex according to Breuer et al. 's (2009) classification (see **Table 3**). The majority (N = 136) were housed in 21 zoos located in the USA and Canada. A further 53 eWLGs were housed in 6 zoological facilities in the Netherlands, and 14 eWLGs were housed in 3 facilities in Japan. Data from the USA, Canada and the Netherlands were collected between January 2011 and November 2012, and in Japan between January 2008 and December 2009. The data from Japan and USA/Canada were kindly shared by Alexander Weiss and James King to be included into this larger data set. The mean number of subjects living in each facility was 6.77 (SD = 3.56). Demographic information for each eWLGs was taken from the International Gorilla Studbook (Wilms & Bender, 2017). All of the zoos which contributed to the research project are listed in Supplemental Material.

Table 3 *Overview of sex and age categories of subjects using Breuer et al.'s (2009) classifications*

Age category	Age-range (years)	N females	N males	N Total[a]
Full-grown silverback	>18	-	40	40 (1)
Young silverback	>14-18	-	13	13 (1)
Blackbacks	>11-14	-	5	5
Sub-adult males	> 7.5 – 11	-	8	8
Adult females	> 10	93	-	93 (9)
Sub-adult females	> 7.5 – 10	6	-	6
Juvenile	> 4 – 7.5	8	14	22 (4)
Infant	0 – 4	8	8	16 (9)
Total		115	88	203 (24)

Note.
[a] Values in parenthesis indicate the number of eWLGs also included in s-dbr observations observed in the two facilities.

3.3.3 Raters

Each eWLG was rated only once by each keeper (within this Chapter 3), field site (in Chapter 4 on iWLGs) - or research assistant, gorilla researcher, or student. Each rater could rate several gorillas with whom they were sufficiently familiar according to the rules and regulations described in the questionnaire (**TableAPP 1**). The raters were given the following instructions for filling out the forms: "*Gorilla personality assessments can be made with this questionnaire by assigning a numerical score for all of the personality traits*." The judgments were made based on their subjective understanding of the trait guided by the short clarifying definition following each trait. The gorilla's own behaviours and interactions with other gorillas were the basis for the numerical ratings. Thus, raters were expected to use their subjective judgments of typical gorilla behaviour (in comparison to all gorillas the raters know) to decide if the gorilla's score was above, below, or average for a trait. The seven-point scale was used when scoring.

I personally rated 53 gorillas at different zoos in the Netherlands. Two research students from the Netherlands (University of Amsterdam and Stichting AAP) have been recording behaviours for additional data collection on one of the study groups (Artis, Amsterdam or Apenheul, NL). They also rated the personality of both gorilla groups. An inter-rater reliability test was conducted on their ratings (Apenheul, 14 individuals or Artis 10 individuals) before they rated a second group. I also discussed the questionnaire with all the animal keepers in the Netherlands before they started to rate their gorillas in ex situ care. I ensured that all definitions of the traits and procedures were clearly understood which included providing a questionnaire translated into Dutch. Further questionnaires in French were also provided on request as language differences seemed to contribute to an unwillingness in the Netherland zoos as well as in the field with research assistants. A Japanese questionnaire was provided to Japanese raters as well as a French translation to Congolese. These Japanese and French translations were previously used for research on personality in bonobos and chimpanzees (see Weiss et al., 2009, 2015).

Ratings from Japan and the US were kindly shared by Alexander Weiss and James King (N=150 gorillas). to be included into this bigger data set for eWLGs (N=203 gorillas).

More information on this topic will be given in Chapter 4 (ex situ), Chapter 5 (in situ), and Chapter 6 (multi-dimensional approach to positive welfare).

Within the eWLG population, each eWLG (N=203) was rated up to seven times by researchers (N=3) or keepers (N=89) working with the eWLGs at each of the facilities. The mean number of raters per individual was 3.34 (SD = 1.61). All keepers had a minimum of one year's experience with each eWLG they rated (range 5-32 years), except with the infants were who less than one year old (N = 4). I only included those infants, as they were members of the two groups, where the behaviours for the validation of the personality structure were collected.

3.3.4 Behavioural Data Collection for Validation of the GPQ

Behavioural data were collected between 2011 and 2014 at two groups of eWLGs (*Gorilla gorilla gorilla*, n=24, more information see below on the groups). Gorillas were housed indoors and outdoors in both zoological facilities in the Netherlands (Natura Artis Magistra and Apenheul Primate Park, see **Picture 5** and **Picture 13** for group composition of both groups).

Observation scheme

Of twelve focal times per observation day (see Table 4, Observation timetable, below), the goal was to randomly compute an observation scheme to achieve a minimum of two different observations per individual per observation times (session 1-12) in a two-monthly scheme. After the two months, I calculated the recorded number of observations per focal time (session 1-3) per individual and readjusted a follow-up observation scheme to achieve the missing observations per individual and block time. The recorded videos were saved on hard drives with the focal time, date and name of the individual, as well as with the information whether the videos were recorded in the indoor or outdoor setting of the facility. The observation schedule was done for both groups.

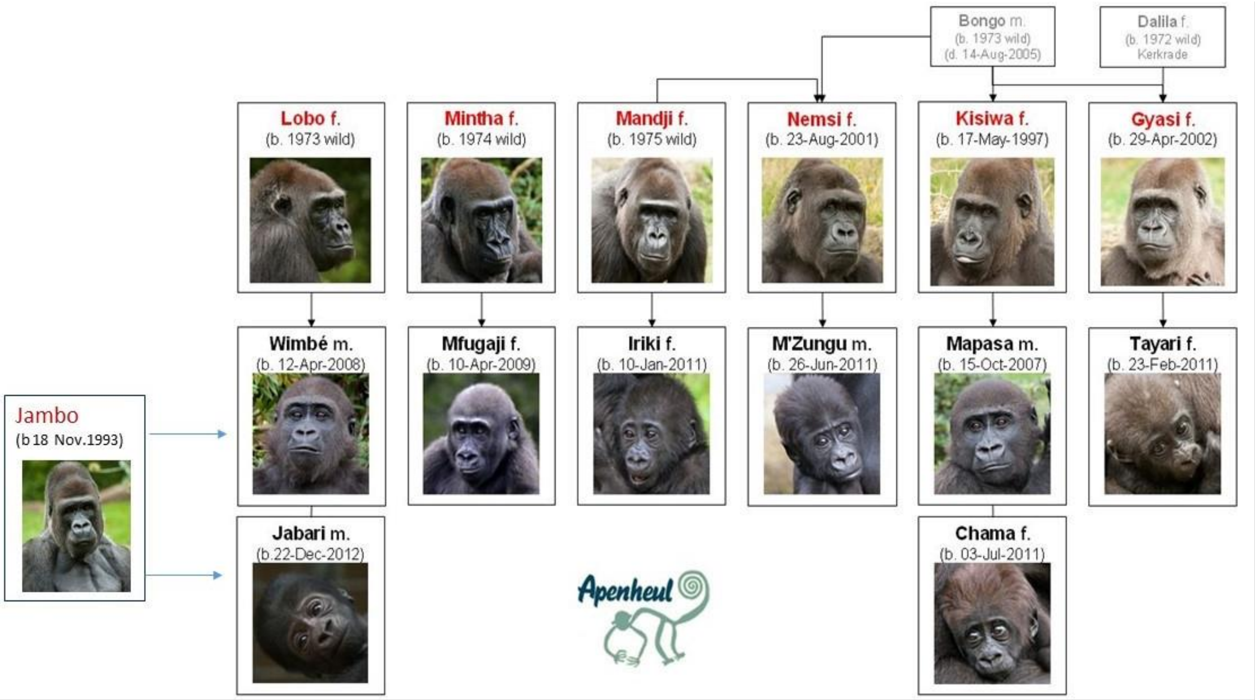
Table 4 *Overview of observation times per day with a 30 min observation schedule*

Focal times	**30 min observations**	**Start**	**End**
1. Session	1	09:00	09:30
	2	09:35	10:05
	3	10:10	10:40
Break-time 10 min			
	4	10:50	11:20
	5	11:25	11:55
	6	12:00	12:30
Break-time 1h			
2. Session	7	13:30	14:00
	8	14:05	14:35
	9	14:40	15:10
Break-time 10 min			
3. Session	10	15:20	15:50
	11	15:55	16:25
	12	16:30	17:00

Coding scheme

For further details on the ethogram, see **TableAPP 2**.

3.3.4.1 Apenheul Primate Park (Apeldoorn, The Netherlands)



Picture 5 *Apenheul Group Composition (graphic by Von Willard, gorillaland 2012)*

Apenheul Primate Park was selected due to its well-functioning gorilla group demonstrated by positive indicators of social enrichment and activity, such as successful breeding. During the years of data collection (2011-2014), four infants were born.

Two main areas were available to the gorillas – outdoors and indoors. The outdoor area of ~10,000m^2 was encircled by a moat (see Pictures 5-8) and shared with patas monkeys (*Erythrocebus patas)*. The indoor enclosure (where they were housed overnight; during poor weather in the summer; and mostly every year in the winter when the park was closed, at end of October until April due to construction on the outside enclosure) comprised of ten different compartments demarcated by movable partition totalling ~330m ^{2}. These two areas facilitated unrestricted movement of gorillas in three-dimensional space, enabling them to avoid one another or hide. The indoor configuration of the enclosure underwent periodic alterations, so gorillas had to occasionally change enclosures. Between May and September, the group was provided with nutrition in the form of fruits, vegetables, seeds, pellets, or tree branches four times a day (8:30am., 12:00pm., 1:45pm., and 3:30pm). Between June and August, the group was fed five times a day, (8:3am., 11:30 a.m., 1:00pm., 2:30 pm., and 4:00pm.), which coincided with public viewings (see Picture 8).

The large outside enclosure contained many features mimicking in situ conditions. Such large naturalistic ex situ environments have the potential to facilitate both the preservation of species and the conservation of their respective habitats during exhibition (Claxton, 2011; Fernandez et al., 2009; Little & Sommer, 2002).

Picture 6 *Apenheul, outdoor area: next to indoor enclosure*

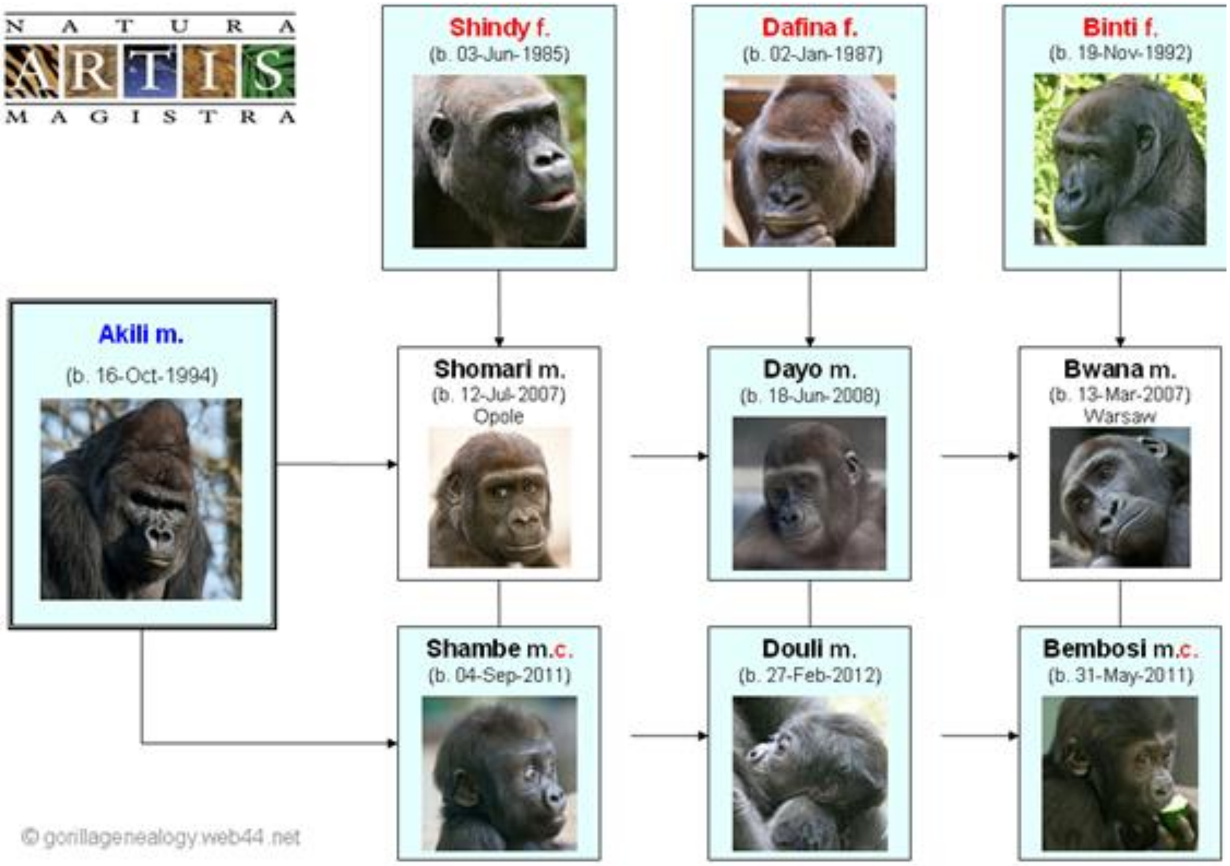
Picture 7 *Apenheul, outdoor area: right side of the island*

Picture 8 *Apenheul, outdoor area: right side of the island, wider angle*

Picture 9 *Apenheul, outdoor area: Feeding presentation*

Picture 10 *Apenheul, Swampy Area (left)*
Picture 11 *Apenheul, Open Clearing (Middle)*
Picture 12 *Apenheul, Climbing Trees (Right)*

3.3.4.2 Natura Artis Magistra (Amsterdam, The Netherlands)



Picture 13 *Natura Artis Magistra Group Composition (graphic by Von Willard, gorillaland, 2012)*

Note: c=castrated; f = female; m= male

Data from the second group of gorillas was collected in Natura Artis Magistra in 2012. This group (**Picture 13**) also exhibited well-functioning behaviours such as successful breeding and experienced mothers. The facility offered an indoor and an outdoor enclosure. The indoor exhibit was inside the Gorilla House and had soft wood-chip substrate flooring, climbing areas and natural plants (**Picture 14** and **Picture 15**). The outside exhibit was shared with white-throated guenons (*Cercopithecus erythrogaster*) and slender-tailed meerkats (*Suricata suricatta*). Both inside and outside were surrounded by large windows and allowed gorillas to explore the space in a three-dimensional environment, affording them the ability to avoid each other or hide themselves.


© Zoo Antwerpen
Gorillas Land | Natura Artis Magistra

Picture 14 *Artis, indoor enclosure*


© Arjan Haverkamp
Gorillas Land | Natura Artis Magistra

Picture 15 *Artis: outdoor enclosure*

3.3.5 Data Analyses

Missing data

The total number of missing ratings per individual was calculated and if a rater had more than 10 traits missing, the whole GPQ was removed from the data set. The missing ratings of any single trait were then replaced with the mean based on all ratings across all gorillas and raters for that trait (Weiss, Adams, Widdig, et al., 2011 on rhesus macaques, Weiss et al., 2017 on Gombe chimps).

Inter-rater reliability

The concept of inter-rater reliability pertains to the degree of agreement between two or more raters who utilise a common rating instrument.

ICC (**Intraclass Correlation Coefficient**) = Variance due to rated subjects (gorillas)/ Variance due to subjects + Variance due to Judges + Residual Variance.

In this case, the GPQ and the SWB were used to evaluate a given set of gorillas, with respect to raters' assessment of the animals' traits. We used two types of intra-class correlation (Shrout & Fleiss, 1979) to estimate the inter-rater reliability of the ratings on each trait. To calculate inter-reliability, ICC (3,1) (= across subject reliability) was used to assess the reliability of individual ratings of a single rater's ratings. ICC (3,k) (= within subject reliability) is used to assess the mean of k ratings scored for each subject gorilla by a set of k raters. Traits were omitted from further analyses if they had an ICC (3,k) that was zero or negative. ICC (3,1) and ICC (3,k) greater than 0.60 indicates good agreement between raters and the rater scores/ rater (Cicchetti, 1994).

Dimension identification/ retention

This section provides an overview of the shared analysis conducted for personality and SWB in Chapter 3, Chapter 4, and Chapter 5. All analyses were carried out using R Core Team (Urbanek, 2022). All functions were used from Revelle (2017). psych: Procedures for personality and psychological research (Version 1.2.12). Evanston, IL: Northwestern University. Retrieved from http://personality project.org/r/psych.manual.pd

Additional questionnaire on rater judgement of importance of the trait to being a gorilla himself

We ran a set of nonparametric tests to be able to make minimal assumptions about the underlying distribution of the data and computed a linear regression for sex rating (see **TableAPP 5**).

Data reduction

To determine how many dimensions to extract, I conducted several exploratory methods that have been used in several primate personality studies (e.g., Weiss, 2017) this reductive process involved Factor rotation and retention as explained in the following:

Factor rotation. Principal Component Analysis (PCA) vs. Exploratory Factor analyses (FA)

A variety of different methods have been used to extract the number of dimensions in studies of personality structure in animals. The most conventional methods are Principal Component Analysis (PCA) or Exploratory Factor Analyses (FA) with diverse rotation and factoring methods. The dimensions extracted via PCA are called “components,” whereas in FA, these are referred to as “factors.” As both procedures were compared with each other, I labelled these “dimensions.” The principal difference between both methods is that PCA extracts as much variance with the fewest number of dimensions, whereas FA is used to explain as many of the correlations between the original variables with a minimum number of dimensions. Therefore, a PCA tends to produce a unique solution while an FA can provide multiple solutions depending on the method used and the estimates of the community. Some authors conduct PCA or FA using both orthogonal and oblique methods; if the correlations between factors in the oblique rotation are minimal and there is no qualitative difference between the factor structures, then according to Weiss, Adams, Widdig, et al. (2011), researchers can confidently use the orthogonal rotation solution for further data interpretation.

Goldberg (1990) examined the FFM in humans using ten different methods of analyses and five-factor rotations for a total of 75 traits and found very consistent results across methods. Others (Ashton et al., 1998; Caprara & Perugini, 1994) have confirmed the universality of the Five Factors running several other rotation approaches from standard axes. Following this approach of comparing different methods of extracting dimensions, I used eight different extraction methods to compare the outcome of the personality structure of our eWLG data-set, containing 54 traits, to test for cross-method consistency.

A scree plot was used to compare the number of dimensions extracted in the original data set in comparison to the recommended number of dimensions from Horns' parallel analysis (1965). Additionally, a Bass-Ackward factoring algorithm was used as a wrapper over the Exploratory Factor Analysis (EFA) and PCA functions (Goldberg, 2006). The number of traits were repeatedly invoked, and the final weights of the solutions were utilised to determine the relationships between the various factors and/or components. By default, all factor solutions from 4 to n factors were performed. This was used to extract a hierarchical structure for the 54 traits to be followed from the top (nfactors, in our case 8 factors) down (in this case, 4factors).

PCA: Varimax vs. Promax

After assessing the retained number of components, I used two rotation procedures, **orthogonal** (varimax) and **oblique** (non-orthogonal, promax), to derive the unit-weighted component loadings into the specific components of the personality structure. A correlation test was used to compare the components and their unit-weighted component loadings to examine whether the rotation procedures produced similar outcomes.

Factor analysis

Different FA methods were used to examine the personality structure obtained from the data set. According to the factoring method used, the data underlie different rotations, orthogonal (varimax) vs. oblique (direct oblimin; non-orthogonal, promax) rotation. More information on the factoring procedure can be found in Revelle (2013). Thus, different FA factoring methods; (1) orthogonal: varimax rotation paired with different factoring methods, such as PAF (Principal Axis Factoring), MinRes (minimum residual) and ML (Factanal, maximum likelihood), and (2) oblique rotation (direct oblimin), paired with different factoring methods, such as Gls (generalised weighted least squares), WLS (weighted least squares) or MinChi (minimum Chi Square), were used to extract the number of factors of the personality questionnaire data-set.

To test the variance of different numbers of factors with the leave-one out procedure, I took 9 randomly chosen zoological sites (3 from the US, 3 from the Netherlands and 3 from Japan), and excluded those in turn.

Dimension identification/ retention

When performing a dimension retention, eigenvalues (EV) are provided, which represent the dimension's substantive significance. According to Kaiser (1960), all factors with EV>1 should be preserved. The magnitudes of EVs are displayed on the y-axis, while their corresponding factors are plotted on the x-axis, arranged in ascending order. The typical form of a graph is a dramatic decline in the curve followed by a gradual flattening. It is suggested that the point of inflection in the curve should represent the "cut off" point, with EV/factors above this point being kept. The minimum average partial (MAP) approach (Velicer, 1976) and Parallel analysis (*psycho* package) are two strategies for deciding which components to keep in studies that are believed to be more accurate than arbitrary "cut-offs" (Horn, 1965). The MAP approach generates a one-factor solution for a data set and computes an index based on the average residual correlation of the one-factor solution. The greater this index, the greater the variation that cannot be explained by this dimension. This procedure is repeated for a two-factor solution and so on, and the index of residual correlations indicates the amount of unaccounted-for variation in the extraction of x dimensions. The index will indicate the number of dimensions (x) that may be retrieved to explain the greatest amount of variation in the data (the index with the lowest residual correlation) The MAP test has been demonstrated to underestimate the number of factors that may be formed from a data source; hence, parallel analysis is the preferable strategy for factor retention. Therefore, I decided to use a combination of different dimension retention methods and compare the outcomes. The statistically significant number of dimensions was identified with the help of parallel analyses (*psycho* package) using the *paran* function (Dinno, 2009). In parallel analyses, a random matrix (i.e. uncorrelated variables) is used with a similar number of raters, ratings, and traits to the original data set. Only those dimensions with an EV greater than expected at chance at the 95% confidence level are extracted. A robustness test targeted orthogonal Procrustes rotation recommended in (Everett, 1983) was used to test the stability of the number of dimensions.

Additionally, I tested the variance of different numbers of dimensions. And lastly, I tested the number of stable dimensions using a leave-one out procedure causing one zoological or field site to be omitted from the analyses. I also ran a PCA to explore the EV and the number of components retained as well as the Scree-plot for a visual inspection of the number of dimensions expected.

Dimension reliability and normality

In the same way as described above on the level of the traits: to determine the inter-rater reliability for each dimension, we generated unit-weighted dimension scores for each rating of each gorilla and computed ICC (3,1) and ICC(3,k) for these scores. To determine the internal consistency of each dimension, I used the psych package https://cran.r-project.org/web/packages/psych/index.html to compute Cronbach's alphas for the mean ratings

Finally, I tested the dimensions for normality using a Shapiro Normality Test for the later behavioural correlation.

Generation of the structure. The structure of personality generated via $\text{EFA}_{\text{MinRes, varimax}}$ served as a baseline for all further analysis (in Chapter 4 for comparison to iWLGs' personality structure; and in Chapter 5 in respect to SWB and welfare).

Dimension labelling. Dimensions were labelled and interpreted according to the similarities found in other non-human great ape species (for eWLGs with other ex situ studies: Gold & Maple, 1994; King & Figueredo, 1997; Weiss et al., 2006, 2009, 2009, 2015; and for in situ gorillas: iVMGs: Eckardt et al., 2015, and humans: Weiss, 2022).

Data Analysis in Respect to Behavioural Observations

A coding scheme based on a social-emotional relationship rating scale in humans (McCall et al., 2010) was established. Specifically, within the scope of the study interests in positive psychology.

An all occurrence, focal-animal sampling method was used to code gorilla behaviours listed in the coded ethogram (***TableAPP 2***, Ethogram) off-site on a personal computer using Observer (observational software from Noldus Information Technology). **All state events** (coding of duration), such as social interactions, proximity to others, play, feeding, and inactivity, and **point events** (coding of frequencies), such as kiss, scratch etc., were coded as continuous behaviour types (every 30-second). Behaviours were also divided into **start-stop categories** (start and end of the behaviour had to be set) or **mutual exclusive, exhaustive group** (meaning when one behaviour started, the other behaviour was stopped automatically within the behavioural category). Additional, information on modifiers (such as the individual, etc.,) were also included. Therefore, the direction towards the behaviours performed was added (e.g., whether received or given, or both together). From the Observer XT output file per individual, all coded state and point event behaviours were exported. From the calculated rate per minute (observation duration (state) or frequency (point)), the mean of all observations was assessed on the individual level. The mean for each state-dependent behaviour (s-dbr) and emotion was calculated within R for further analyses to validate the personality structure. The coded s-dbrs have been regrouped in behavioural categories as shown in the ethogram (***TableAPP 2***, Ethogram). For instance, all coded s-dbrs in respect to feeding have been clumped together (such as foraging and food manipulation). Another example shown here is activity, all activity related s-dbrs have been grouped together (following, leaving, approaching, locomotion and play). Seven s-dbr categories have been built in total. Single behaviours can be used for additional purposes, e.g. to correlate with single traits or lower-order facets. In respect to the validation of the personality structure, only the regrouped s-dbr categories have been applied. For consistent comparison between three populations (in situ and ex situ WLGs and Virunga mountain gorillas), I tried to build similar s-dbr categories.

In conducting multiple correlational analyses using the same datasets within this chapter, the issue of non-independence of data points arises. Non-independence occurs when the same data points are used in multiple analyses, which can inflate Type I error rates and lead to spurious findings. Various methodologies were employed to address this issue. Below, I outline the strategies used, as well as reasons for not implementing certain methods in my thesis. Examples of datasets and the analysis process are provided. Additionally, all R scripts can be made available to support the findings.

Strategies to Deal with Non-Independence of Data Points

Validation of Ex Situ Personality Data and Coded Behaviors

The personality structure of ex situ gorillas consists of six personality factors. The validation process included a dataset of 156 coded behaviors.

1. **Bonferroni Correction**:
    - **Method**: Adjusted the significance level by dividing it by the number of tests conducted in R, controlling the family-wise error rate.
    - **Outcome**: No significant results for Spearman and Pearson correlations.
    - **Reason for Not Using**: The Bonferroni correction was overly conservative, increasing the risk of Type II errors (false negatives), particularly in studies with many tests (6 factors x 156 behaviors).

2. **Holm’s Correction**:
    - **Method**: Used Holm's procedure to correct p-values as an alternative to Bonferroni.
    - **Outcome**: Similar issues as with the Bonferroni correction.
    - **Reason for Not Using**: The same conservativeness led to complications in interpretation and no significant results.

3. **False Discovery Rate (FDR) Control**:
    - **Method**: Applied the Benjamini-Hochberg procedure to control the expected proportion of false discoveries among the rejected hypotheses.
    - **Outcome**: Less conservative than Bonferroni, but still yielded no significant results and complicated interpretation.
    - **Reason for Not Using**: Despite being less conservative, FDR control still did not produce significant results.

To mitigate the risk of Type I errors, behaviours were regrouped into broader behavioural categories (a total of 8 categories) as detailed in the ethogram. This grouping aggregated related behaviours (e.g., locomotion, following, approaching) into single categories. These categories were chosen for their similarity to in situ gorilla behaviours, facilitating comparison to the iVMG (Eckardt et al., 2015).

Following the regrouping, the same steps (Bonferroni, Holm, and FDR) were applied, resulting in significant correlations for only four of the six factors. This limitation could stem from the consolidation of behavioural categories, which reduced the granularity of the data.

Final Methodology

Given these findings, the analysis proceeded with the 8 behavioural categories, using Spearman correlations for non-normally distributed behaviours and Pearson correlations for normally distributed data. To avoid the issue of multiple correlational analyses on the same behaviours, different behaviour groups were used to validate personality (Chapter 3) and subjective well-being (SWB, Chapter 5).

The ethogram contained all behaviours of interest, but it was not necessary to use all behaviors for validation. Therefore, behavioural categories were employed as explained in Chapter 3, allowing for optimal comparison to iWLGs and iVMGs. In Chapter 5, coded emotions, data on positive and negative affect, another level of proximity (contact-resting with body contact instead of close proximity), and other behaviours were used to address the research questions without repeating behaviours multiple times. Play behaviour was used repetitively, but other behaviours were included in the regrouped category to circumvent this issue.

The strategies and reasons for their use or exclusion in this thesis were guided by the need to balance methodological rigor with practical constraints. By grouping behaviours and using appropriate correlation methods, the analysis aims to provide robust findings while acknowledging the limitations inherent in handling non-independence of data points.

To reduce the increased risk of Type I error (false positives) when conducting multiple behavioural tests, I adjusted the significance threshold (alpha-level) based on a Bonferroni correction on the p-value. The validation and Bonferroni correction was done separately for each of the personality factor, as previously be done in Eckardt et al., (2015). The reason for this is as the Bonferroni correction can otherwise be overly conservative, especially with many tests, potentially increasing the risk of Type II errors (false negatives).

Video focal samples of 24 eWLGs ((**Picture 5** Apenheul Group Composition (graphic by Von Willard) Picture 12 Artis Group Composition (graphic by Von Willard)) from two family groups in the Netherlands were collected between May and September 2012: Apenheul Primate Park, Apeldoorn (4 males and 10 females, mean age = 10.69 years) and Artis Zoo, Amsterdam (7 males and 3 females, mean age = 13.38 years). A minimum of six 30-minute videos per eWLG (mean = 7.5), were randomly chosen from different days of observations and spread across the data collection period. The behavioural coding was done in three phases, first, a total round of all individuals were coded before the 2nd round of videos was coded for each gorilla (N=24). This was done to avoid a bias during coding and to make sure that at least 3 videos got coded per individual.

To ensure different observers (JC and YB) could identify and code for identical behaviours (s-dbr) and emotions, inter-observer reliability tests were conducted before the beginning of video coding for each of the observed behaviours (s-dbr) and emotion until all were coded reliably. The inter-observer reliability test was validated by a Kappa Index of agreement (Cohen's kappa: Fleiss, 1981). The value of Kappa is considered moderate between 0.40-0.59, substantial between 0.60-0.79 and outstanding above 0.80 (Landis & Koch, 1977). The inter-observer reliability between both coders was good (kappa =.82). Behavioural coding was performed by JC and YP.

A test for normality (Shapiro Normality Test) was performed on the behavioural data (N=24 gorillas, all coded behaviours) as well as on the personality dimensions before further analyses was done in R. For normal distributed data, Pearson was used for the correlation between the behaviour or emotion and the personality dimensions. Spearman's two-tailed rank was used for non-normally distributed data, accordingly.

Effects of age and sex differences on personality. To test the possibility that an extracted personality factor is underpinned by differences in sex, age, and sex x age interaction, I conducted a linear regression model on each personality factors t-scores. I used a scatter plot to show the regression lines and confidence intervals ill depict the relationship between age for male and female gorillas.

Cross species comparison:

Cross eWLGs comparisons (US eWLGs)

When considering the personality structure in relation to previously described personality dimensions in eWLGs, there were some methodological issues that constrained the direct comparison of the results. For example, Gold & Maple's (1994) Gorilla Behavioural Index uses fewer traits and not all are congruent with the traits represented in our GPQ; only 57% items were identical. If the trait had a slightly different name, I renamed the trait when the defined meanings of the traits were very similar. For Extraversion, six out of seven traits matched**.** Slow was renamed Lazy and Popular was excluded. For Dominance, four of the six traits matched, Strong was renamed Dominance, and Effective and Opportunistic were excluded. Gold and Maple's third factor was congruent. Subordinate was renamed Submissive; Eccentric was renamed Autistic and Confident was renamed Decisive. In Gold and Maples' fourth factor Understanding (Und), Protective was identical to the GPQ trait and Motherly was seen as like GPQ's Gentle and Sympathetic in the Und factor; while Equable was assumed to be like Cool and (not) Excitable, Gold and Maple's Understanding was renamed Stable.

I did not compare our outcome with those shown in Schaefer & Steklis, (2014), even though they used the same variant of the HPQ questionnaire to assess the personality structure of eWLGs. This was because the personality structure was based on a total of only 8 males, all of which were housed in a bachelor group (Sedgwick County Zoo in Witchita, Kansas) and were rated by only 9 raters.

Cross great ape comparisons

A) **Procrustes rotation.** For those great ape species which also have a sixth personality dimension such as bonobos and chimpanzees, I ran a targeted orthogonal Procrustes rotation (McCrae et al., 1996; Weiss et al., 2015). I rotated the personality structure of bonobos and chimpanzees towards the generated personality structure of eWLGs. I used different rotation methods (see below) and calculated the congruence coefficient of the traits. In each rotation, a structure produced from one of the three chimpanzee samples was compared to a structure derived from the current eWLGs sample; the same was done for the bonobos. The research on bonobos and chimpanzees varied in terms of whether factors or components were extracted and the number of traits that were submitted to data reduction. For each targeted rotation, I ensured that the extraction procedure and set of traits used to construct the eWLGs target matrix were identical to those used for the bonobos and chimpanzee sample. I evaluated congruence coefficients using recommendations drawn from research in which experts assessed the resemblance of structures with varying degrees of congruence (Lorenzo-Seva & Ten Berge, 2006). Congruence coefficients below .85 do not show factor similarity, between .85 and .94 suggesting "fair similarity," whereas above .94 they hence "excellent similarity" (Lorenzo-Seva & Ten Berge, 2006, p. 61).

In the following, I list first the rotation methods used in the eWLG personality data vs. the rotation method used for ex situ bonobos or chimpanzees:

1. eWLG,$_{\text{EFA,min,var}}$ (EFA, minres, varimax) vs. eBonobo$_{\text{FA}}$ (FA on personality structure of bonobos), Data be=Bonobos: Weiss and colleagues (2015), 54 trait rating form.
2. eWLG,$_{\text{PCA}}$ (Principal Component Analysis) vs. eBonobo$_{\text{PCA}}$ (PCA on personality structure of bonobos), Data eBonobos: Weiss and colleagues (2015), 54 trait rating form.
3. eWLG,$_{\text{EFA,min,var}}$ (EFA, minres, varimax) vs. eJapan$_{\text{FA}}$ (FA on personality structure of Japanese chimpanzees), Data eJapan: Weiss and colleagues (2009). 54 trait rating form.
4. eWLG,$_{\text{PCA}}$ (Principal Component Analysis) vs. eJapan$_{\text{PCA}}$ (PCA on personality structure of Japanese chimpanzees), Data eJapan: Weiss and colleagues (2009). 54 trait rating form.
5. eWLG,$_{\text{FA,min}}$ (FA, minres) vs. eYerkes$_{\text{FA}}$ (FA on personality structure of zoo chimpanzees), Data eYerkes: Weiss and colleagues (2007). 43 trait rating form.
6. eWLG,$_{\text{PA}}$ (Principal Analysis) vs. eYerkes$_{\text{PA}}$ (PA on personality structure of chimpanzees housed at Yerkes), Data eYerkes: Weiss and colleagues (2007). 43 trait rating form.
7. eWLG,$_{\text{FA,min}}$ (EFA, minres, varimax) vs. eChimp$_{\text{FA}}$ (FA on personality structure of chimpanzees), Data eChimp: King & Figueredo (1997). 43 trait rating form.
8. eWLG,$_{\text{PA}}$ (Principal Analysis) vs. eChimp$_{\text{PA}}$ (PA on personality structure of chimpanzees), Data eChimp: King & Figueredo (1997). 43 trait rating form.

B) I used **unit-weighted dimension scores** to compare the personality dimensions derived in eWLGs to those identified in previous studies of ex situ populations: 154 bonobos living in zoological parks and a research centre in the United States and Europe (Weiss et al., 2015); 152 orangutans in zoos in the United States, Canada, Australia, and Singapore (Weiss et al., 2006); 100 chimpanzees in U.S. and Australian zoological parks (King & Figueredo, 1997), 1997; 175 chimpanzees from Yerkes National Primate Research Center, U.S (Weiss et al., 2007); 146 chimpanzees living in Japanese zoological parks, research centres, and a sanctuary (Weiss et al., 2009); and to humans (Weiss, 2022). I created unit-weighted dimensions scores based on gorillas' personality structure, and defined loadings that were ≥ |.4| as salient. I then assigned positive, salient loadings a weight of +1 and negative, salient loadings a weight of -1. If more than two dimensions loaded on a trait, I defined the trait as belonging to the dimensions with the highest absolute loading.

An additional comparison of evolutionary integrated low-order facets across close related species was carried out using the categorisation of Weiss, King, et al. (2011); see Cladogram **Figure 7** for full information). Gorillas filling the missing link in the great ape collection on data generated with variants on the HPQ.

3.3.6 Ethical Considerations and Approval

Ethical considerations

The acknowledgment of animal personalities highlights the need to see each animal as a unique being with its own distinct needs, dispositions, and preferences. This promotes respect for their autonomy and intrinsic value. Recognising their personalities can lead to more ethical practices in respect to animal welfare and conservation. The knowledge of individual-like characteristics can lead to better behavioural interventions in confinement and when addressing human-wildlife conflicts, which should be considered. Recognising animals as sentient beings with complex emotions, emotional states, and behavioural requirements may increase the moral obligation of caretakers, researchers, and conservationists to provide adequate care and protection. However, it also requires careful consideration of the ethical implications and potential challenges that may arise in different contexts. The ongoing discourse surrounding the personhood, moral standing, and legal status of great apes presents a significant ethical quandary that demands careful consideration. Ultimately, navigating this dilemma necessitates striking a balance between recognizing their cognitive, emotional, and personhood capacities, while also addressing the complexities and challenges inherent in altering their legal status. However, delving into the intricacies of these legal changes falls outside the scope of my personal investigations.

Ethical approval

This study was non-invasive, purely observational and conducted according to the “Guidelines for the Treatment of Animals in Behavioural Research and Teaching” (2012), which also meets the latest ethical standards of the Association for the Study of Animal Behaviour (ASAB Ethical Committee/ABS Animal Care Committee, 2023). Ethical approval and permission to conduct the research was granted by all zoological facilities and field sites involved. The EAZA Accreditation system was implemented to ensure that EAZA Accredited Members complied with EAZA's Standards of Accommodation and Care of Animals in Zoos and Aquaria, as well as EAZA's Guidelines, including the EAZA Guidelines on the use of animals in public demonstrations. The Psychology Research Ethics Committee, University of Stirling, Scotland approved my application at the start of the thesis.

3.4 Results

In the following section, I give detailed information on the generated results from the methodology described above.

Missing data

A total of 678 questionnaires were returned from 30 zoos and 94 raters, and of these, seven were excluded because there were more than nine missing responses. From the 36,234 potential trait ratings of the remaining questionnaires (N=671) from 90 raters and 203 gorillas, all missing responses (N=72, <0.001%) were replaced with the mean for the relevant trait, based on all ratings across all eWLGs.

Inter-rater reliabilities for GPQ traits

None of the traits were excluded based on an ICCs ≤ 0 cut-off criteria (Eckardt et al., 2015; Gosling & John, 1999; Gosling & Vazire, 2002; King & Figueredo, 1997; Weiss et al., 2007, 2009). The consistency across raters for each trait ranged from .18 (*Unperceptive*) to .64 (*Submissive*) with a mean ICC (3, 1) of .39. ICC (3, k) indicates the reliability of mean ratings, the overall mean was .67 (range from .44 to .86) (see **TableAPP 3**).

Personality structure in eWLGs

Parallel Analysis identified six principal factors with adjusted eigenvalues of 8.85, 8.04, 7.27, 2.18, 1.49 and 1.09. Therefore, six factors (Adjusted eigenvalues > 1) were retained with 1620 iterations using 95 centile estimates.

The visual interpretation of the scree plot (**Figure 4**) also showed the cut-off at 6 factors (see red -. line of the re sampled data like the actual data (blue x-line)

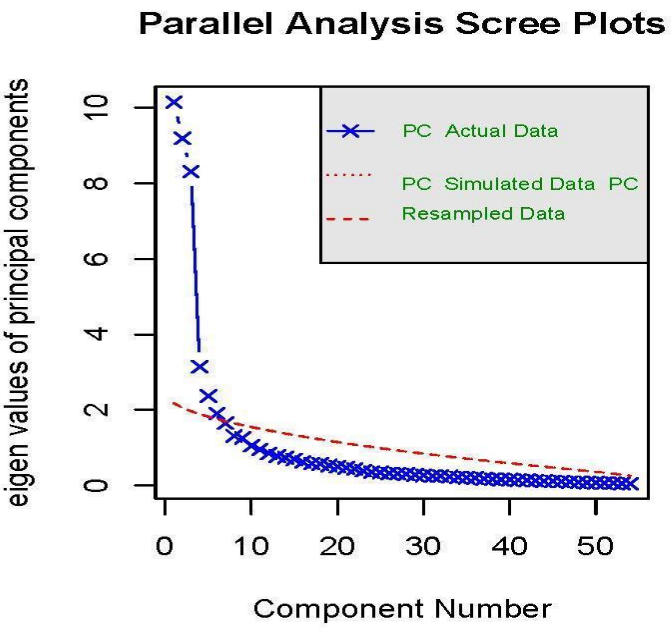


Figure 4 *Scree Plot according to Parallel Analysis*

Testing for variance on different numbers of factors showed a cumulative variance of .65 at six factors. The graphical distribution of the variances also shows a cut-off at six factors.

Cross-method comparison

I compared the personality factors identified using the different analyses techniques (see Chapter 3), independently from the labelling of the factors. Both the EFA and PCA methods were used to extract the personality structure, with a fixed number of six, five and four factor, allowing a comparison of how each trait loads onto a given factor and to check for general coherence between these traits for each solution (-.

Six different extraction methods are presented in **Table 5** to highlight results of the cross-method comparison and these corroborate the findings of Goldberg (1990).

Table 5 *Traits loading on personality factors in eWLGs: a comparison of EFA,minres, varimax vs. PCA, varimax within a six factor solution*

	EFA, minres, varimax, 6 factor							PCA, varimax, 6 factor						
Traits	**Dom**	**Opn**	**Con**	**Agr**	**Neu**	**Ext**	**h2**	**Dom**	**Agr**	**Con**	**Opn**	**Neu**	**Ext**	**h2**
Stingy	**.84**	-.03	.04	-.09	-.08	.05	.73	**.86**	-.10	.02	-.03	.06	.06	.75
Bullying	**.83**	.04	-.12	-.16	.05	.01	.74	**.83**	-.15	-.14	.04	.16	-.03	.75
Aggressive	**.81**	.07	-.16	-.19	.20	.00	.76	**.78**	-.16	-.18	.06	.29	-.11	.77
Dominant	**.79**	-.12	.18	-.08	-.33	.06	.80	**.83**	-.13	.17	-.11	-.17	.18	.80
Persistent	**.74**	.22	.14	.02	-.26	.02	.69	**.78**	.01	.14	.23	-.14	.10	.71
Jealous	**.74**	.13	-.10	.04	.08	.04	.58	**.75**	.07	-.11	.11	.17	-.04	.62
Submissive	**-.69**	.06	-.14	.17	**.47**	-.23	.81	**-.74**	.18	-.14	.04	.20	-.41	.81
Irritable	**.52**	-.10	-.18	-.28	.25	-.25	.52	**.51**	-.30	-.20	-.10	.21	-.35	.56
Reckless	**.51**	.35	**-.45**	.02	.13	.12	.62	**.50**	.08	-.47	.34	.22	.03	.65
Manipulative	**.49**	.25	-.05	.28	-.02	-.03	.38	**.53**	.32	-.05	.21	-.03	-.09	.44
Defiant	**.47**	.27	-.27	.04	.15	-.14	.41	**.48**	.05	-.29	.28	.11	-.25	.47
Cautious	**-.47**	-.33	.16	-.06	.19	-.10	.41	**-.51**	-.09	.18	-.36	.10	-.16	.46
Impulsive	**.41**	.39	-.37	-.08	.36	.05	.60	.37	.00	-.39	.38	**.42**	-.14	.63
Innovative	.04	**.84**	.08	.23	-.04	-.07	.77	.05	.29	.09	**.82**	-.05	-.08	.78
Inventive	.07	**.83**	.18	.25	-.10	-.04	.80	.09	.31	.18	**.80**	-.09	-.03	.79
Inquisitive	.09	**.78**	.15	.31	.00	.12	.75	.09	.40	.15	**.75**	.07	.06	.76
Curious	.16	**.74**	.13	.25	-.06	.11	.67	.18	.32	.14	**.73**	.01	.08	.70
Active	.05	**.68**	-.20	.32	.12	.36	.74	.04	.45	-.19	**.64**	.25	.22	.76
Playful	.04	**.62**	-.18	**.41**	.03	.38	.73	.04	.54	-.17	**.58**	.16	.27	.74
Lazy	.04	**-.60**	-.12	-.22	-.11	**-.52**	.71	.05	-.38	-.13	**-.56**	-.34	-.39	.74
Conventional	-.21	**-.53**	.19	.13	.18	-.27	.48	-.22	.07	.22	**-.59**	-.01	-.35	.57
Imitative	-.16	**.52**	**-.40**	**.44**	.19	.05	.69	-.18	.52	-.39	**.48**	.11	-.09	.71
Disorganized	.02	.07	**-.78**	.14	.19	-.18	.70	.00	.15	**-.79**	.05	.04	-.27	.72
Thoughtless	.30	.08	**-.72**	.06	.23	-.10	.67	.27	.09	**-.73**	.07	.17	-.21	.70
Intelligent	.01	.16	**.68**	.16	-.12	-.12	.55	.04	.13	**.73**	.17	-.16	-.12	.61
Distractible	.04	.09	**-.68**	.09	.24	.05	.54	.00	.14	**-.71**	.07	.21	-.06	.58
Clumsy	-.05	-.03	**-.66**	.21	.15	-.25	.57	-.07	.19	**-.68**	-.04	-.06	-.33	.62
Unperceptive	.08	-.10	**-.63**	-.09	.01	-.24	.48	.07	-.13	**-.68**	-.08	-.14	-.20	.55
Decisive	.23	.12	**.59**	.10	-.11	-.16	.46	.26	.06	**.64**	.14	-.14	-.18	.55
Sensitive	-.24	.08	**.52**	**.48**	-.03	-.10	.58	-.22	**.47**	**.56**	.05	-.16	-.15	.64
Predictable	-.26	-.35	**.49**	.16	-.17	-.16	.51	-.23	.08	**.52**	-.36	-.29	-.09	.55
Erratic	.38	.17	**-.49**	-.08	.35	-.32	.65	.35	-.07	**-.51**	.17	.22	**-.47**	.68
Quitting	.01	-.25	**-.40**	.05	.28	-.15	.32	-.02	.05	**-.42**	-.29	.16	-.28	.37
Sympathetic	-.11	.14	-.02	**.77**	-.15	-.07	.65	-.07	**.76**	-.01	.09	-.31	-.08	.69
Affectionate	-.01	.36	-.02	**.74**	.07	.31	.78	.00	**.82**	-.01	.28	.09	.16	.79
Friendly	-.30	.34	-.03	**.70**	-.05	.23	.75	-.28	**.76**	-.01	.28	-.08	.16	.77
Sociable	.05	.38	-.01	**.69**	.03	**.47**	.84	.05	**.78**	.00	.32	.14	.31	.83
Helpful	-.08	.14	.00	**.68**	-.06	.08	.49	-.05	**.73**	.01	.08	-.14	.01	.56
Gentle	**-.60**	.04	.05	**.60**	-.06	-.16	.75	**-.58**	**.56**	.07	.02	-.29	-.16	.76
Protective	.30	-.17	.16	**.52**	-.11	-.07	.43	.37	**.53**	.19	-.28	-.18	-.09	.57
Dependent	-.38	.24	-.33	**.47**	.39	.11	.70	**-.42**	**.56**	-.32	.17	.28	-.13	.72
Fearful	-.13	-.08	-.25	.00	**.62**	.02	.48	-.20	.08	-.26	-.15	**.59**	-.27	.55
Stable	-.15	-.02	.26	.33	**-.61**	-.11	.59	-.08	.24	.28	.02	**-.69**	.15	.64
Vulnerable	-.39	-.02	-.18	.11	**.59**	-.23	.60	**-.46**	.14	-.18	-.06	.36	**-.49**	.64
Anxious	.09	-.16	-.38	-.08	**.58**	-.27	.60	.02	-.08	-.39	-.17	**.40**	-.53	.64
Cool	-.16	-.35	.12	.26	**-.57**	-.30	.65	-.09	.11	.13	-.32	**-.75**	-.02	.70
Excitable	**.44**	.28	-.09	-.18	**.51**	.02	.57	.39	-.09	-.10	.26	**.58**	-.23	.63
Timid	**-.49**	-.18	-.29	-.10	**.50**	-.22	.67	**-.56**	-.10	-.30	-.18	.29	**-.40**	.69
Independent	.31	.06	.29	-.26	**-.46**	-.17	.49	.36	-.37	.29	.16	**-.44**	.06	.57
Depressed	-.05	-.27	-.28	-.11	.27	**-.67**	.69	-.08	-.22	-.29	-.25	-.08	**-.72**	.72
Solitary	-.11	-.30	.06	**-.46**	.06	**-.66**	.75	-.12	-.60	.05	-.24	-.20	**-.55**	.77

Unemotionality	-.29	-.36	-.29	.08	-.16	**-.45**	.54	-.28	-.04	-.31	-.34	**-.47**	-.34	.62
Individualistic	.09	.30	.02	-.17	.06	.01	.13	.05	-.21	.03	**.43**	.09	-.05	.24
Autistic	-.01	.03	-.08	-.04	.39	-.33	.27	-.06	-.07	-.06	.06	.20	**-.58**	.39
[8]Total traits	52							54						
[9]FA,min,pro	.98	.94	.95	.98	.97	.99								
[10]PCA,var	1.00	.99	1.00	.98	.87	.86								
[11]FA,min,var (5)	.90	.99	.77	.57	.99	.70*								
[12]FA,min,var (4)	.91	.99	.76	.61	.95*	-.62*								

Note.
Values in bold font indicate highest salient loadings; '+' = positive loadings; '-' = negative loadings.
1. Raw: 6 factor solutions are compared in respect to EFA,minres,varimax. vs PCA,varimax rotation method.
2. Raw: factor labelling: Column 2-7: Dom=Dominance. Opn=Openness (to Experience). Con=Conscientiousness. Agr=Agreeableness. Neu=Neuroticism. Ext= Extraversion; h2=communality (*indicates communalities under 0.5).
Column 8-13: Same listening of factors in the eWLG,$_{\text{PCA,min,var,6}}$ as in eWLG,$_{\text{EFA,min,var,6}}$.
Column 1: listening of 54 traits according to their associated factors in the eWLG,$_{\text{EFA,min,var,6}}$ sorted in a descending order of their silent trait loadings.
[8]Total traits = number of traits included into the factor solution. either eWLG,$_{\text{EFA,min,var,6}}$ or eWLG,$_{\text{PCA,min,var,6}}$.
Factor congruence between eWLG,$_{\text{PCA,min,var,6}}$ and [9]FA,minres,promax (6 factors), [10]PCA,varimax (6 factors); [11]FA,minres,varimax (5 factor solution), and [12]FA,minres,varimax (4 factor solution) to each factor is presented.

I present the solution for the following cross-method analyses eWLG$_{\text{,EFA,min,var,6}}$ (6 factor solution) vs. eWLG$_{\text{,PCA,var,6}}$ (6 factors). Total number of traits included into the factor solution is for eWLG$_{\text{,EFA,min,var}}$ N=52 and for eWLG$_{\text{,PCA,var}}$ N=54.

Using eWLG,$_{\text{EFA,min,var,6}}$ as a reference, the first 13 traits, from *Stingy* to *Impulsive*, are grouped on the first factor labelled Dominance (Dom$_{\text{eWLG}}$). The following 9 traits, from *Innovative* to *Imitative* are grouped in the factor Openness (Opn$_{\text{eWLG}}$), the 11 traits *Disorganised* to *Quitting* belong to the Conscientiousness (Con$_{\text{eWLG}}$) factor. The following 8 traits, from *Sympathetic* to Dependent, belong to the factor labelled Agreeableness (Agr$_{\text{eWLG}}$). The following 8 traits listed from *Fearful* to *Independent* are structured into the dimension labelled Neuroticism (Neu$_{\text{eWLG}}$), the last 3 traits *Depressed* to *Unemotionality* describe the factor labelled as the negative continuum of Extraversion (Ext$_{\text{eWLG}}$). The traits *Individualistic* and *Autistic* had to be excluded as these did not meet the criteria for inclusion (≥ |.4) in the personality structure generated with eWLG,$_{\text{EFA,min,var,6}}$.

In total, only seven traits were not consistent across the different analyses procedures eWLG,$_{\text{EFA,min,var,6}}$ vs. eWLG,$_{\text{PCA,var,6}}$ *(Gentle, Dependent, Vulnerable, Excitable, Unemotional, Individualistic* and *Autistic.* Cross-method correlations are represented in the last 4 rows, confirm that the rotation methods of eWLG$_{\text{FA,min,promax,6}}$ as well as the eWLG,$_{\text{FA,min,var,5 and 4}}$ (5 and 4 factor solution) showed that the factors and dimensions are very robust. Overall, 4 of the 6 factors eWLG,$_{\text{FA,min,var,6}}$ were strongly replicated across all compared methods, these were Dominance, Openness, Conscientiousness and Neuroticism. Two factors, Agreeableness and Extraversion showed modest replication. For the outcome of the distribution of traits across different numbers of factors according to the Bass-Ackward factoring algorithm, see **TableAPP 6**.

Additionally, I tested the absolute inter-factor correlation between EFA,$_{\text{Minres,promax}}$ on 6 factors with the mean of 0.16 and SD of 0.17.

Inter-rater reliability of the personality factors, analysed using FA$_{\text{Minres,v}}$.

The internal consistency (Cronbach’s alpha) of the factors was highest for Openness (.89), and lowest for Extraversion (.66) (see **TableAPP 4** for more information).

The eWLG,$_{\text{EFA,min,var,6}}$ is the basis for all the subsequent analyses. These analyses are:

a. validation using coded behaviour on a subgroup of 24 eWLGs.
b. effects of sex and age differences on personality.
c. the cross-species comparison (Procrustes rotation and unit-weighted dimension scores) of the personality structure.
d. Personality factors were compared between sexes and according to age

Correlations between personality factors and state-dependent behaviour responses (s-dbr) for validation

Table 6, below, presents the result of the correlation between the six personality factors and the categorized s-dbr categories. This allowed the validation of the personality structure. Significant results are highlighted in bold.

Table 6 *Correlations between personality factors and state-dependent behavioural responses in eWLGs (N= 24)*

s-dpr	**DomeWLG**	**OpneWLGa**	**ConeWLGa**	**AgreWLGa**	**NeueWLG**	**ExteWLG**
Feeding	-.14	.30	.01	.11	-.19	.51**
Activitya	-.24	.50**	.12	.26	-.13	.34
Agonistic	.40*	-.09	-.25	-.02	-.28	.06
Self-directed_negative	.22	.26	.21	.34	-.50**	.45*
Play	.07	.72***	.05	.40*	.15	.21
Prosocial	-.06	.46	.32	.23	-.38	.41*
Proximity	.33	.45*	.46*	.56***	-.18	.35

Note.
All behaviours are calculated as all occurrences and calculated as a mean rate per minute and grouped as following:
The s-dbr have been regrouped in the following categories:
Feeding: foraging and food manipulation.
Action: Following, leaving, approaching, nest building, locomotion, Passing another individual and play.
Agonistic behaviour: Contact aggression, non-contact aggression, such as displacement and staring.
Self-directed behaviour: nose-touch.
Play: Play behaviour, Object manipulation, drumming, chestbeat, initiate and join play.
Prosocial: touch, groom, hold on, contact resting (direct body contact with another gorilla), share attention, positive affect
Proximity: individual in close proximity > 1.5m (no direct body contact) to another gorilla.
a Pearson correlation, all others are Spearman rank correlations.
Column 1: coded s-dbr, see ethogram for definition.
Column 2 – 7: Correlations between rated personality structure generated via FAminres,v (6 factors) and observed s-dbr.
Factors: a = normally distributed. DomeWLG = Dominance, OpneWLGa = Openness, ConeWLGa = Conscientiousness, AgreWLGa = Agreeableness, NeueWLG = Neuroticism, and ExteWLG = Extraversion.
Bold font indicates significant correlations *p< .05, ** p<.01 *** p < .001.

As shown in **Table 6**, each personality factor showed significant correlations to the mentioned behavioural categories (see Notes, **Table 6**). The factor DomeWLG is significant positive correlated with agonistic behaviour, implying that more dominant gorillas exhibit more agonistic behaviours. OpneWLG is significant correlated with activity, play and proximity, indicates that more open eWLGs are more likely to engage in play, physical activities and seek close social contact to other eWLGs. The positive significant correlation of ConeWLG with proximity shows, that more conscientious eWLGs tend to stay closer to their conspecifics. Same was found for eWLGs rated higher on the factor Agr$_{eWLG}$. Additionally, they also tend to be more playful. Self-directed behaviours are significant negative correlated with Neu_{eWLG}, but positive correlated with ExteWLG. Additionally, feeding shows a significant positive correlation with Ext_{eWLG}., indicating that more extraverted gorillas are more likely to engage in feeding behaviours. Ext_{eWLG} is also significant positively correlated with prosocial behaviour, indicating that eWLGs higher on Extraversion show more prosocial behaviours.

In **Table** 7, I included the personality factors (six factors) in the middle. They are surrounded by positive (right) and negative (left) loaded traits which represent the personality structure. Additionally, I included single s-dbr, which I predicted to be correlated with those personality factors. The results from **Table 6**, are presented within the 1st and last column, to show the significant correlations to the s-dbr categories and to understand which traits have been included in the each personality factor.

Table 7 *Personality structure (N=203) with predicted behaviours, and correlations found (N=24)*

Correlation found	Low loaded: Predicted behaviour	Negative Loaded Traits	Personality Factors	Positive Loaded Traits	High loaded: Predicted behaviour	Correlation found
	Hold on^{p} Being stared on^{r} Approach^{p}	Submissive, Cautious	**Dominance**	Stingy, Bullying, Aggressive, Dominant, Persistent, Jealous, Irritable, Reckless, Manipulative, Defiant, Impulsive	Contact aggression^{p} Displace^{p} Staring^{p} Approach^{p}	Agonistic behaviour
	Mother neg. detach^{p}	Lazy, Conventional	**Openness**	Innovative, Inventive, Inquisitive, Curious, Active, Playful, Individualistic, Imitative	Social Play^{p,r}, Locomotion, Contact resting^{p,r} Social Play^{p,r} Solitary Play^{p} Start Play^{p} Join Play^{p} Object manipulation Food manipulation	Activity Play Proximity (close)
	Abnormal behaviour	Disorganized, Thoughtless, Distractible, Clumsy, Unperceptive, Erratic, Quitting	**Conscientiousness**	Intelligent, Decisive, Sensitive, Predictable	Object manipulation, Watch attentively^{p}	Proximity (close)
	Limited social behaviour, Such as proximity, or Prosocial behaviour		**Agreeableness**	Sympathetic, Affectionate, Friendly, Sociable, Helpful, Gentle Protective, Dependent	Contact resting Prosocial behaviour Touch Proximity	Play Proximity (close)

Self-directed	Inactive, Contact resting	Stable, Cool Independent	**Neuroticism**	Fearful, Vulnerable, Anxious, Excitable, Timid, Independent	Self-directed beh., Out of sight, Negative Emotion	
	Self-directed behaviour, Negative emotion, Limited social behaviour	Depressed, Solitary, Unemotional	**Extraversion**		Social behaviours	Feeding Self-directed Prosocial

Another way to illustrate the personality factors is the trait distribution and the examined correlation to behaviours as shown in **Figure 5**. The Figure represents a circular model with multidimensional axes that illustrates the distribution of the six personality factors of eWLGs and the clustered traits within the factors as well as alongside multiple axes representing a constitution of a continuum between two opposite ends. For instance, the factor Agreeableness, is a spectrum that spans from highly agreeable to highly disagreeable. The majority of gorillas fall somewhere in the middle of each dimension, rather than at the extremes. The model also includes the dimension a) emotional stability to emotional instability, representing neurotic behaviours, shown with the factor Neuroticism on top of the wheel and clustered traits representing neurotic traits, such as anxious and fearful etc. The other dimensions representing the axes on b) high to low arousal, c) high to low vitality, and d) pleasure to displeasure. The measured behaviours are grouped in purple at the outside of the cycle and represents correlated behaviours observed.

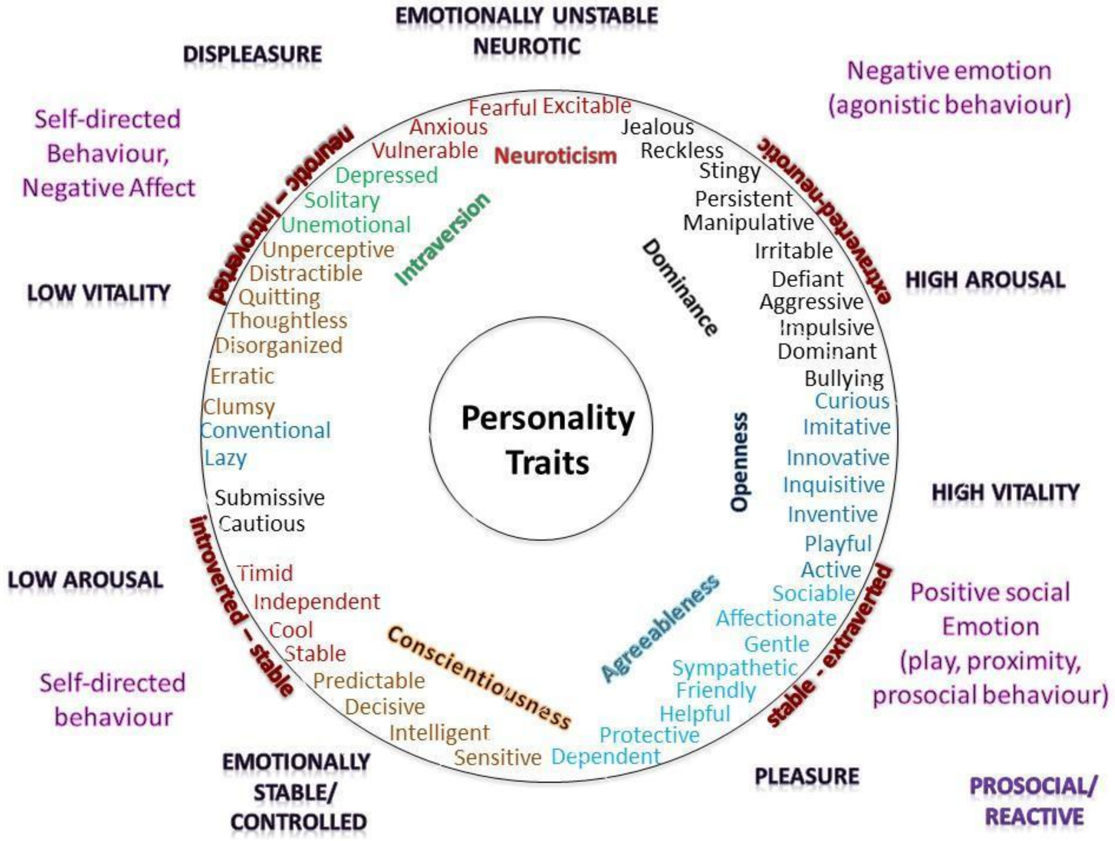


Figure 5 *Distribution of the traits of the six personality factors and correlated behaviours*

Note.

The 52 personality traits of the personality structure generated via EFA$_{\mathrm{Minres,v}}$ remaining in the following colour coded factors:
Green: Extraversion (opposite side: Introversion); red: Neuroticism, black: Dominance; dark blue: Openness, light blue: Agreeableness, brown: Conscientiousness.
The correlated behaviours are distributed over the six personality factors and represented in purple.
There are multiple dimensions included from emotionally unstable/ neurotic to emotionally stable/ controlled: from high arousal to low arousal, from low vitality to high vitality and from pleasure to displeasure.

Effects of sex and age differences on personality

Below the analyses on the effect of sex or age, or the interaction between both factors on the personality structure in eWLGs. For results see **Table 8** and **Figure 6**.

Table 8 *Age, Sex and Age x Sex Differences on Personality factors of eWLGs (N=203)*

Factor	**Tested effect**	***B***	***SE$_b$***	***t***	***p***
Dom$_{\mathrm{eWLG,}}$	Age	-.16	.07	-2.47	.13
	Sex	-1.27	2.57	-.49	**.02***
	Age x Sex	.23	.11	2.10	**.03***
Opn$_{\mathrm{eWLG,}}$	**Age**	-.50	.05	-10.26	**< 0.001*****
	Sex	1.15	1.92	.60	.52
	Age x Sex	-.09	.08	-1.11	0.27
Con$_{\mathrm{eWLG,}}$	**Age**	.10	.05	1.98	**.02***
	Sex	-2.42	2.06	-1.17	**.02***
	Age x Sex	-.01	.09	-.16	.87
Agr$_{\mathrm{eWLG,}}$	**Age**	-.24	.06	-.4.19	**< 0.001*****
	Sex	1.41	2.27	.62	**. 04***
	Age x Sex	-.20	.10	-2.04	**. 04***
Neu$_{\mathrm{eWLG,}}$	**Age**	-.04	.06	-.68	**.02***
	Sex	2.63	2.49	1.06	.18
	Age x Sex	-.23	.11	-2.12	**.03***
Ext$_{\mathrm{eWLG,}}$	**Age**	-.31	.05	-.5.81	**< 0.001*****
	Sex	2.65	2.13	1.24	.25
	Age x Sex	-.07	.09	-.74	.46

Note.
Dom$_{\mathrm{eWLG}}$=Dominance, Opn$_{\mathrm{eWLG}}$=Openness, Con$_{\mathrm{eWLG}}$=Conscientiousness, Agr$_{\mathrm{eWLG}}$=Agreeableness/ Sociability, Neu$_{\mathrm{eWLG}}$=Neuroticism, Ext$_{\mathrm{eWLG}}$=Extraversion.
B = unstandardized linear regression coefficient
SE$_b$ = SE of linear regression coefficient
t = t value
p = correlation coefficient, bold font indicates significant correlations *p< .05, ** p< .01 *** p < 0.001.
green=increasing, red=decreasing.

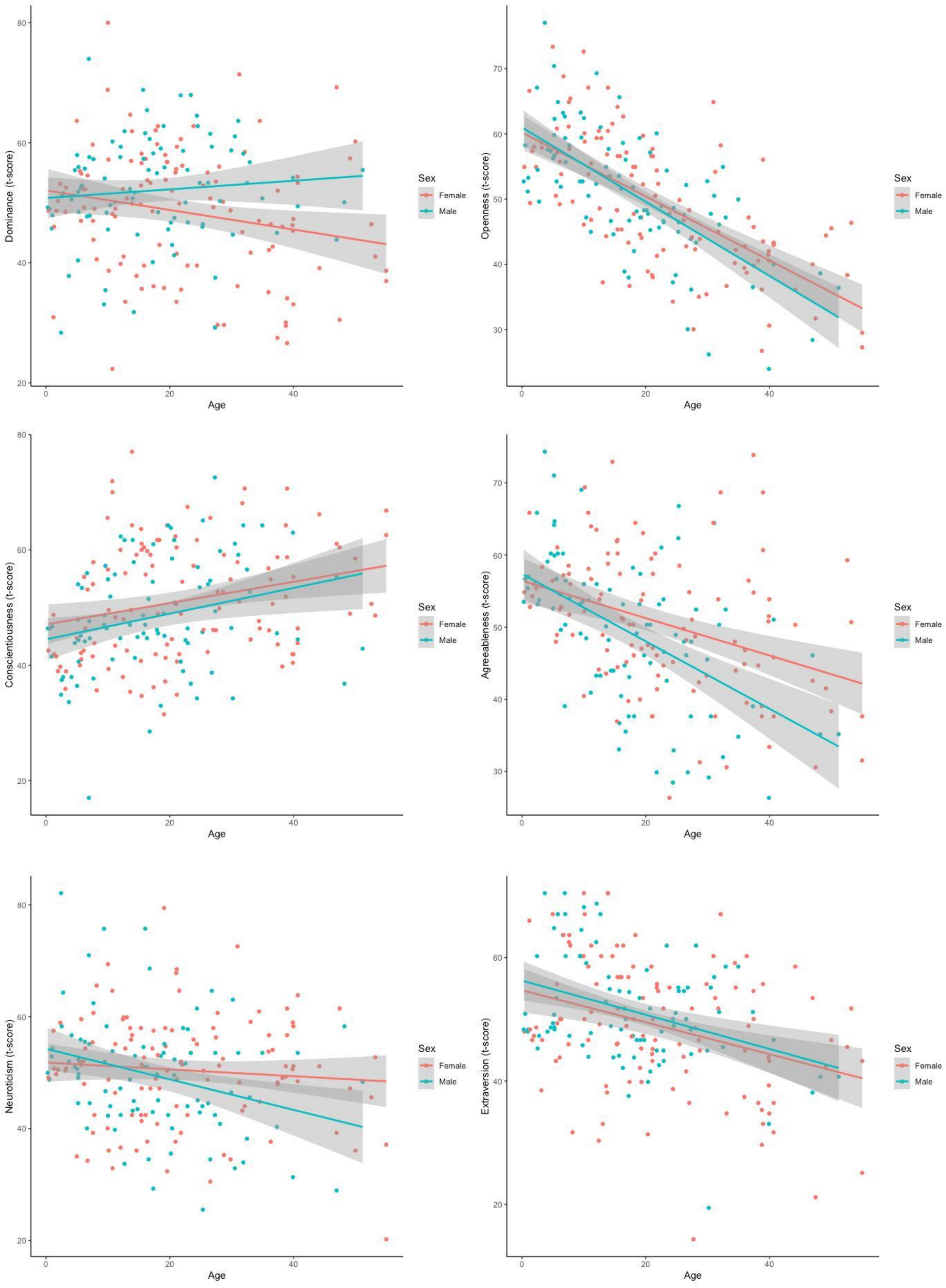


Figure 6 *Age Differences on Personality factors of eWLGs*

Note.
Graphs are shown in the following order of the personality factor of eWLGs: Dom$_{\text{eWLG}}$, Opn$_{\text{eWLG}}$, Con$_{\text{eWLG}}$, Agr$_{\text{eWLG}}$, Neu$_{\text{eWLG}}$ and Ext$_{\text{eWLG}}$.
Score distribution of female (red) and male (blue) on each of the personality factor presented by eWLG ages.

Significant age or sex effects for all factors are represented in **Table 8**. On all factors, apart from Dom$_{\text{eWLG}}$, an age effect was found. The graphical representation of the regression in **Figure 4** shows a negative effect on age for the following factors: Opn$_{\text{eWLG}}$, Agr$_{\text{eWLG}}$ Neu$_{\text{eWLG}}$ and Ext$_{\text{eWLG}}$, meaning that there is a decline with age. A positive effect, however, has been found for Con$_{\text{eWLG}}$.

An negative effect on the gender (females) was shown for Dom$_{\text{eWLG}}$ and Con$_{\text{eWLG}}$, for Agr$_{\text{eWLG}}$, it was positively. In all factors, except for Con$_{\text{eWLG}}$, females showed a slight downward trend, indicating a more pronounced decrease with age. Same for males, except for Dom$_{\text{eWLG}}$ and Con$_{\text{eWLG}}$ which increased with age. Individual variability within all factors was found to high for both sexes and across all age. The interaction between sex and age influenced Dom$_{\text{eWLG}}$, Agr$_{\text{eWLG}}$ and Neu$_{\text{eWLG}}$, negatively.

Cross-great ape comparison

A comparison of diverse rotated factor structures of the data on eWLG,$_{\text{EFA,min,var}}$ vs the personality structure of other ex situ great ape species using Procrustes rotation can be found in **Table 9**. All traits are tested highly robustly in all the different comparisons.

Table 9 *Comparing diverse rotated factor structures of eWLG versus the personality structure of other ex situ primate species using Procrustes rotation*

	1	2	3	4	5	6	7	8
Traits	eWLGs personality structure							
	EFA, min, var	PCA	EFA, min, var	PCA	EFA, min, var	PA	EFA, min, var	FA, minres
	rotated subspecies							
	eBonobo[1] FA	eBonobo[1] PCA	eJapan[2] FA	eJapan[2] PCA	eYerkes[3] FA	eYerkes[3] PA	eChimp[4] FA	eChimp[4] PA
Stingy	.95	.95	.96	.96	.93	.93	.66	.66
Bullying	.97	.97	.98	.98	.98	.98	.97	.97
Aggressive	.95	.95	.94	.94	.95	.95	.95	.95
Dominant	.97	.96	.96	.97	.91	.91	.95	.95
Persistent	.96	.96	.89	.89	.88	.88	.96	.96
Jealous	.94	.93	.94	.93	.89	.89	.73	.73
Submissive	.98	.98	.95	.95	.88	.88	.91	.91

Irritable	.99	.99	.94	.94	.94	.94	.94	.94
Reckless	.93	.99	.88	.89	.90	.90	.99	.99
Manipulative	.82	.82	.89	.89	.82	.82	.74	.74
Defiant	.88	.87	.84	.85	.90	.90	.91	.91
Cautious	.77	.77	.65	.65	.79	.79	.83	.83
Impulsive	.99	.99	.85	.86	.88	.88	.97	.97
Innovative	.94	.94	.98	.98				
Inventive	.95	.95	.99	.98	.76	.76	.98	.98
Inquisitive	.97	.97	.96	.96	.92	.92	.98	.98
Curious	.98	.98	.98	.98				
Active	.99	.99	.95	.95	.91	.91	.95	.95
Playful	.97	.97	.95	.96	.97	.97	.944	.94
Lazy	.95	.95	.92	.92	.96	.96	.97	.97
Conventional	.94	.95	.75	.75				
Imitative	.95	.95	.93	.94	.71	.71	.87	.87
Disorganized	.92	.92	.97	.96	.95	.95	.83	.83
Thoughtless	.89	.89	.86	.86				
Intelligent	.93	.92	.80	.81	.94	.94	.83	.83
Distractible	.97	.98	.99	.99				
Clumsy	.85	.86	.85	.86	.94	.94	.85	.85
Unperceptive	.88	.86	.95	.95				
Decisive	.87	.84	.89	.90	.86	.86	.81	.81
Sensitive	.90	.90	.86	.87	.92	.92	.95	.95
Predictable	.82	.81	.78	.79	.79	.79	.98	.98
Erratic	.95	.95	.53	.53	.99	.99	.90	.95
Quitting	.88	.89	.76	.76				
Sympathetic	.82	.81	.81	.81	.90	.90	.83	.83
Affectionate	.83	.83	.89	.88	.80	.80	.80	.80
Friendly	.92	.91	.82	.82	.89	.89	.95	.96
Sociable	.95	.95	.94	.94	.95	.95	.96	.96
Helpful	.83	.83	.82	.83	.84	.84	.94	.94
Gentle	.97	.97	.94	.93	.98	.98	.91	.91
Protective	.93	.92	.80	.78	.75	.75	.95	.95
Dependent	.89	.89	.87	.87	.85	.85	.88	.88
Fearful	.95	.94	.79	.81	.89	.89	.86	.86
Stable	.95	.95	.99	.99	.79	.78	.96	.96
Vulnerable	.88	.88	.88	.87				
Anxious	.89	.89	.89	.89				
Cool	.82	.82	.94	.95				
Excitable	.75	.75	.84	.84	.88	.88	.78	.78
Timid	.97	.97	.83	.83	.93	.93	.95	.95
Independent	.93	.93	.84	.86	.96	.96	.91	.91
Depressed	.95	.95	.57	.56	.98	.98	.92	.91
Solitary	.94	.94	.94	.94	.97	.97	.99	.99
Unemotional	.77	.77	.91	.92	.69	.69	.74	.74
Individualistic	.54	.63	.37	.48				
Autistic	.89	.86	.77	.73	.85	.85	.79	.79

Note.

Procrust rotations: with ex situ populations of:

1. eWLG,$_{\text{EFA,min,var}}$ vs. eBonobo$_{\text{FA}}$, Weiss et al., (2015), 54 trait form.
2. eWLG,$_{\text{PCA}}$ vs. eBonobo$_{\text{PCA}}$, Weiss et al., (2015), 54 trait rating form.
3. eWLG,$_{\text{EFA,min,var}}$ vs. eJapan$_{\text{FA}}$, Weiss et al., (2009). 54 trait rating form.
4. eWLG,$_{\text{PCA}}$ vs. eJapan$_{\text{PCA}}$, Weiss et al., (2009). 54 trait rating form.
5. eWLG,$_{\text{EFA,min}}$ vs. eYerkes$_{\text{FA,}}$ Weiss and colleagues (2007). 43 trait rating form.
6. eWLG,$_{\text{PA}}$ vs. eYerkes$_{\text{PA}}$, Weiss et al., (2007). 43 trait rating form.
7. eWLG,$_{\text{EFA,min,var}}$ vs. eChimp$_{\text{FA}}$, King & Figueredo (1997). 43 trait rating form.
8. eWLG,$_{\text{FA,minres}}$ vs. eChimp$_{\text{PA}}$, King & Figueredo (1997). 43 trait rating form.

Correlations between eWLG,$_{\text{EFA,min,var}}$ unit-weighted scores and those of ex situ populations: eWLGs (Gold and Maple, 1994), bonobos (Weiss et al., 2015), orangutans (Weiss et al., 2006), two data sets of chimpanzees (Chimp, King and Figueredo (1997); Japan, Weiss et al. (2009)), and humans (Weiss, 2022) are shown in **Table 10**.

Table 10 *Correlations between eWLGs personality factors (unit-weighted scores) and those of ex situ great ape populations: eWLGs (US), bonobos, orangutans, chimpanzees*[1&2]*, and humans*

cWLGs	**Dom$_{cWLG}$**	**Opn$_{cWLG}$**	**Con$_{cWLG}$**	**Agr/ Soc$_{cWLG}$**	**Neu$_{cWLG}$**	**Ext$_{cWLG}$**
cWLGs$_{1994}$[1]						
Extraversion	.19 (.05, .32)	.90 (.87, .92)	.03 (-.16, .11)	.68 (.60, .75)	-.02 (-.15, .12)	.74 (.67, .80)
Dominance	.76 (.70, .82)	.01 (-.13, .15)	-.41 (-.52, -.25)	-.34 (-.46, -.21)	.36 (.24, .48)	-.01 (-.15, .12)
Fearful	-.12 (-.26, .02)	-.03 (-.17, .11)	-.37 (-.48, -.25)	.03 (-.11, .16)	.78 (.72,.83)	-.14 (-.27, .00)
Understanding	.19 (.05, .32)	.02 (-.11, .16)	.13 (-.01, .26)	.44 (.32, .54)	-.19 (-.32, .05)	.07 (-.06, .21)
Bonobo[2]						
Assertiveness	.42 (.29, .52)	-.04 (-.17, .01)	.47 (.36, .57)	-.17 (-.30, -.03)	-.09 (-.92, -.87)	.22 (.09, .35)
Conscientiousness	-.93 (-.94, -.90)	-.19 (-.32, -.06)	.47 (.36, .57)	.23 (.10, .36)	-.02 (-.33, -.07)	-.01 (-.24, .04)
Openness	.19 (.06, .32)	***1.0*** (.95, 98)	-.02 (-.16, .11)	.56 (.46, .65)	.01 (.02, .44)	.06 (.05, .68)
Attentiveness	-.17 (-.30, .04)	-.04 (-.17, .01)	***.96*** (.94, .97)	-.06 (-.20, .07)	-.49 (-.13, .14)	.24 (.11, .37)
Agreeableness	-.09 (-.23, .05)	.56 (.46, .65)	.18 (.04, .31)	***.96*** *(.95, .97)*	-.15 (-.59, -.38)	.46 (.35, .56)
Extraversion	.05 (-.09, .18)	.37 (.24, .48)	.24 (.11, .37)	.04 (.28, .51)	-.35 (-.28, -.01)	.75 (.68, .80)
Orangutan[3]						
Extraversion	.21 (.08, .34)	.96 (.95, .97)	.04 (-.10, .17)	.57 (.47, .65)	-.05 (-.44, -.19)	.78 (.72, .83)
Dominance	***.99*** (.99, .99)	.11 (-.03, .24)	-.02 (-.33, -.06)	-.28 (-.04,- .15)	-.01 (-.18, .09)	.18 (.04, .31)
Neuroticism	.01 (-.03, .24)	.06 (-.08,.19)	-.64 (-.72, -.56)	-.01 (-.23, .04)	***.94*** (-.24, .03)	-.19 (-.32,- .05)
Agreeableness	-.09 (-.23, .05)	.56 (.46, .65)	.18 (.04, .31)	***.96*** (.95, .97)	-.15 (.92, .96)	.46 (.35, .56)
Intellect	.16 (.03, .03)	-.12 (-.28, .01)	.80 (.74, .84)	-.32 (-.44, -.19)	-.61 (-.28, -.01)	.13 (-.01, .26)
Chimpanzee[4]						
Dominance	.83 (.07, .33)	.06 (.89, .93)	-.79 (-.01, .26)	-.27 (.35, .57)	.43 (-.24, .03)	.18 (.36, .57)
Extraversion	.19 (.78, .87)	.86 (.06, .32)	-.24 (.05, .32)	.29 (-.25, .03)	.26 (-.06, -.39)	.89 (.22, .46)
Conscientiousness	.19 (-.07, .02)	.01 (.83, .90)	.67 (-.13, .14)	.26 (.71, .82)	-.24 (-.15, .13)	.16 (.68, .80)
Agreeableness	-.11 (-.84, -.74)	.77 (-.36, -.10)	.12 (.59, .74)	.85 (-.02, .26)	-.14 (-.48,-.25)	.47 (-.16, .12)
Neuroticism	-.05 (-.40, -.14)	-.01 (.16, .41)	-.37 (.13, .38)	-.21 (.81, .89)	.52 (-.34, -.07)	-.11 (.03, .30)
Openness	.35 (.31, .53)	.75 (.12, .38)	-.02 (-.37, -.11)	.17 (-.27, .00)	.36 (.41, .61)	.47 (.23, .47)
Chimpanzee[5]						
Dominance	.83 (-.72, .56)	.19 (-.55, -.33)	.19 (.56, .72)	-.11 (-.15, .13)	-.05 (-.50, -.27)	.35 (-.35, -.09)
Extraversion	.06 (.66, .79)	.86 (-.04, .23)	.01 (.18, .43)	.77 (-.34, -.08)	-.01 (-.74, -.59)	.75 (.18, .43)

Conscientiousness	-.79 (-.09, .18)	-.24 (.80, .88)	.67 (-.13, .15)	.12 (.72, .83)	-.37 (-.15, .12)	-.02 (.67, .80)
Agreeableness	-.27 (-.72, -.56)	.29 (-.30,-.04)	.26 (.81, .89)	.85 (-.08, .20)	-.21 (-.57,-.35)	.17 (-.04, .23)
Neuroticism	.43 (-.45, -.21)	.26 (.01, .28)	-.24 (.15, .40)	-.14 (.74, .84)	.52 (-.31, -.04)	.36 (-.08, .20)
Openness	.18 (.21, .45)	.89 (.09, .35)	.16 (-.44, .32)	.47 (-.27, .00)	-.11 (.55, .71)	.47 (.07, .34)
Humans[6]						
Openness	.35 (.22, .47)	.94 (.92, .96)	-.02 (-.15, .12)	.55 (.44, .64)	-.06 (-.02, .07)	.58 (.49, .67)
Agreeableness	-.93 (-.95, -.91)	.02 (-.11, .16)	.24 (.01, .36)	.47 (.35, .57)	-.01 (-.15, .13)	-.05 (-.19, .09)
Conscientiousness	-.18 (-.31, -.05)	-.02 (-.16,.12)	.94 (.92, .95)	-.11 (-.24, .03)	-.57 (-.65, -.46)	.27 (.14, .39)
Neuroticism	-.03 (-.16, .11)	.09 (-.05, .22)	-.31 (-.43, -.18)	-.01 (-.14, .13)	.90 (.88, .93)	.00 (-.14, .14)
Extraversion	.15 (.01, .28)	.67 (.58, .74)	.23 (.09, .35)	.68 (.06, .75)	-.34 (-.45, -.21)	.87 (.83, .90)

Note.

Column 1: listing of compared species:[1]Gold and Maple, 1994), [2]Weiss et al. (2015), [3]Weiss et al. (2006), [4]King and Figueredo, 1997: zoochimps=data chimpanZoo sample, [5]Weiss et al. (2007): JPchimps=Yerkes chimpanzee, [6]Weiss (2022).

Column 2-7: personality factors of eWLGs: $\text{Dom}_{\textbf{eWLG}}$ = Dominance, $\text{Opn}_{\textbf{eWLG}}$ = Openness, $\text{Con}_{\textbf{eWLG}}$ = Conscientiousness, Agr/ $\text{Soc}_{\textbf{eWLG}}$ = Agreeableness/ Sociability, $\text{Neu}_{\textbf{eWLG}}$ = Neuroticism, $\text{Ext}_{\textbf{eWLG}}$ = Extraversion. Bold font indicates highest correlation coefficients (Confidence Interval). $p < .05$, underscored values indicate the highest overall correlation with eWLGs factor.

Cross-gorilla comparison: A comparison to the personality structure generated by Gold and Maple (1994) on eWLGs

Extraversion (Opn$_{cWL}$ (.90/Extraverted). The factors congruence for Dom$_{eWLG}$ (.76/Dominance), Neu$_{eWLG}$(.78/Fearful), and Ext$_{eWLG}$ (.74/Extroverted) remained high. The emergence of two additional factors (Conscientiousness and Openness) has been previously reported in chimpanzees (Weiss, 2007) and seem to be due to the underrepresentation of the traits in the rating form in the earlier study of Gold & Maple, (1994).

Cross- great ape and human comparison

Overall, the eWLGs personality structure had the highest agreement with the following factors of ex situ great ape populations:

To bonobos: Dom$_{eWLG}$ and Conscientiousness (-.93), Opn$_{eWLG}$ and Openness (1.0), Con$_{eWLG}$ and Attentiveness (.96), Agr$_{eWLG}$ and Agreeableness (.96), and Neu$_{eWLG}$ and Assertiveness (.90) in Weiss et al. 2009);

To orangutans: Dom$_{eWLG}$ and Dominance (.99), Opn$_{eWLG}$ and Openness (.96), Agr$_{eWLG}$ and Agreeableness (.96), and Neu$_{eWLG}$ and Neuroticism (.94) in Weiss et al. 2009);

And to humans: Dom$_{eWLG}$ and Agreeableness (-.93), Opn$_{eWLG}$ and Openness (.94), Con$_{eWLG}$ and Conscientiousness (.94), and Neu$_{eWLG}$ and Neuroticism (.90), and Ext$_{eWLG}$ and Extraversion (.87) in (Weiss, 2022).

Comparison of evolutionary integrated low-order facets across closely related species. The missing link!

Anxiety (ANX) and Confidence (CNF), blend to the factor Neu$_{eWLG}$, as previously reported for all great apes and capuchin monkeys (Morton et al., 2015; Weiss, King, et al., 2011). The factor OPN$_{eWLG}$ consists of the typical OPN lower-order facets (such as e.g., Inquisitiveness, Unconventionality), and the ACT (Activity = lower-order facet). In humans, chimpanzees, and orangutans SOC and ACT blend to Extraversion (EXT). However, such as with the *Cercopithecidae*, our Agreeableness (AGR) factor includes the lower-order facet of Sociability

(SOC), and Altruism (ALT), a combination also mentioned as Friendliness (see Weiss et al., 2011). In eWLGs, I found three basic dimensions: Dom_{eWLG}, Con_{eWLG} and Ext_{eWLG}. Two low-order facets. Conscientiousness (CON) is a unitary factor in our eWLGs, as in chimpanzees, bonobos, and humans, and to some extent, brown capuchin monkeys (labelled Attentiveness), although in orangutans an Intellect factor comprises the two facets of Openness and Conscientiousness.

For more information see **Figure 7**, where I have included the extracted personality structure of eWLGs into the Cladogram of Weiss and colleagues (2011).

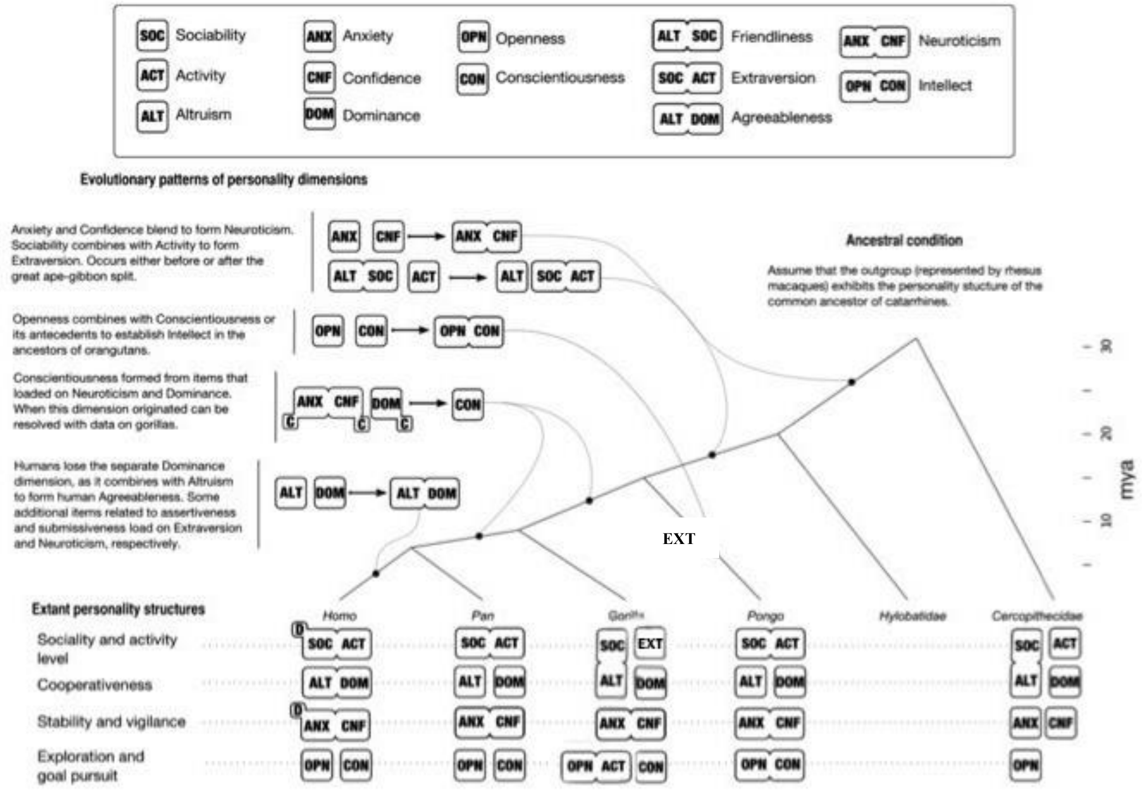


Figure 7 *Cladogram of Weiss, Adams, Widdig, et al. (2011)*

Note.
Adding additional great ape species (iVMG, iWLG and eWLG) and bonobos into the Cladogram of Weiss et al., (2011), we cannot hold on to the suggested ancestral evolutionary patterns of primate personality as suggested/ proposed in the earlier publication. Within this Figure, I added eWLGs as a representative of the others to show that the suggested phylogenetic distribution is no longer supported.

In **Table 11**, the higher-order factors are listed as well as the lower-order facets (trait constructs). This gives a better understanding of how the higher/lower-order factors are distributed by adding additional species into the existing cladogram of Weiss et al. (2011), such as bonobos and eWLGs.

Table 11 *Comparison of higher-order factors as well as lower-order facets of compared great apes (cWLGs, (in situ is not listed as analysis follows in* Chapter 4*), humans, orangutans, bonobos, and chimpanzees*

Dimension	eWLG	humans	orangutan	bonobos	chimpanzee
DOM	DOM = COM: Emotionality, RR + AGR		DOM (Dominant) / - neg AGR (human)	EMO + DOM (Dominant, -Vulnerable) + less ANX	DOM
OPN	ACT + typ OPN (CREA + EXP)	CREA + EXP		ACT + typ OPN (CREA + EXP)	CREA + EXP
CON	CON = ACH + INT	CON = ACH + INT	Intelligent = NEU + CON + OPN	less AGR+ ACH	CON = ACH + INT
AGR	SOC + ALT + AUP	ALT + SUP + less ANX +less CNF + NEGAFF + INT+ AGR	ALT + SUP = AGR (human)	SOC + ALT + SUP	DOM (Dominant) = inverse of the AGR (human)
NEU	Emotional stability = EMO + ANX + CNF	ANX + CNF + DOM	ANX + CNF +EMO + NEGAFF		ANX + CNF
EXT	SOC + NEGAFF (inverse)	SOC + ACT - DOM	ACT + OPN/ SOC Could be OPN, too	could be NEGAFF	SOC + ACT

Note.

Lower-order facets (trait constructs):
SOC = Sociability = traits such as: Sociable and Solitary
ACT = Activity = traits such as: Playful, Active
ALT = Altruism = traits such as: Friendly, Sympathetic, Helpful
ANX = Anxiety = traits such as: Anxious, Depressed, Timid, Fearful, Vulnerable
CNF= Confidence = traits such as: Confident, Independent
EMO = Emotional stability / Self-Control= traits such as: Cool, Stable
NEGAFF = Negative affect = traits such as: (NEGAFF)
SUP = Supportive = trait Protective
CREA = Creativity
EXP = Explorative tendencies
INT = Intelligence
ACH = Achievement
Dominance = DOM = Dominance = Competitive prowess (COM), Emotionality, Risk taking and Resource monopolisation (RR)+ Aggressive (AGG) + Impulsive + Vulnerable

Higher-order dimensions:
Neuroticism = NEU = ANX + CNF = Anxious + Less confident
Intelligent= INT = OPN + CON
Friendliness = FRI = ALT + SOC
Agreeableness = AGR = ALT + DOM
Extraversion = EXT = SOC + ACT
Dominance = DOM = Dominance = Competitive prowess: Emotionality, Risk taking and Resource monopolisation + Aggressive + Impulsive + Vulnerable
Openness = OPN = Creativity + Exploratory tendencies
Conscientiousness = CON = Achievement, Intelligence

3.5 Discussion

One of the main goals of the current study was to identify the personality structure of eWLGs and test the robustness of the structure with different methodical procedures (EFA vs. PCA), using different rotation and factoring techniques. In terms of the cross-method comparison on eWLGs personality structure, the findings were consistent with previous findings in humans (Ashton et al., 1998; Caprara & Perugini, 1994; Goldberg, 1990) and other studies on non-human primates, where different factoring rotations result in high factor agreement (Morton, Lee, & Buchanan-Smith, 2013; Weiss, King, et al., 2011), even with inter-method comparisons (Weiss et al., 2007). Previous studies have used regularised exploratory factor analysis (Jung & Takane, 2008) for very small sample sizes, and the results of these studies are also consistent with those obtained using PCA (varimax) (Konečná et al., 2012; Schaefer & Steklis, 2014).

The use of the standardised HPQ (Weiss et al., 2006), in this case the GPQ, facilitated comparisons based on the same list of traits to identify the presence and absence of factors in a cross-great ape comparison (Weiss, King, et al., 2011). The six personality factors identified in eWLGs - labelled as Dominance ($\mathrm{Dom}_{\mathrm{eWLG}}$), Openness ($\mathrm{Opn}_{\mathrm{eWLG}}$), Conscientiousness ($\mathrm{Con}_{\mathrm{eWLG}}$), Agreeableness/Sociability ($\mathrm{Agr}_{\mathrm{eWLG}}$), Neuroticism ($\mathrm{Neu}_{\mathrm{eWLG}}$), and Extraversion ($\mathrm{Ext}_{\mathrm{eWLG}}$) - demonstrated a robust and reliable data-set and replicated comparable results as found for humans (Goldberg, 1990; Weiss, 2022) and other non-human primate species and animals (Eckardt et al., 2015; Freeman & Gosling, 2010; Gosling, 2001; Weiss et al., 2007, 2009; Weiss, King, et al., 2011).

I was able to confirm the personality factors generated by Gold & Maple (1994) using the Gorilla Behavioural Index (GBI, Stevenson-Hinde & Zunz, 1978). The rating form (GPQ) consists of 54 traits whereas Gold and Maple (1994) used 25 traits in their GBI. One of the reasons for the still high agreement of the factors might be due the fact that some of the US eWLGs have been rated on both questionnaires. Gold and Maple (1994) included 298 US eWLGs in their personality analysis, 136 US eWLGs are rated for this data set. There will be some overlap in ratings of the overall US eWLGs population (N=344) as registered in the International Studbook 2012. I extend their findings, and the structure generated via the GPQ maps well onto personality factors reported in other ex situ non-human primates (capuchin monkeys: Morton et al., 2015; rhesus macaques: Weiss, Adams, et al., 2011) and especially onto those of ex situ great ape species: bonobos, orangutans, and chimpanzees, but also humans (Costa & McCrae, 1992; Goldberg, 1990; King & Figueredo, 1997; McCrae & Costa, 1987; Weiss, 2022; Weiss et al., 2007, 2009, 2015; Weiss, King, et al., 2011). The results of this analysis indicate that both social (according to the trait loadings) and phylogenetic relationships play a significant role in the emergence, maintenance, and evolution of personality traits.

In the following sections, I discuss the importance of each of the six personality factors in respect to the composition of trait loadings, cross-species comparison, the existence of communalities in shared higher-order and lower-order personality factors across Hominidae, and the implications for eWLGs' lives, demographic variables, and correlation with eWLGs behaviours.

Dominance (Dom$_{eWLG}$)

In eWLGs, the Dom$_{eWLG}$ factor describes negative destructive streaks and their negative counterparts. Thirteen negative social traits, from the facet aggressiveness (AGR) and competitive prowess (COM) (Bullying, Aggression, Dominant, Reckless, Manipulative, (un-) Submissive), emotionality (EMO) and risk-taking facets (Irritable, Defiant, Impulsive), (un-) Cautious), Jealous, Persistent) and resource monopolization (RR)/ greed (Stingy/Greedy) are grouped into this factor. A good trait consistency with the Dominance factor previously identified using the GBI in eWLGs (Gold & Maple, 1994) was found, but might be due to the general lack of overlapping traits. A similar Dominance factor has been reported in other primate species (Weiss, Adams, Widdig, et al., 2011), sometimes labelled as Confidence (Bolig et al., 1992; Caine et al., 1983, 1983; Murray, 1998), Aggression (Buirski et al., 1978), or Assertiveness (Morton et al., 2015). Dominance is one of the most identified personality factors and is phylogenetically old, as it is also widely found across the animal kingdom (Freeman & Gosling, 2010; Gosling, 2008; Gosling & John, 1999). Humans, however, lack a separate Dominance factor as these traits loaded negatively on the Agreeableness dimension (Weiss, 2022). Traits that load on the Dom$_{eWLG}$ factor in my eWLGs, load positively and with high congruence on the Dominance factor in ex situ populations, such as orangutans, negatively on the Conscientiousness factor in bonobos, and Agreeableness in humans (Weiss, 2022). The Dominance factor is correlated with dominance rank in baboons (Sapolsky & Ray, 1989) and is considered to play a central role in chimpanzee personality (King & Figueredo, 1997).

In the case of eWLGs, I observed that agonistic interactions (such as contact and non-contact aggression, display, and staring) was significant positive correlated with the factor Dom$_{eWLG}$. Studies on eWLGs living in bachelor groups have identified a similar relationship between Dominance and rates of displacement (Kuhar et al., 2006; Racevska & Hill, 2017; Schaefer & Steklis, 2014). These findings are consistent with behavioural observations in eWLGs (Kuhar et al., 2006; Stoinski, Kuhar, et al., 2004; Stoinski, Lukas, et al., 2004). However, it is mentioned, that aggression is higher in bachelor groups, especially in groups including silverbacks, than in family groups. The observed behaviours in the study of Kuhar and colleagues (2006) included initiated and received displacement behaviours (N=25). Murray (1995) also found a strong positive correlation of ratings on Tense and Aggression in female and immature eWLGs (N=13), and positive correlations with rates of aggression in chimpanzees and the factor Excitability. A significant correlation of the Dominance factor was found with expressed watching/staring in in situ Virunga mountain gorillas (iVMGs, Eckardt et al., 2015), but not to aggression. However, the level of aggression observed is in general low in iWLGs and no dominance hierarchy could be found in female iWLGs (in situ WLGs, Stokes, 2004; Maguette, pers. comm., 2022).

Openness to explore (Opn$_{eWLG}$)

Traits such as Innovative, Inventive, Inquisitive, Imitative, and Curious belong to the facet resembling creativity (CREA) or exploratory tendencies (EXT) in other non-human primate studies (King & Figueredo, 1997; Weiss et al., 2009) and in human studies (Weiss, King, et al., 2011). Individuals' exploitativeness is characterised by their curiosity in their social and physical contexts and their behavioural responses to novel situations, according to Réale and colleagues (2007). Evidence of an exploratory dimension in a wide range of animals has been compiled, demonstrating the consistency of this characteristic/facet across the animal kingdom (Gosling, 2001; Réale et al., 2007) and especially in non-human primates (Murray, 1995; Pederson et al., 2005; Réale et al., 2007)

Our eWLG facet of Activity (ACT) contained the two traits; Active and Playful. McGuire and colleagues called the facet Playful/Curious, (Byrne & Suomi, 2002) Play and Exploration behaviour. Our Activity facets/traits confirm what was found in the personality structures of Assamese macaques (Ebenau et al., 2019), barbary macaques (Konečná et al., 2012), bonobos

(Garai et al., 2016; Uher & Visalberghi, 2016), chimpanzees (Anestis, 2005; Anestis et al., 2006; Bard & Gardner, 1996; Uher & Asendorpf, 2008), grey mouse lemur (Dammhahn, 2012), Japanese macaques (French, 1981), lion-tailed macaques (Wergård et al., 2016), pig-tailed macaque (Reite & Short, 1980), rhesus macaques (Altschul et al., 2019), in several other monkey species (Adams et al., 2015; Stevenson-Hinde & Zunz, 1978; Weiss, King, et al., 2011, Clark and Snipes, 1998), and small-eared bushbaby (Watson et al., 1996).

The Conventional facet (CON) included the trait (not) Conventional and (not) Lazy. Overall, OPN is a factor shared within primates to benefit living in complex social systems and here, especially for those with some kind of fission-fusion tendency. The combination out of the Opn$_{eWLG}$ factor was identical to the one found in ex situ bonobos (Weiss et al., 2015) and highly congruent in a similar dimension (labelled Extraversion) identified in the earlier study on ex situ eWLGs rated on the GBI (Gold & Maple, 1994), highly congruent in orangutans (dimension was labelled Extraversion), and humans (dimension labelled Openness), and fair agreement was found for Openness in chimpanzees (.86 in King & Figueredo, 1997; Weiss et al., 2009), and VMGs Openness dimension.

In OpneWLG and AgreWLG, I found positive correlations to activity, play and proximity, supporting the interpretation that these personality factors underpin strong social affiliations and highlight the overall egalitarian social system in eWLGs. Murray (1995), found that immature eWLGs with high scores on Confident are groomed more, but surprisingly, play behaviour was adversely associated with ratings of Sociable in her study. This finding was in direct contrast to the positive connection she found among chimpanzees. Her observations also showed that playful activities were quite uncommon, and when they occurred, they were characterised by single or non-social play activities, such as running, climbing, and playing with aspects of their habitat. My findings stand in contrast to Murray's, as I found significant positive correlations to social play. Exploration (Dammhahn, 2012; Watson et al., 1996), staring (Forss et al., 2015; Schuppli et al., 2017), proximity (Massen et al., 2013; Santillán-Doherty et al., 2010), and manipulation (touching or manipulating an item) has also been shown to be correlated with Openness in other studies and are described as good indicators of this personality factor (Damerius et al., 2017; Uher, 2008a). Additionally, it is examined that more explorative individuals have a greater probability of surviving (Dingemanse et al., 2004b; Réale et al., 2007; B. R. Smith & Blumstein, 2007). A high pace of activity behaviour may improve the likelihood that individuals (particularly young ones) may acquire new abilities, in addition to play. This may help adults to survive (Russon, 2006; Schuppli et al., 2017; Schuppli, Forss, et al., 2016; Schuppli, Graber, et al., 2016; Schuppli, Meulman, et al., 2016; Van Adrichem et al., 2006; van Noordwijk & van Schaik, 2005), as new resources are explored and young once to learn new skills.

Conscientiousness (Con$_{\mathrm{eWLG}}$)

Trait loadings were like those seen in humans and ex situ chimpanzees and bonobos with positive traits, such as Intelligent, Decisive, Sensitive and Predictable and negatively loaded traits, (not) Disorganised, (not) Thoughtless, (not) Distractible, (not) Clumsy, (not) Unperceptive, Erratic, and Quitting. The Con$_{\mathrm{eWLG}}$ factor might be shaped as an artefact of captivity, as we could not confirm this factor in our iWLGs (see Chapter 4). The generated factor might be the result of the fact that enrichment items and cognitive stimuli to ex situ animals keep up their mental health and keep them busy. Not to forget to mention the fact, that cognitive tasks are often used in captivity to measure individual differences (Morten et al., 2015). Adjusting the complexity of tasks, incorporating medical training sessions and enrichment activities that engage animal's cognitive abilities and encourage problem-solving might have resulted in this distinct factor in eWLGs. This might also explain the fact that ex situ chimpanzees and ex situ bonobos show similar results.

The finding that Con$_{\mathrm{eWLG}}$ is positively correlated with proximity, shows that more conscious individuals tend to seek for closer contact to other conspecifics. This might can be explained through the social dynamics in eWLGs behaviours. A conscientious eWLG might prioritize group cohesion and stability, understanding that close proximity to group members can help maintain harmony and reduce conflicts. Being near others allows for better monitoring of group dynamics and quicker intervention in disputes. Additionally, by staying close to others, conscientious eWLGs can better manage and influence group activities, ensuring that the group remains organized and functions smoothly. Furthermore, close proximity enables better communication, both verbal and non-verbal. Conscientious gorillas might use their proximity to engage in more frequent and effective communication, which can help in coordinating activities and reinforcing social structures within the group. Also, close proximity allows for better monitoring and protection of young, ensuring their safety and wellbeing.

Agreeableness/ Sociability (Agr$_{\text{eWLG}}$)

I labelled this extracted factor Agreeableness/Sociability as the factor is characterised by multiple trait loadings with similarities in their semantic meaning, e.g., sociability, the expression of positive affect, and gregariousness. It is a combination of the sociable-related facet, SOC = Sociable, combined with the facet of altruism (ALT), with Sympathetic, Helpful, Gentle, and warmth (with the trait Affectionate), and amiability (with the trait Friendly), and a protective facet, with Protective and Dependent. This confirms earlier research, which suggested that personality dimensions could be further broken down into sub-traits (Carter, Marshall, et al., 2012; Koski, 2011; Tkaczynski et al., 2019). In fact, sociability has been broken down into several components, including tactility, equitability, and pleasant affect (Koski, 2011; Tkaczynski et al., 2019). The findings confirm this sub-trait reorganisation in facets. The lower-order facets also allow better comparison to other species or subspecies (see also Chapter 4 for cross gorilla comparison).

In rhesus macaques, as in eWLG, the Sociability and Activity constructs are separated into two dimensions, whereas it is divided into the two "basic" dimensions, i.e., Sociable + Altruism = Friendliness and Activity in rhesus macaques, Activity is loaded under Openness, and Sociable under this dimension named Agr$_{\text{eWLG}}$. Weiss and colleagues (2011) suggest that this pattern results from an evolutionary convergence into one dimension in great apes. However, our results do not support this finding, but this could be an artefact of captivity. Therefore, it seems that eWLGs' Agr$_{\text{eWLG}}$ factor resembles a combination of several "blended" facets, such as SOC and ALT and this seems like the description of humans' "ultra-social" tendency (Dachner et al., 2009). The incorporation of human Agreeableness traits (Friendly, Helpful, and Affectionate) in the Agr$_{\text{eWLG}}$ factor may reflect the mild and gentle nature of eWLGs interactions and the distribution of tolerance and protectiveness as their social compounds.

Similarly, the Agr$_{\text{eWLG}}$ factor identified in eWLG was similar to factors extracted from the personality of bonobos, orangutans, and iVMGs (see Chapter 4). Also, the Agreeableness dimension of ex situ chimpanzees shows a high degree of agreement. Kuhar and colleagues (2006) have demonstrated that the Understanding (Und) factor in Gold & Maple (1994) is analogous to the Agreeableness factor in human personality. Thus, I consider Und (Gold & Maple, 1994) to fit with this interpretation. Both the Agreeableness and Understanding dimensions describe traits that contribute to harmonious social relationships and low levels of conflict.

The positive relationship between Agr_{eWLG} is consistent with the evidence that sociability may be described as an individual's s-dbr to the presence or absence of conspecifics and the proximity of others. Earlier research found that proximity to others (Koski, 2011), behaviours related to food (sharing: (Silk et al., 2013), begging: (Freeman et al., 2013), physical contact (Ebenau et al., 2019), grooming (Eckardt et al., 2015; Neumann et al., 2013), and play are all ways in which the factor sociability may be expressed in real life situations (Koski, 2011). My findings confirm these earlier reports, as I found significant positive relationships between Agr_{eWLG} and proximity (close, < 1.5 m), and play. As mentioned earlier, close proximity might increases more frequent and effective communication, which can allow all kind of social information to be shared. Maybe also conducted when social needs are not met or to inform others of a need (such as the need to be groomed, e.g., **Picture 19**, below, grooming of Mandji and Nemsi). Overall, I found that proximity and play activities, thus, social, gregarious interactions are also correlated with the factor Openness. This can be explained, especially with play behaviour, the exploratory activity, and social aspects of play. Furthermore, the positive correlation to time spent in social proximity confirms similar findings in iVMGs with the relationship between social proximity and their Proto-Agreeableness dimension (Eckardt et al., 2015). In general, measures of proximity to conspecifics (Byrne & Suomi, 1995) and frequencies of social events (Chamove et al., 1972) have been used to validate sociability measures in nonhuman primates.

Neuroticism (Neu_{eWLG})

The Neu_{eWLG} factor comprises traits characterised by the facet of emotional instability (EMO) with the traits (not) Stable, (not) Cool, a high arousal sub-category, including Fearful, Excitable and Anxious traits (facet of ANX), and negative affect, such as Timid, Vulnerable, (not) Independent (CNF). This facet which characterises fear is said to be linked to reactions to threats and dangerous encounters (Boissy, 1995). The factor reflects most notably the Neuroticism factor in orangutans (Weiss et al., 2006) and humans (Weiss, 2022). Gold & Maple (1994) identified a Fearful factor in eWLGs, comprising the traits Fearful, Apprehensive, Insecure, and tense, like Neuroticism in humans (Gosling & John, 1999). A negative association was identified between the Fearful dimension and the frequency of initiated displacements in a bachelor group of ex situ males (Kuhar et al., 2006). The Neu_{eWLG} factor shows the lowest congruence in cross-species comparisons of personality structure in animals (Freeman & Gosling, 2010). Neuroticism was also not replicated in 3 of 4 studies on chimpanzee personality that used variants of the HPQ (King et al., 2005; King & Figueredo, 1997; Weiss et al., 2007, 2009). This dimension is also less robust across human cultures (Saucier & Goldberg, 2001). In situ VMGs do not show, and bonobos lack, a clear Neuroticism factor, this might be due to the relatively stable environment in which iVMGs live, where competition for food resources is low (Eckardt et al., 2015). The same has been demonstrated for in situ bonobos as competition in this population is low in general compared to other great apes (Garai et al., 2016). In rhesus monkeys, Neuroticism was divided into two components, Confidence (CNF) and Anxiety (ANX) but these seem to have converged into a single dimension in great apes (Weiss, King, et al., 2011). Additionally, the dimension has also been labelled "Emotionality/Emotional stability" (Chamove et al., 1972; Goldberg, 1990; Gosling & John, 1999; Nash & Chamove, 1981; Reite & Short, 1980; Weiss & Adams, 2010) and it is considered to be negative as it captures traits sometimes characterised as anxiety or depression related disorders. It is quite possible that anxiety will have significant effects on the health and fitness of an individual. For instance, maintaining vigilance over one's environment by keeping an eye out for potential dangers (Elgar, 1989) may improve an individual's chances of surviving, given that they will be able to respond more alert and appropriately to any given circumstance. This may confirm the finding in iWLGs (for more interpretation see Chapter 4). Nevertheless, displaying a high degree of anxiousness may also have negative long-term effects on one's health (Maestripieri & Hoffman, 2011).

Earlier studies on rhesus macaques' Neuroticism factor using a 25-trait personality list from Stevenson-Hinde and colleagues (1980) differentiated between two phenotypes, "up-tight", e.g. Insecure and Tense, and "laid-back", Confident and Understanding (Bolig et al., 1992; Suomi, 1987; Suomi & Novak, 1991). When compared to Neuroticism in rhesus macaques (Weiss, Adams, Widdig, et al., 2011), our Neu_{eWLG} dimension showed a high overall correlation with the Anxiety dimension in rhesus macaques. Costa & McCrae (1998) categorise humans as "easy-going" when they are low in Neuroticism and high in Agreeableness, e.g. expressing less or reserved anger and being more "laid-back" in general. Accordingly, eWLGs could be categorised as "laid back" and "easy going," as they show low rates of aggressive interactions and few signs of Neuroticism or abnormal (e.g. autistic) behaviour in general and are high on Agreeableness. The trait Autistic was also not reliable and was excluded from the personality structure.

An earlier study of eWLGs using the GBI (Gold & Maple, 1994) identified a Fearful dimension, comprising the traits fearful, apprehensive, insecure, and tense, like Neuroticism in humans (Gosling & John, 1999). A negative association was identified between the Fearful factor and the frequency of initiated displacements in a bachelor group of eWLG males (Kuhar et al., 2006). Self-directed behaviour (nose touch) a behaviour that might be similar to the tendency to self-scratch, was found to be negatively correlated to our Neu_{eWLG} factor. In contrast, the relationship between self-scratching and the trait anxiety (Canli, 2004; Revelle & Scherer, 2009) and the Neuroticism factor in chimpanzees (Herrelko et al., 2012) has been reported. However, there has been a limited evaluation of self-directed behaviours as potential indicators of anxiety or arousal in eWLGs, and the findings are inconsistent across contexts (Carder & Semple, 2008; Cordoni & Palagi, 2007). The lack of behavioural correlates identified for Neu_{eWLG} may be constrained by the low rates of self-scratching observed, or alternative behaviours or contexts may be required to validate Neu_{eWLG}.

Extraversion (Ext_{eWLG})

Ext_{eWLG} consists of traits: (not) Depressed, and (not) Unemotional, and the second half of the sociality facet (SOC) with (not) Solitary. As all the traits are negative, representing Introversion, the inverse of the factor can be seen as (not) Solitary=Social (SOC), and (not) Unemotional=Emotionality/ Emotional stability (Chamove et al., 1972; Goldberg, 1990; Gosling & John, 1999; Nash & Chamove, 1981; Reite & Short, 1980; Weiss & Adams, 2010). In general, the factor showed the lowest overall factor consistency across the compared great ape studies, however, it resembles best the EXT factor in ex situ chimpanzees (Weiss et al., 2009) and humans (Weiss, 2022), as well as the Unemotionality dimension of in situ bonobos. Similar to ex situ bonobos the facet was separated where Solitary loads negatively on Extraversion and Sociable positively on Agreeableness.

In eWLG, the positive relationship between Ext_{eWLG} and prosocial behaviours is consistent with evidence for a positive correlation between affiliative behaviour, initiated or received (Kuhar et al., 2006; Racevska & Hill, 2017; Schaefer & Steklis, 2014). More extroverted humans and chimpanzees have been found to show higher rates on positive emotions and play (Freeman et al., 2013), both behaviours with a social component, however, I found no significant correlation to play. Instead, a positive association with time spent feeding/ foraging was shown. This might be explained by the fact that feeding is mainly socially associated in eWLGs and there might be a circularity with prosocial as a measurer. Additionally, I found positive correlations of the factor Ext_{eWLG} and self-directed behaviours, which might be a communication signal to express certain needs and wants to conspecifics.

Sex and age differences on the personality structure

Age

Study of animal personality allows researchers to document species-specific personality maturation, and to make comparisons with the development and stability of human personality. The stability of personality over lengthy periods of time is an area of research that has been overlooked despite the increasing interest in animal psychology, especially in great apes. To chronicle species-specific personality development and draw analogies to the maturity and stability of human personality, researchers need to know whether great ape personalities change over time. Within my results, I confirm the findings of Weiss & King (2015) and others who have shown, similar to studies of humans, that personality changes through time with older chimpanzees, orangutans, bonobos, and eWLGs are evaluated as less extraverted than younger ones (for more information see Roberts et al., 2006; Srivastava et al., 2003; Staes et al., 2016; Weiss & King, 2015). The present finding in respect to the Extraversion factor seem to be consistent with other research on eWLGs and iVMGs, which found that gorillas become less affiliative with age (for eWLGs: Kuhar et al., 2006); for iVMGs: (Eckardt et al., 2015). On the additional factors, Kuhar and colleagues (2006) found no age-effect for the factors: Dominance, Understanding and Fearful. In humans, Agreeableness and Conscientiousness rise with age (Dutton, 2008; King et al., 2008; Staes et al., 2016; Weiss & King, 2015), while Neuroticism and Openness falls with age (McCrae & Costa, 2003). The findings do support the previous research in humans, chimpanzees, and orangutans, as they found a decline in Neuroticism (as I did), and in humans on the Openness factor. In terms of the factor Agreeableness, an increase with age is measured for chimpanzees (Weiss & King, 2015) and a decrease with age in ex situ orangutans and iVMGs (Eckardt et al., 2015; Weiss & King, 2015). I confirm the decrease in Agreeableness similar to orangutans and iVMGs, however, I did not find an age effect on Dominance, as shown for iVMGs, ex situ orangutans and female chimpanzees (Eckardt et al., 2015; Weiss & King, 2015) A decline within age and sex was also found for the factor $\mathrm{Agr}_{\mathrm{eWLG}}$ and $\mathrm{Neu}_{\mathrm{eWLG}}$, with the opposite direction on the $\mathrm{Dom}_{\mathrm{eWLG}}$ factor. To sum up, five of the six personality factors showed age-effects, only $\mathrm{Dom}_{\mathrm{eWLG}}$ did not (only with the interaction of sex). This also accords with the Five-Factor Theory hypothesis, which explains age-related variations in personality factors (McCrae & Costa, 2003).

Sex

In respect to the life cycles in Chapter 4, **Figure 14** and the highlighted differences in male and female WLG, differences within their personality structure are expected. Previous studies on the eWLGs personality generated with the GBI (Gold and Maple, 1994) found no sex-effect on the personality factors (Weiss et al., 2013). This contrasts to results found for iVMGs (Eckardt et al., 2015), where male VMGs scored higher than females on the **Dominance** factor. Eckardt argues that the largest dimorphic difference between the sexes, which is the most extremist in all great apes, is the result of sexual selection in males (Eckardt et al., 2015). In terms of the $\mathrm{Dom}_{\mathrm{eWLG}}$, my data confirm their findings (males>females), but contrast their results for Openness, where males are shown to be more open than females. I instead found sex differences on the factor $\mathrm{Agr}_{\mathrm{eWLG}}$ and $\mathrm{Con}_{\mathrm{eWLG}}$. I also found similar results as shown in earlier studies, where females are pointed out to be more agreeable than males across species, with humans (Srivastava et al., 2003; Weisberg et al., 2011) and chimpanzees and iVMGs (Eckardt et al., 2015, King et al., 2008; Weiss & King, 2015,), as examples. $\mathrm{Con}_{\mathrm{eWLG}}$ was also found to be higher in females and increased with age in both sexes. In addition, there is considerable similarity between humans and chimpanzees in terms of sex differences in age-related changes in personality traits. Sexual selection (Schmitt et al., 2008), social factors/life events (such as status competition/cooperation; De Waal, 2000; King et al., 2008; Srivastava et al., 2003); and sex differences in human cultural norms/social inequality are all hypothesised to contribute to sex differences in personality. The above suggests, while further study is necessary, that there are certain personality traits that show evolutionary continuity between humans, chimpanzees (Weiss & King, 2015) and eWLGs.

It's reasonable to assume that people of all ages will exhibit a wide range of behaviour across social and physical settings; older individuals, however, may benefit from greater stability in their decisions and behaviour because they are still acquiring some of the personality traits that helped them survive childhood. This variety of social structures is going to influence how males and females display personality-based behaviours. The social patterns in eWLGs are considered dispersal-egalitarian in social style (Sterck et al., 1997), with male dominance over females resulting in weak social relationships between females (Doran & McNeilage, 1998; Harcourt & Stewart, 2007; Stokes, 2004). This might also explain the effect of sex and age, or the interaction on the behaviours found. Here I sum up our findings on behaviours that underlie differences on sex or age or the interaction between both in our eWLGs which goes well in line with the age and sex effects described on the different personality structures generated, above. For instance, age effects were found on the behaviours such as inactivity, contact resting, prosocial behaviour, touch, display, play, and object manipulation. Those behaviours were all correlated with Openness and openness factor might be explained by the factor as an age effect on the factor was found as well. A sex effect was found for approach, positive affect, touch (received), and scratching behaviour. Interactions could be found in the behaviour: contact resting, proximity (close), positive affect and holding on (initiated), scratching, and feeding behaviour.

3.6 Limitations and Future Directions

3.6.1 Limitations

Below, I will investigate the limitation of the usage of the GPQ and its interpretation.

Anthropomorphism. The underlying principles of personality psychology and the lexical hypothesis have been criticised, including the notions that personality characteristics are unobservable and that lexical repertoires are separate from the events believed to be contained by such repertoires (Uher, 2013). These objections may be especially applicable to research employing non-human animal research on personality, where individuals are incapable of self-reporting their cognitive processes. In addition, since the adjectives employed in the animal personality were borrowed from human literature (Goldberg, 1990), some traits may have less significance for the species under study. For instance, Morton and colleagues (2013) utilised the trait "autistic" and "individualistic" and describe that such descriptors may be more applicable to humans than to animals, I found this to be similarly in the eWLGs study. Therefore, when framing animal personality questionnaires, researchers may need to be more cautious with the projection of human-like traits onto animals, or at least very conscious of the definitions that the risk of an anthropomorphic language is limited. Another point which should be discussed here is that non-native English speakers should be provided with a questionnaire in their mother-tongue to makes sure that the assessment form is fully understood. I personally explained to each of the raters in the Netherlands each of the traits to avoid mis-understandings or -interpretations.

Limited range of behavioural representatives. The least disadvantageous method to rate is using the approach on behavioural description when describing the traits. The behavioural descriptions give a descriptive evaluation of the targeted personality trait of the particular species in relation to a full spectrum of the animal’s behaviours and context, though there are limitations while attempting a cross-species comparison. Therefore, the best tool should be selected for the study at hand. Within my thesis, I aimed for a cross-species comparison to use a phylogenetic and socio-ecological framework as the basis for the comparison to other great apes’ species and to generate shared social personality constructs, therefore, using the Gorilla Personality Questionaire (GPQ) makes here the most sense.

Human interpretation bias. Human raters are subject to recall biases, tending to remember salient life events more vividly than daily occurrences and negative experiences more than positive ones (Kensinger & Schacter, 2006; Koppel et al., 2013). The presence of recall bias might impact the assessment of personality in animal research, perhaps resulting in an overestimation or underreporting of traits due to the influence of recent noteworthy events or the experiences of other raters.

Consistency over time. The evaluation was not repeated. The nature of gorillas' behaviour and personality is based on iWLGs and eWLGs set on a specific moment in time to compare the both populations (see **Figure 16**, Chapter 5). Since there remains the risk that they may be influenced by several variables including developmental stages, life experiences, and changes in the confined environment repetition is advisable.

Limitation on the analysis procedures. It should be noted that in cross-species comparison the usage of a consistent analytical tool on all species, as well as similar sample sizes should improve the preciseness of the comparison. Instead of using simple correlation tests, in some cases, linear regression models (such as regression lines, model estimates) could have brought a more sophisticated analysis. However, as correlations have been used in earlier studies, I repeated for consistency of methodology I tried best possible to use the same methods, behaviours, questionnaire and analysis, as used in Eckardt et al. 2015, and others.

3.6.2 Future Directions

Importance of lower-order personality trait constructs, which are more specific and narrowly defined than broad, higher-order personality factors, can offer detailed insights into individual differences. These traits can be crucial for improving welfare and happiness in WLGs by enabling more tailored and effective management practices. Such as **individualised care**, as understanding specific traits such as sociability, aggression, or timidity can help caretakers provide personalised care and enrichment that meets each animal's unique needs. For example, an animal with a high level of sociability may benefit from increased social interactions, while a more timid animal might need quieter, less stimulating environments. It can also be used to enhance the effect of environmental enrichment, as tailoring enrichment activities to match individual personality traits can improve engagement and reduce stress. For instance, exploratory and curious animals might enjoy complex puzzles, whereas animals with lower curiosity might benefit more from predictable and routine enrichment.

Collaboration and Data Sharing. I encourage collaboration among institutions and researchers to share questionnaires, data and insights on personality research. Best would be if one instance or personal would run all shared data on similar methodologies to compare across species in best possible manner. This can lead to more robust and generalizable findings and facilitate the development of best practices for using personality research in conservation.

3.7 Conclusion

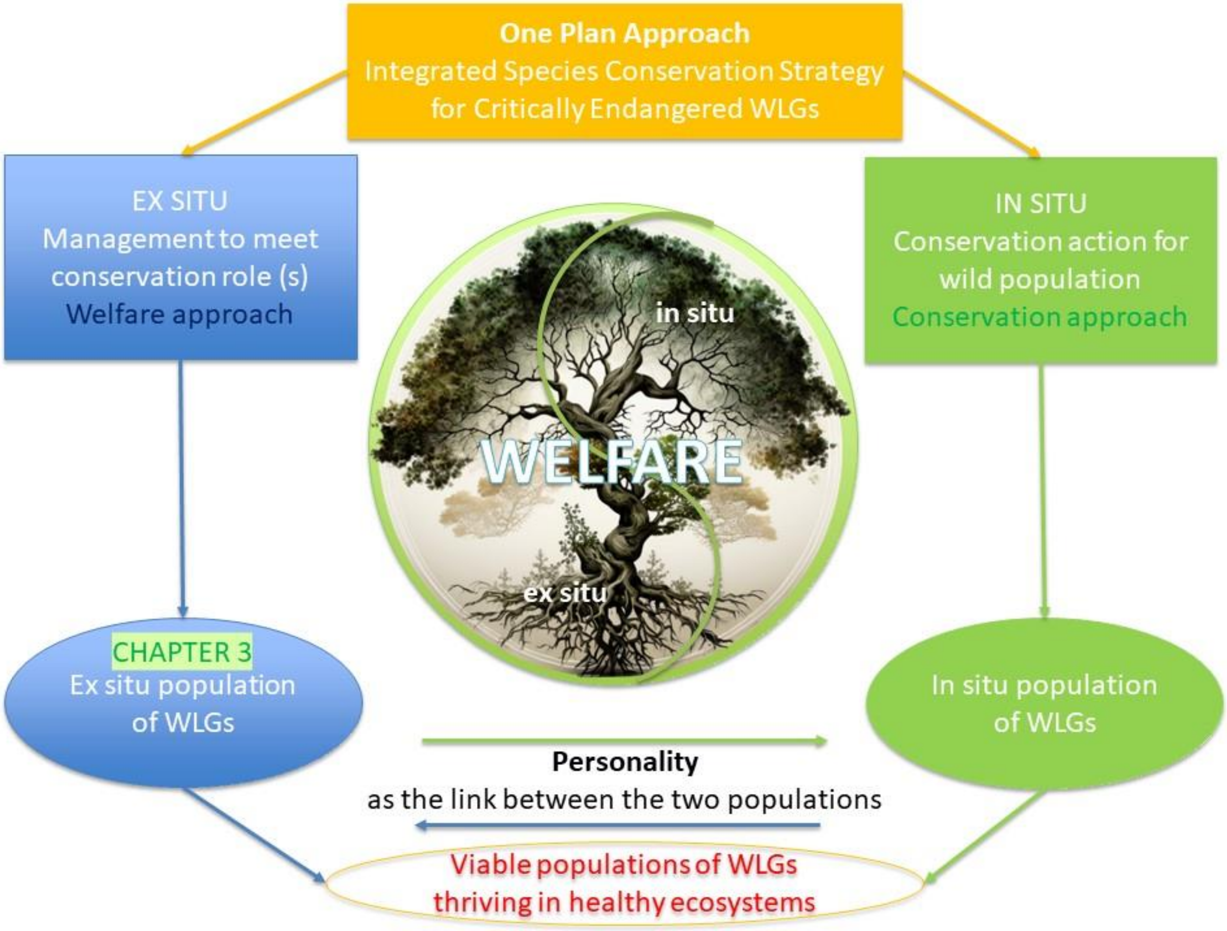


Figure 8 *Road Map Including Chapter 3*

I generated ex situ WLGs' personality structure and elucidated the phylogenetic relationship to other ex situ great ape species, such as bonobos, orangutans, and chimpanzees. The personality structure is the basis of the ex situ population in respect to the One Plan approach. It serves for the comparison to the in situ WLG population, and for the overall welfare approach, in situ as well as ex situ (see **Figure 8**).

Within this chapter, I shed light on the phylogenetical continuity (consistency and differences) of the personality structure (on the level of factors and low-level trait constructs) of eWLGs. Overall, the highest similarity between the personality structures of eWLGs in a cross-great ape comparison was found to ex situ bonobos, orangutans, and to humans. The comparison of low-level facets and their corresponding higher-order factors helped to understand the evolutionary history of personality and adds to the phylogenetically related species of closely related great ape species.

Further, I extracted personality factors (Dom$_{\text{eWLG}}$, Opn$_{\text{eWLG}}$, Con$_{\text{eWLG}}$, Agr$_{\text{eWLG}}$, Neu$_{\text{eWLG}}$, Ext$_{\text{eWLG}}$) similar to those generated by Gold & Maple (1994) from a previous data-set collected on a modification of the Madingley Questionnaire (created by Stevenson-Hinde & Zunz, 1978) with Extraversion (Ext), Dominance (Dom), Fearful (Fef) and Understanding (Und) and confirm thereby the earlier personality structure.

I validated the conclusions drawn by Weiss & King, (2015) and other researchers who have observed that, akin to studies conducted on humans, personality traits in older chimpanzees, orangutans, bonobos, and eWLGs tend to exhibit lower levels of Extraversion compared to their younger counterparts (see Roberts et al., 2006; Srivastava et al., 2003; Staes et al., 2016; Weiss & King, 2015). This observation aligns with the hypothesis proposed by McCrae & Costa (2003) known as the Five-Factor Theory, which seeks to elucidate the influence of age on personality factors. With regards to sex differences, it was possible to demonstrate the existence of specific personality traits that exhibit evolutionary continuity across humans, chimpanzees (Weiss & King, 2015), and our common eWLGs.

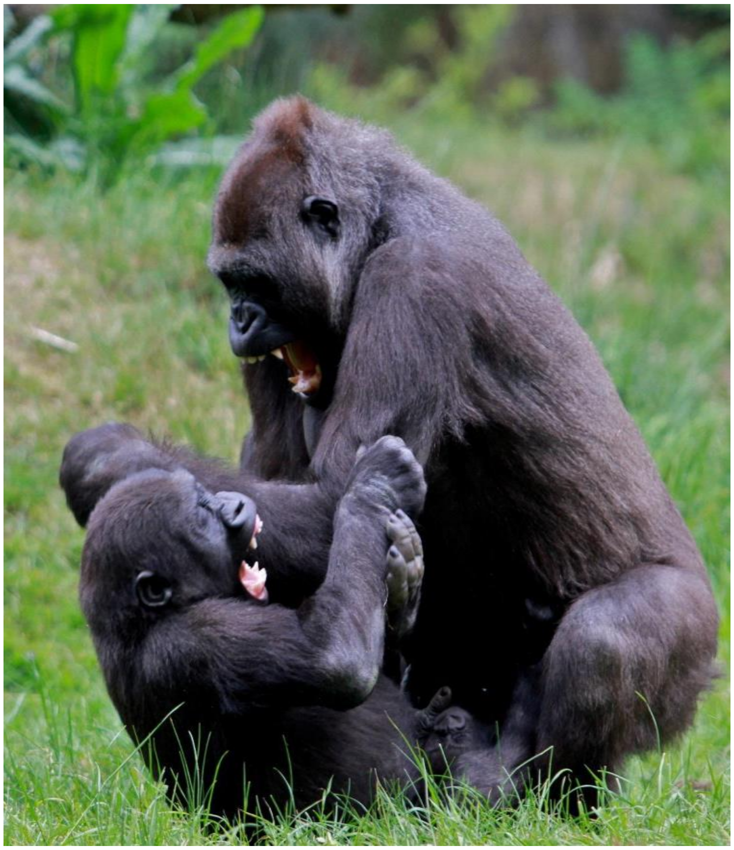
Introduction to Chapter 4

The next chapter assesses iWLG personality structure to allow me to compare the number of factors generated and try to explain whether a six factor personality structure might be an artefact of captivity in our eWLG data, as it may be in ex situ bonobos and chimpanzees (Weiss, 2017b; Weiss et al., 2015, 2017). At the ultimate level, a direct comparison of iWLG and iVMGs is required to evaluate the impact of context, ex situ versus in situ, and the role of socio-ecological differences in shaping personality structure in the genus *Gorilla*. The use of standardised methods to assess the personality structure facilitates direct comparisons of higher-order personality dimensions and lower-order facets, which can help us identify similarities/ differences in socio-ecological relationships between the two sub-species and the settings. In addition, an extraction of shared social personality factors in the genus *Gorilla*, allows us to understand the evolution of shared gorilla dimensions across great apes.

3.7 Appendices

Picture 16 *Adult male and female are playing together with youngsters*

Picture 17 *Adult male and female are playing together with youngsters*



Picture 18 *Adult female playing. Infant is hanging on her belly, next to the legs of the playful youngster*

Picture 19 *Grooming between two adult female*

Chapter 4

The Difference Matters!
Identifying In Situ Western Lowland Gorillas' Personality Structure
A Comparison Across the Genus *Gorilla*

Picture 20 *Graphic is © Thomas Breuer*

"Our love and concern for animals should go beyond those within our personal environment. We should see the world as a whole, see nature in its entirety and realise the importance of humans being part of the animal world and animals being part of theirs. It is only in this way that we can prevent the complete destruction of our environment and perhaps, ultimately, of ourselves." Dame Virginia McKenna DBE.

4.1 Abstract

Socio-ecological factors play a pivotal role in shaping personality dimensions across species, influencing behavioural patterns crucial for conservation strategies. This study aims to delineate the personality structure of in situ Western lowland gorillas (iWLG, *Gorilla gorilla gorilla*) utilizing the Hominoid Personality Questionnaire (HPQ), a standardized tool for comparative personality assessment. A total of 198 iWLGs from five African field sites were assessed by 25 field researchers using a variant of the 54-trait HPQ. Exploratory Factor Analysis with varimax rotation extracted a four-factor personality structure comprising Neuroticism, Sociability, Dominance, and Tolerance/Self-Control, explaining 70% of total variances. All factors and traits, except for the Autistic trait, demonstrated high reliability and validation. Comparisons with ex situ gorilla populations (eWLGs) and in situ Virunga mountain gorillas (iVMGs) revealed similarities in Dominance and Sociability dimensions but distinctions in Tolerance/Self-Control (iWLGs), Proto-Agreeableness (iVMGs), and Neuroticism/Conscientiousness (eWLGs). These differences are attributed to varying socio-ecological contexts, including resource availability, diet, habitat use, predator risk, social structure, and behavioural adaptations. The results underscore the profound influence of socio-ecological factors on personality traits within and across closely related species. These findings have significant implications for conservation, management, and reintroduction programs, particularly within the One Plan Approach framework. By integrating personality research, conservation efforts can be tailored to account for species-specific behavioural responses to environmental changes and management interventions. In conclusion, this study highlights the relevance of personality research in wildlife conservation, emphasizing the need to incorporate personality considerations into conservation strategies, especially in the context of ex situ breeding and translocation programs. Understanding how socio-ecological factors shape personality can enhance the effectiveness of conservation initiatives and mitigate potential risks associated with altering natural evolutionary trajectories through human intervention.

4.2 Introduction

Personality influences the structuring of animal social relationships for populations, subspecies, and species (Bergmüller & Taborsky, 2010; Bolnick et al., 2003; Dingemanse & Wolf, 2013; Koski, 2011; Koski & Burkart, 2015; Sih & Watters, 2005; Wolf & Weissing, 2010). Between-species comparisons of personality structure address questions of phylogeny, examining how environmental (socio-ecological) factors have shaped the evolution of specific traits and broader personality dimensions (e.g., Adams et al., 2015b; Budaev, 2000; Freeman & Gosling, 2010b; Gosling, 2008; Gosling & John, 1999; Sih et al., 2004, 2015b). For example, species-typical social structure, including social group stability, e.g., levels of fission-fusion dynamics, and social style, have been used to explain variance in primate personality structures (Adams et al., 2015; Eckardt et al., 2015; Weiss et al., 2015).

Socio-ecological comparison between the genus *Gorilla*.

In this chapter, I examine the personality structure of in situ Western lowland gorillas (iWLGs, *Gorilla gorilla gorilla*) by conducting a detailed social-ecological comparison within the genus *Gorilla*. This involved comparing the personality structure of iWLGs to eWLGs (ex situ WLG population, see Chapter 3) and in situ Virunga mountain gorillas (iVMGs, *Gorilla beringei beringei*) based on published data by Eckardt et al., (2015). To maintain methodological consistency between this cross-gorilla and cross-setting comparison, I used the same methodological procedure as described in Chapter 3. Chapter 2 on gorilla biology serves as the foundation for the socio-ecological comparison in respect to the personality structures derived from the different populations.

There is a growing body of research investigating personality within in situ animals. However, few studies have compared ex situ and in situ populations. Personality studies of in situ animals provide valuable insights into individual variation in behaviours, which can have significant implications for conservation and ecological understanding (Dingemanse & Wolf, 2013). Other research has recognised the possible impact of ex situ conditions on the expression of certain personality traits (Garai et al., 2016; Koski, 2011) and these studies accept that personality traits have heritable characteristics and may be influenced by selection pressures. The notion known as “contemporary evolution" (McDougall et al., 2006) refers to the occurrence of fast evolutionary changes in personality traits over short time periods, often ranging from a centuries to only a few decades, or even generations (Hendry & Kinnison, 1999; Stockwell et al., 2003). In some circumstances, it is possible for alterations to occur during the span of an individual's lifetime (Ashley et al., 2003).

Both ex situ and in situ populations – as well as reintroduction initiatives – could potentially drive rapid evolution due to the prevalence of robust selection pressures acting on hereditary traits. Consequently, selection pressures have the capacity to manipulate functional associations among and within personality traits, leading to remarkably swift alterations in structure (McDougall et al., 2006). Moreover, understanding differences in individual traits may aid conservationists in predicting, conserving, and adapting population responses to environmental changes (Merrick & Koprowski, 2017; Wolf & Weissing, 2012).

Analysing the personality of both iVMGs and iWLGs provides insight into how social-ecological disparities might influence variations in in situ subspecies (Bremner-Harrison et al., 2004; Watters & Meehan, 2007; Weiss & Adams, 2013; Wolf & Krause, 2014). Such comparisons also aid in understanding the collective impact of entire ecosystems – encompassing social, ecological and developmental aspects as well as evolutionary timescales – on the development of primate personality (Dall et al., 2004; Dingemanse & Dochtermann, 2013; Sih et al., 2004, 2015; Sih & Bell, 2008; Sih & Watters, 2005; Wolf et al., 2008; Wolf & Weissing, 2012). In captivity, gorillas encounter selection pressures affected by artificial environmental factors and social constraints, all of which can significantly shape their personalities and influence breeding or reintroduction success as the ex situ back-up population.

Considering their phylogenetic relatedness, a heightened level of congruence can be anticipated between personality structures extracted using the HPQ in iVMGs and iWLGs (Eckardt et al., 2015; Weiss et al., 2009). However, these two sub-species do exhibit differences in certain aspects of their socio-ecology (Harcourt & Stewart, 2007; M. Robbins et al., 2004, 2016, 2017; Stokes, 2004; Watts, 1996) as highlighted in Chapter 2.

An understanding of the behaviour of animals in their natural habitat can be used to enhance the manifestation of natural behaviours ex situ. This practice can be beneficial in terms of increasing the chances of survival of primates that are kept as part of a breeding program and can also aid in enhancing public education. The notion that any animal welfare model within the zoo community must incorporate in situ-type behaviour has been deeply embedded since the 1950s with Hedger's first declaration of that importance (Watters et al., 2021).

The concept that animal welfare is based on natural living proposes that animals exhibiting natural behaviours are experiencing a state of positive welfare (see D. Fraser, 2008). However, this model has been criticized primarily due to the argument that the frequency of displayed natural or in situ-type behaviours does not necessarily imply positive welfare, unless welfare is defined as the expression of natural behaviour (Hutchins, 2006; Veasey et al., 1996). Hence, this theory can be subjected to additional scrutiny as it appears to have originated from circular logic (Watters et al., 2021). It is imperative to classify a behaviour as a "need" prior to recognising its value to the individual (Howell & Cheyne, 2019). To address this, it is necessary to consider whether nature embodies a predetermined set of behaviours that ex situ management must adhere to avoid compromising the wellbeing of the animals under their supervision. The precise replication of nature by zoos is deemed impossible according to Hutchins (2006) and so raises the question of how can we measure the extent to which ex situ settings offer conditions for adequate welfare.

To address this, I did not use a direct comparison of the activity budgets. It has been found that allocation of time to various activities among in situ conspecific groups varies in response to diverse environmental factors (Sih et al., 2015), distribution of resources (King & Landau, 2003), and group size (Schaefer & Steklis, 2014), and so the use of time budgets as a comparative diagnostic tool is complicated (Lyubomirsky, King, et al., 2005). Instead, I used the behaviours assessed in gorillas to validate the personality structure and the subjective wellbeing questionnaire of and to compare the ex-and in situ personality structure of WLGs based on a wider socio-ecological comparison as shown in Chapter 2.

a. Generate the personality structure of iWLG (data from N=198 gorillas across five in situ populations) and assess its robustness and reliability. I aim to explore potential similarities between the social aspects of personality structure and anecdotal attributes associated with WLGs, such as gentleness, peacefulness, emotional stability, and introversion.

b. This study included behavioural data of 124 iWLGs from Mbeli Bai, Republic of Congo, which have been provided by Manguette to validate the personality structure. Data collection lasted four years, from 2013 to 2016, and included the activity budget, the frequency of Bai visits, and occurrences of inter- and intra-unit encounters.

c. Explore the impact of age and sex on personality structure, as previous primate studies have shown that age and sex variations are influenced by socio-ecological variables.

d. Provide a comprehensive analysis of differences and similarities in personality structure of in situ gorilla populations (iWLGs and iVMGs) compared to eWLG and compare those to social ecological differences within the different populations and subspecies.

e. Compare the personality structure of iWLGs with that of other great ape species studied in situ and humans to provide insight into the evolutionary origins of the personality structure.

f. Investigate the impact that ultimate causes have on the evolutionary development of the sociable personality trait constructs within the genus *Gorilla*. This involves analysing correlated trait facets using a fuzzy set analysis, with the goal of ascertaining common social constructs. This provides a better understanding of the origins and persistence of personality structures within the gorilla subspecies from a social-ecological perspective.

4.3 Methods and Materials

4.3.1 Field Sites

This section provides the background of the five African field sites where data on personality and behaviours for validation (at Mbeli Bai) were collected by collaborators. These data will be analysed, and results will be compared with iVMGs and eWLG (Chapter 3).

In **Figure 9**, five locations of iWLGs field sites are marked in West Africa. In the East of Africa, one MG field site is marked for comparison (iVMGs). The divergence between the two subspecies of the genus *Gorilla* occurred around 1.2-1.3 million years ago (Robbins et al., 2016). Personality structure on iVMGs has been described and published by Eckardt et al. (2016) and the findings will be used for comparing our iWLG with iVMGs and the eWLGs data on personality.

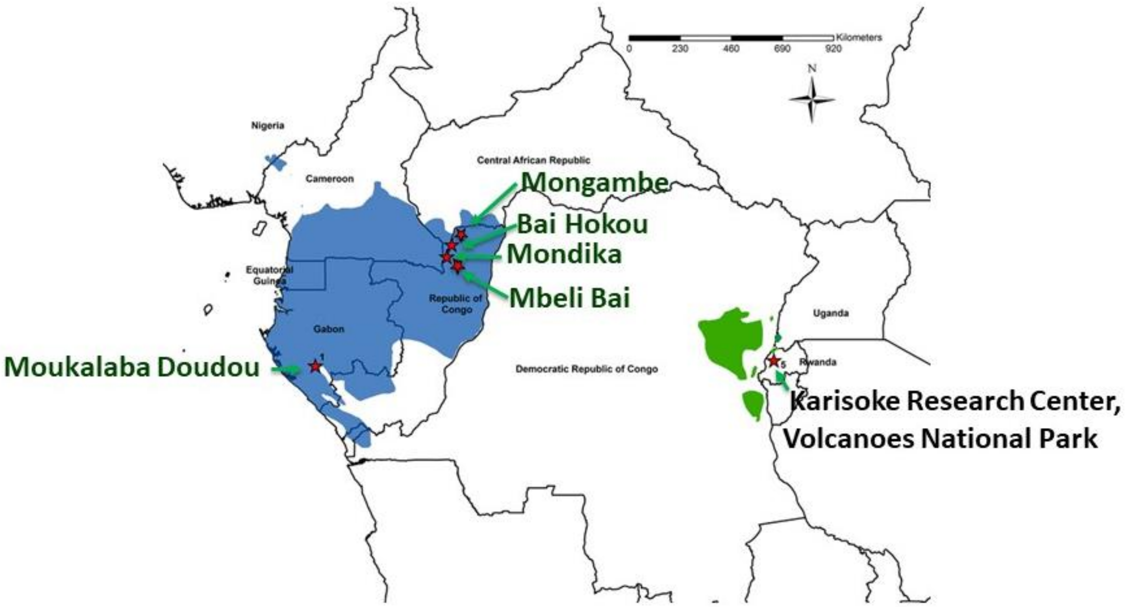


Figure 9 *Distribution of study sites and gorilla subspecies used in this study*

Note.
Graphic is (©(M. Robbins et al., 2016)*, Fig 1, Robbins et al., 2016).*
blue area = iWLGs, green area=MG area. Comparison is made to iVMGs.
Collaboration partner: in iWLGs from the left to the right: Moukalaba Doudou (Gabon), Mongabme (CAR), Bai Hokou (CAR), Mondika (CAR), and Mbeli Bai (CAR). Data on iVMGs is collected by Eckardt and colleagues in the VNP (RWA).

4.3.1.1 Moukalaba Doudou, Gabon

Moukalaba-Doudou Nature Reserve is located south-east of Gabon (2°26'S, 10°25'E). A patchwork of woodland, savanna, and wetland encompasses a total area of 5,028 km^2 inside the park. The research location (about 30 km^2) is situated in the park's southeast corner. The flora of the research area consists of primary forest, forest dominated by *Musanga cecropioides*, and Savannah. The average yearly temperature is between 24-28 °C (with variation from time of the year and specific location), and yearly precipitation ranges from 1,300-1,800 millimetres. Since 2001, field research on the social ecology of WLG has been conducted by the research team of the Wildlife Research Centre, Kyoto University, Japan. Since 2004, a group of 20–23 gorillas has been habituated (Ando et al., 2008). The area is home to a greater population of iWLGs than other research locations (Takenoshita & Yamagiwa, 2008; Tutin & Fernandez, 1984). Each individual's sex was established by both first-hand observations and DNA analysis from faeces (Inoue et al., 2013).

4.3.1.2 Sangha Tri-National Protected Area

The Sangha Tri-National Protected Area is home to 4 field sites: Mongabme, Bai Hokou, Mondika and Mbeli Bai. The Wildlife Conservation Society and the Ministry of Forestry and Economy of the Democratic Republic of the Congo jointly administer the 42,00km^2 sized Nouabalé-Ndoki National Park (NNNP) (Ruggiero, 1998). The NNNP, together with the neighbouring Dzanga-Ndoki National Park in Central African Republic and Lobéké National Park in Cameroon, form the **Sangha Tri-National Protected Area complex (TNS)**. The TNS encompasses 25,000km^2 and is the greatest swath of pristine forest left in central Africa (Wilkie et al., 1992). The area is characterised by a main mono dominant *Gilbertiodendron dewevrei* forest and mixed forest, as well as secondary Marantaceae forest patches, swamps, and natural forest clearings (“bais", which are maintained and created by buffaloes and elephants according to Ruggiero & Fay (1994)). The seasonal climate is characterized by a dry season (100mm monthly rainfall) from December to February and a rainy season, with a peak from September to October (Lilly et al., 2002; Masi et al., 2009; Moutsamboté et al., 1994). The climate in this region is characterized by high humidity, high rainfall, and stable temperatures (24-28 °C) throughout the year, due to the typical equatorial climate. UNESCO declared this area as a World Heritage Site in 2012 due to its crucial importance to the region's biodiversity (Parnell, 2002).

The TNS encompasses four out of the five study areas designated for data collection. The initial three sites focused on gathering information about successfully habituated iWLGs, a practice initiated in the early 1990s. These sites include Mongabme (2°55’N, 16°23’E) and Bai Hokou (2°52’N, 16° 28’E) situated within the Dzanga-Sangha Protected Areas (DSPA) in the southwestern region of the Central African Republic (CAR) (Cipolletta, 2003; Fuh et al., 2022; Goldsmith, 1999; Remis, 1994). Additionally, Mondika (4°39’N, 18°56’E) is positioned on the periphery of the NNNP in the Central African Republic - Republic of Congo (Brazzaville) (Doran & McNeilage, 1998; Doran-Sheehy et al., 2004, 2007), close to where Mbeli Bai (2°16'N, 16°25'E) is also located in Congo. At Mbeli Bai, the groups are habituated to the presence of the observers but only observed when they visit the large open bai of around 12.9 hectares. The environment is swampy, with continually flooded soil and a depth of 1-2m on average, apart from a dry area in the eastern part of the bai, which is considered solid ground. The year-round growth of vegetation is dominated by *Hydrocharis chevalieri*, *Rynchospora corumbosa*, *Cyperaceae* spp., and *Poaceaea* spp. It is a mineral-rich area with all year-round food availability (Fay et al., 1990; Parnell, 2002). Since 1995, long-term demographic data has been gathered at Mbeli Bai. Behavioural data collection for the validation of the personality structure were also collected there following their protocols.

Note: Photos provided by Marie Manguette

Picture 21 *Top row, left: observation platform at Mbeli Bai*

Picture 22 *Top row, right: collaboration partner Marie Manguette, Mbeli Bai*

Picture 23 *Bottom row, left: view from above on Mbeli Bai clearing*

Picture 24 *Bottom row, right: a group of iWLGs at the clearing in Mbeli Bai*

4.3.2 Study Subjects for Trait Assessment

On the above mentioned five African field sites, data on personality were collected on a total of 198 gorilla, from 25 raters (field researchers or assistants) and on a total of 501 personality questionnaires: data on 8 iWLGs were collected at Moukalaba Doudou (Gabon), 15 iWLGs at Bai Hokou (Central African Republic), 17 iWLGs at Mondika (Central African Republic – Republic of Congo), 14 iWLGs in Mongabme (Republic of Congo) and 143 iWLGs at Mbeli Bai, Republic of Congo. Age and sex of gorillas were categorized according to Breuer et al.'s (2009) classification as shown in **Table 12**.

Table 12 *Overview of sex and age categories of subjects using Breuer et al.'s (2009) classifications*

Age category	Age-range (years)	N females	N males	N Total[a]
Full-grown silverback	>18	-	40	40 (30)[a]
Young silverback	>14-18	-	4	4 (2)[a]
Blackbacks	>11-14	-	-	-
Sub-adult males	> 7.5 – 11	-	24	24 (12)[a]
Adult females	> 10	71	-	71 (43)[a]
Sub-adult females	> 7.5 – 10	12	-	12 (7)[a]
Juvenile	> 4 – 7.5	11	11	22 (13)[a]
Infant	0 – 4	5	10	15 (10)[a]
Total				198 (124)[a]

Note.
[a] Values in parenthesis indicate the number of iWLGs included as observations at Mbeli Bai.

4.3.3 Behavioural validation of iWLGs from Mbeli Bai

4.3.3.1 Identification of Individual Gorillas

Identification was facilitated using identification cards, and in situations of doubt, digital images were taken to permit confirmation later. Observers scanned the Bai and listened for noises or movements around the edges to determine whether nearby groups were waiting to enter the clearing. Gorillas may be seen in the Bai at any time of day, but most depart after sunset to build their nighttime nests in the nearby forest.

4.3.3.2 Behavioural Data Collection for Validation of the Personality Structure

The current study on personality differences used behavioural data from Mbeli Bai. This was provided by field site manager Marie Manguette and was collected between 2013-2016 by Vidrich Kandza, Jana Robeys and Marie Manguette. Since 1995, the Mbeli Bai Study has accumulated long-term demographic data of 463 iWLGs including 229 infants and 118 adult females. Behaviours were recorded following "The Mbeli Bai Study protocol," and all observers received training to increase reliability. Data included the behavioural activity, Bai visits, and inter and intra unit encounters. Of the 37 reproductive groups, data concerning group compositions, birth, and transfer rates were documented and used to determine male and female breeding ages, tenure length, weaning ages, solitary time, and intervals between demographic events. Dictaphones were used by two observers to record all activities during visits to the Bai using all-occurrence behaviour sample methodology (Altmann, 1974) to record continuous behaviours. Notes were transferred into Excel spreadsheets in mutual agreement of both observers.

I used these behavioural records to validate iWLG personality structure and discuss socio-ecological differences between iVMGs and eWLGs. Behaviours were sorted according to Manguette (2022) into behavioural categories (see **Table 13**, below) to match best the recorded behaviours of iVMG in the study of Eckardt et al. (2015) for comparison.

All data were collected from a 9 high wooden platform (mirador) which was situated on the edge of the Bai. The area was split into separate zones with each zone subdivided into portions and natural characteristics used as visual cues to demarcate these zone boundaries. This allowed observers to record points of entrance, departure, relative animal position, and estimate distances between individuals with reasonable accuracy (more information on Mbeli Bai can be found in Parnell (2002). Gorillas were seen in almost all regions of the Bai. Consequently, the distance between observers and subjects varied from 10 to 500m, and observations were conducted using high-definition telescopes and cameras to identify and follow each gorilla along the clearing, which is 700m long and 150m wide. (Photos provided by Manguette 2022). Each day, at least one researcher or field assistant recorded at the Bai for an average of 9-10 hours. Normal observation started 7:00-7:30am and ended 4:30-5:30pm with data transferred to Excel tables.

Table 13 *Behaviours collected on 124 iWLGs and combined into the following categories according to Manguette (2022)*

Behaviour	Description of behaviour according to Mbeli Bai protocol
Agonistic	Physical contact between individuals such as grabbing, shaking, pushing, barging, flinching, pulling, aggressive biting, clapping Non-contact aggression such as chasing, lunging, swiping, excessive staring, displacement of another individual and bristling (raises hairs to stand on end)
Activity	Locomoting or performing some form of action behaviour (inactive includes climbing, jumping, general locomotion patterns, crossing, lying and making minimal movements)
Approach	Approaching another
Vigilance	Vigilant to another individual; prolonged staring with body frozen, more aggressive in nature than "looking" or "om staring"
Submissive	Avoiding gaze, moving away, fleeing, hiding, screaming
Sexual	Any kind of sexual behaviour, such as sniffing, precopulatory behaviour, mounting, touching, inspection of genitals, etc.
Playing	Solitary and social playing, including parallel playing, running, wrestling, rolling, clapping. It contains intra and interplay behaviour
Affiliative	Friendly/prosocial behaviour (e.g., embracing, nuzzling, hugging, hand contact, kissing, reconciling after aggression, playing)
MI-Affiliative	Mother-infant weaning, including food transfers, clinging, transporting, suckling, grooming, etc.

Note.
Grouped behaviours according to Manguette in Rscript, definitions according to the protocol of Mbeli Bai.

4.3.4 Data Analyses

Missing data. is described in Chapter 3.3.5

Inter-rater reliability of trait assessment is described in Chapter 3.3.5

Data rotation is described in Chapter 3.3.5

PCA. Varimax vs. Promax is described in Chapter 3.3.5

Factor analysis is described in Chapter 3.3.5

Dimension identification is described in Chapter 3.3.5

The statistically relevant number of **four factors** was determined using parallel analyses (Horn, 1965) and the paran function (Dinno, 2009). In the parallel analysis, a random matrix with the same number of raters, ratings, and characteristics as the original data set was used. Only those dimensions having an eigenvalue larger than expected by chance with a 95% degree of confidence were retrieved. The stability of the number of factors was evaluated using a targeted orthogonal Procrustes rotation as robustness test (Everett, 1983; McCrae et al., 1996). The variance of various numbers of factors was also tested. Using a leave-one-out technique, I determined the number of stable dimensions by excluding one field site from each set of studies.

Effects of age and sex differences on personality is described in Chapter 3.3.5

Dimension reliability is described in Chapter 3.3.5

Behaviour analyses.

The average length of time a gorilla of a certain group was observed (calculated by the length of time the group visited the Bai) was divided by the total time spent in a certain behavioural category. Behaviours were correlated with the personality structure for validation.

During each visitation of a known gorilla group or a solitary male in the Bai, the identity of the gorilla unit name, gorillas' identity, time and place of arrival, and departure time, as well as all activities in the ethogram ("The Mbeli Bai Study protocol"), were documented. A unit could visit the Bai several times on a given day of observation. If all members of a unit left the Bai for more than four hours before returning, it was considered two separate visits.

Gorillas were grouped into their units, then the total time the gorilla's unit spent at the Bai (not an individual's time) was calculated as total observation time per unit (N=33 groups, Total Number of observation hours between 2013 and 2016 of all groups=4746.8). The frequency of observed behaviours according to the ethogram of an individual gorilla (N=124 iWLGs) was divided by the total time of the unit's visit. The assortment of the behaviour was done by Manguette via PivotTable and provided for behavioural validation of the personality structure.

Extraction of sociality trait constructs for the genus *Gorillas'* personality structures is described in Chapter 3.3.5. R script is attached in Supplementary Materials.

The extraction of sociality trait constructs for great apes' personality structures. Sociality trait constructs representing clusters of social personality traits (Adams et al., 2015) across different dimensions of great ape species were evaluated. Fuzzy set analysis was used to extract the social personality construct; for more information on the analysis procedure and R source code, see supplementary material in Adams and colleagues (2015). This was done because each personality dimension of a species is represented using a species-specific composition of traits. Further, each trait is characterised by a continuum of different individuals (i.e. plasticity in the expression of the trait) which is defined as a "fuzzy set."

The different dimensions of the personality structure of each great ape species formed the basis for the membership function, which meant that social traits could be mapped on new sociality trait constructs, called shared "social" personality dimension for great apes. All data on the personality structure of each species was extracted from the original articles (bonobos: Weiss et al. (2016); humans: Weiss (2022), Goldberg (1990); orangutan: Weiss et al., (2011); mountain gorilla: Eckardt et al. (2015); chimpanzees: Weiss et al., (2009).

Additional information: Fourteen of the 54 traits from the HPQ were missing. Traits have either not been listed in the previous personality structure of the species (especially in the ex situ Japanese chimpanzees generated structure).

A permutation test was used to examine the cut-off of the salient loading for each trait in the fuzzy set as mentioned in Adams and colleagues (2015).

List of dimensions used to run fuzzy-set analyses:

The number in the bracket resembles the personality dimension used to run the analyses. The number is based on the order of the appropriate dimension in the personality structure of the species.

Dominance: eWLG(1); iWLG (3); iVMG(4)
Sociability: eWLG(4); iWLG (2); iVMG(3)
Conscientiousness: eWLG(3); iWLG (4); iVMG(2)
Neuroticism: eWLG(5); iWLG (1); iVMG(1)
Openness: eWLG(2); iWLG (2); iVMG(2)
Proto-Agreeableness: eWLG(3); iWLG (3); iVMG(4) (similar to Dominance)

4.3.4.1 Cross Species Comparisons

Cross-gorilla comparison. The personality factors of the iWLGs were compared within the genus *Gorilla*: to the eWLGs personality structure (identified in Chapter 3), and to the iVMGs (Eckardt et al., 2015). See **Figure 10**, below for information on variation of data collection (Age categories, etc, see below) across sites and populations.

Variation in data collection

	iWLGs	eWLGs	iVMGs
Sites / Zoos	5	30	1
Total personality ratings	499	671	556
Total raters on the GPQ	25	90	8
Total gorillas rated:	198	203	116
Females / Males	109 / 98	115 / 88	60 / 56
Infants (females/ males)	15 (5/10)	16 (8/8)	15 (4/11)
Juveniles (females/ males)	22 (11/11)	22 (8/14)	15 (9/6)
Subadult (females/ males)	36 (12/24)	14 (6/8)	14 (7/7)
Adult females	71	93	40
Blackbacks	0	5	8
Young silverbacks	4	13	6
Full-grown silverbacks	40	40	18
Total gorillas, behavioural observations for validation	124 (1 site)	24 (2 zoos)	116

Figure 10 *Variation in data collection across gorilla populations*

Cross great ape comparisons. Additionally, I compared the iWLG personality structure with two other in situ great ape studies and a human study: chimpanzees (N=128, Weiss et al., 2017), bonobos (N=16, Garai et al., 2016); and humans (N=1147; Weiss, 2022). I also compared the iWLG personality structure to ex situ studies: to bonobos (N=154, Weiss et al., 2015), to orangutans (N=152, Weiss et al., 2006); to chimpanzees (N=100, King & Figueredo, 1997); additional chimpanzees (N=146, Weiss et al., 2009). Unit-weighted dimension scores were calculated based on the personality structures derived from those samples according to their personality structure, and these were correlated with unit-weighted scores for the present sample of our iWLGs (as already shown in Chapter 3 for eWLGs).

A final comparison of evolutionary integrated low-order facets across close related species was carried out using the categorisations shown in within this Chapter 4.

4.4 Results

Missing data. A total of 501 questionnaires were returned by 25 raters. Of these, 29 gorillas were excluded as they were rated only once. An additional two gorillas were excluded as they had 10 missing traits. From the received questionnaires all missing traits (N = 401, out of a total of N = 27,054 traits, <1.5%) were replaced with the mean for the relevant trait (based on all ratings across all subjects).

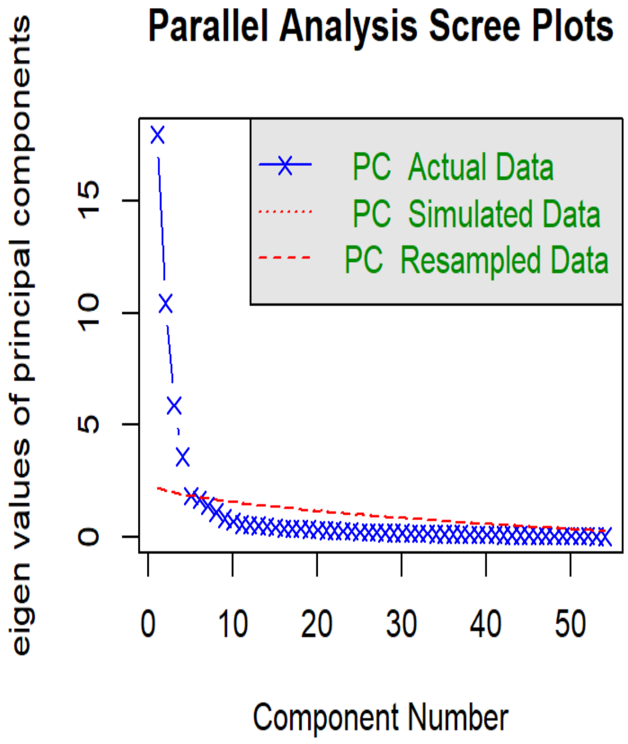
Inter-rater reliabilities for GPQ traits. None of the traits were rejected based on the ICCs 0 criterion (Eckardt et al., 2015; Gosling & John, 1999; Gosling & Vazire, 2002; King & Figueredo, 1997; Weiss et al., 2007, 2009). Consistency between raters for each trait varied from .01 (*Unperceptive*) to .58 (*Dependent*), with an average ICC (3, 1) of .29. ICC (3, k) represents the dependability of mean ratings, and the overall mean was .50 (range from .02 to .79). See **TableAPP 7**.

Personality structure in iWLGs

Horns Parallel Analysis identified **four** principal factors. The adjusted eigenvalues are 16.65, 9.28, 4.83 and 2.60). Four factors (Adjusted eigenvalues > 1) were retained with 1620 iterations using 95th centile estimates.

Additionally, the visual interpretation of the scree plot (**Table 14**) also revealed the cut-off at four factors (note the red line of the re-sampled data, which is comparable to the original data seen in blue).

Table 14 *Parallel Analysis Scree Plot*



Testing for variance on different numbers of factors showed a variance of 0.70 at four factors (see **Table 15** for comparison to the variance from one to four factors).

Cross-method comparison.

I compared the personality factors found by the various analysis methodologies (see above) regardless of the dimension's labelling. PCA and FA were used to extract the personality structure with a set number of four, five, and six dimensions, allowing for a comparison of how each trait loads onto a particular factor and a general coherence check between these characteristics for each solution.

The findings of the cross-method comparison are highlighted in the table below (**Table 15**) by comparing the four dimensions across the extraction techniques.

Table 15 *Traits loading on personality dimensions in iWLGs: a comparison of EFA,minres, varimax vs. promax in a four dimension solution*

	EFA, minres, varimax					EFA, promax				
Traits	**Neu[1]**	**Soc[2]**	**Dom[3]**	**T/SC[4]**	**h^2**	**Neu[1]**	**Soc[2]**	**Dom[3]**	**T/SC[4]**	**h^2**
Anxious	**0.88**	0.02	0.1	-0.05	0.78	**0.96**	-0.21	-0.02	-0.05	0.78
Timid	**0.86**	-0.03	-0.06	0.12	0.75	**0.97**	-0.28	-0.14	0.11	0.75
Depressed	**0.83**	0.07	0.3	-0.13	0.8	**0.87**	-0.14	0.18	-0.11	0.8
Quitting	**0.8**	0.31	0.14	0.02	0.75	**0.79**	0.12	0.03	0.02	0.75
Clumsy	**0.79**	0.25	0.38	-0.12	0.84	**0.77**	0.07	0.26	-0.09	0.84
Erratic	**0.79**	0.18	0.41	-0.24	0.89	**0.78**	0.01	0.26	-0.21	0.89
Disorganized	**0.79**	0.31	0.34	-0.17	0.86	**0.76**	0.14	0.2	-0.15	0.86
Lazy	**0.77**	-0.06	0.37	0.19	0.77	**0.84**	-0.31	0.37	0.27	0.77
Fearful	**0.73**	0.13	-0.27	0.13	0.63	**0.81**	-0.05	-0.36	0.07	0.63
Unperceptive	**0.73**	0.10	0.37	-0.10	0.69	**0.75**	-0.08	0.27	-0.06	0.69
Imitative	**0.71**	0.45	0	0.05	0.71	**0.68**	0.30	-0.11	0.02	0.71
Irritable	**0.60**	0.06	0.56	-0.34	0.79	**0.58**	-0.07	0.43	-0.29	0.79
Vulnerable	**0.57**	0.42	-0.44	0.18	0.73	**0.58**	0.31	-0.53	0.09	0.73
Thoughtless	**0.55**	0.30	0.41	-0.46	0.77	**0.47**	0.23	0.22	-0.45	0.77
Dependent	**0.55**	0.42	-0.48	0.17	0.74	**0.56**	0.31	-0.58	0.07	0.74
Unemotional	**0.55**	-0.09	0.4	0.15	0.49	**0.60**	-0.28	0.41	0.23	0.49
Independent	**-0.51**	-0.33	0.37	-0.13	0.53	**-0.53**	-0.22	0.46	-0.05	0.53
Inventive	0.42	**0.72**	0.25	-0.07	0.77	0.26	**0.68**	0.14	-0.09	0.77
Playful	0.05	**0.87**	-0.03	-0.12	0.78	-0.16	**0.96**	-0.14	-0.19	0.78
Inquisitive	0.07	**0.85**	0.21	-0.11	0.78	-0.16	**0.92**	0.12	-0.14	0.78
Curious	0	**0.83**	0.25	-0.14	0.77	-0.24	**0.92**	0.16	-0.16	0.77
Friendly	0.24	**0.8**	-0.3	0.15	0.82	0.1	**0.82**	-0.38	0.05	0.82
Active	-0.09	**0.8**	0.08	-0.07	0.66	-0.31	**0.91**	0.01	-0.12	0.66
Sociable	0.03	**0.78**	-0.08	0.08	0.62	-0.15	**0.85**	-0.13	0.03	0.62
Affectionate	0.27	**0.77**	-0.08	0.31	0.77	0.13	**0.73**	-0.1	0.28	0.77
Helpful	0.31	**0.71**	0.19	0.31	0.74	0.16	**0.65**	0.2	0.33	0.74
Innovative	0.49	**0.71**	0.17	-0.02	0.77	0.35	**0.64**	0.06	-0.04	0.77
Sympathetic	0.31	**0.64**	0.12	0.27	0.59	0.52	0.3	***-0.62***	0.11	0.76
Distractible	0.48	**0.61**	0.14	-0.09	0.63	0.37	**0.55**	0.02	-0.12	0.63
Gentle	0.26	**0.57**	-0.23	0.53	0.72	0.19	**0.5**	-0.17	0.50	0.72
Intelligent	-0.02	**0.57**	0.22	0.35	0.5	-0.17	**0.58**	0.30	0.38	0.5
Sensitive	0.2	**0.45**	0.33	0.35	0.47[*]	0.1	0.37	0.39	***0.41***	0.47[*]
Solitary	0.27	**-0.47**	0.21	-0.27	0.41[*]	0.38	**-0.56**	0.15	-0.23	0.41[*]
Dominant	-0.15	-0.13	**0.88**	0.03	0.81	-0.22	-0.15	**0.99**	0.2	0.81
Persistent	-0.05	-0.03	**0.84**	-0.07	0.71	-0.13	-0.05	**0.9**	0.07	0.71
Bullying	0.16	0.19	**0.82**	-0.16	0.76	0.04	0.15	**0.81**	-0.04	0.76
Aggressive	0.18	-0.04	**0.79**	-0.32	0.76	0.12	-0.09	**0.75**	-0.20	0.76
Decisive	-0.19	-0.18	**0.74**	-0.12	0.63	-0.24	-0.16	**0.8**	0.01	0.63
Stingy	0.24	0.20	**0.73**	0.09	0.64	0.15	0.11	**0.77**	0.21	0.64
Jealous	0.26	0.14	**0.73**	-0.04	0.62	0.18	0.06	**0.74**	0.08	0.62

Defiant	0.35	0.18	**0.7**	-0.35	0.76	0.26	0.12	**0.6**	-0.27	0.76
Reckless	0.3	0.33	**0.61**	-0.46	0.78	0.17	0.32	**0.47**	-0.41	0.78
Protective	0.15	0	**0.61**	0.11	0.41^{*}	0.11	-0.08	**0.68**	0.22	0.41^{*}
Excitable	0.51	0.27	**0.54**	-0.34	0.73	***0.43***	0.19	0.4	-0.29	0.73
Impulsive	0.46	0.36	**0.48**	-0.39	0.72	0.36	0.31	0.32	***-0.37***	0.72
Manipulative	0.44	0.36	**0.68**	-0.16	0.81	0.33	0.26	**0.61**	-0.08	0.81
Individualistic	0.23	0.13	**0.45**	-0.24	0.34^{*}	0.17	0.1	***0.38***	-0.2	0.34^{*}
Submissive	0.5	0.4	**-0.54**	0.22	0.76	0.52	0.3	**-0.62**	0.11	0.76
Predictable	0.02	0.05	-0.17	**0.77**	0.62	0.06	-0.05	0.03	**0.81**	0.62
Stable	-0.21	0.29	-0.04	**0.7**	0.62	-0.28	0.28	0.16	**0.74**	0.62
Cool	-0.2	0.21	-0.03	**0.69**	0.56	-0.25	0.19	0.17	**0.73**	0.56
Conventional	0.42	0.02	-0.09	**0.66**	0.61	0.49	-0.17	0.03	**0.69**	0.61
Cautious	0.43	-0.11	-0.28	**0.53**	0.56	0.56	-0.3	-0.2	**0.53**	0.56
Autistic	0.12	0.15	0.25	0.13	0.12^{*}	0.07	0.11	***0.28***	0.18	0.12^{*}
^{8}Total traits	53					52				
^{9}FA,min,pro	0.97	0.96	0.97	0.97						
^{10}PCA,var	1.00	1.00	1.00	1.00						
^{11}FA,min,var (5)	0.92	1.00	0.96	0.69	0.97					
^{12}FA,min,var (6)	0.91	0.99	0.64	0.94	0.95	0.47				

Note.
Values in bold font indicate highest salient loadings; '+' = positive loadings; '-' = negative loadings.
1. Raw: 6 factor solutions are compared in respect to EFA,minres,varimax$_{.}$ vs PCA,varimax rotation method.
2. Raw: factor labelling: Column 2-5: Neu^{1}=Neuroticism, Soc^{2}=Sociability, Dom^{3}=Dominance, S/T^{4}=Self-Control/ Tolerance; h^{2}=communality (*indicates communalities under 0.5).
Column 8-13: Same listening of factors in the eWLG,$_{PCA,min,pro,4}$ as in eWLG,$_{EFA,min,var,4}$.
Column 1: listening of 54 traits according to their associated factors in the iWLG,$_{EFA,min,var,4}$ sorted in a descending order of their silent trait loadings.
^{8}Total traits = number of traits included into the factor solution. Either iWLG,$_{EFA,min,var,4}$ or iWLG,$_{PCA,min,pro,4}$.
Factor congruence between iWLG,$_{PCA,min,var,4}$ and ^{9}FA,minres,promax (4 factors), ^{10}PCA,varimax (factors);4 ^{11}FA,minres,varimax (5 factor solution), and ^{12}FA,minres,varimax (6 factor solution) to each factor is presented.

I provide the four factor solution for iWLG,$_{EFA,min,var,4}$ (4 factor solution) vs. iWLG,$_{PCA,pro,4}$ (4 factor solution) to emphasise the influence that a certain approach may have on the structure of personality (labelled factors) and, therefore, on the absolute silent loadings on each personality trait within the dimension. In relation to the silent loading defined as |.4, different numbers of traits were loaded in each personality factor; see total number of traits iWLG,$_{EFA,min,var,4}$: N=53 and iWLG,$_{PCA,pro,4}$: N=52, respectively).

Using iWLG,$_{EFA,min,var,4}$ four factors were extracted. The first 17 traits, from *Anxious* to *Independent*, are clustered around the first factor named Neuroticism (Neu$_{iWLG}$). The following 16 traits, from *Inventive* to *Solitary*, belong to the Sociability (Soc$_{iWLG}$) factor, whereas the following 15 traits, from *Dominant* to *Submissive*, belong to the Dominance (Dom$_{iWLG}$) factor. The following five traits, from *Predictable* to *Cautious*, define the Tolerance /Self-Control (T-SC$_{iWLG}$) factor the personality structure created using iWLG,$_{EFA,min,var,4}$, the trait *Autistic* had to be eliminated since it did not match the inclusion criterion (|.4).

In total, only four traits were not consistent across the different analyses procedures iWLG,$_{\text{EFA,min,var,4}}$ vs. iWLG,$_{\text{PCA,pro,4}}$ *(Sympathetic, Sensitive, Excitable, Impulsive)*. Factor congruence coefficient (last 4 raws) confirm that the iWLG,$_{\text{EFA,min,var,4}}$ and the iWLG,$_{\text{EFA,min,var,5}}$ (5 factors), as well as the iWLG,$_{\text{EFA,min,var,6}}$ (6 factor solution) showed that the factors and dimensions are very robust. Overall, 4 of the 4 factors (EFA; MinRes,varimax) were strongly replicated across all compared methods. Additionally, we tested the absolute inter-factor correlation between iWLG,$_{\text{EFA,min}}$ and iWLG,$_{\text{PCA,pro}}$ on 4 factors with the mean of 0.23 and SD of 0.16.

The four factor personality solution iWLG,$_{\text{EFA,min,var,4}}$ serves as the foundation for all subsequent analyses, including the cross-species comparison of the personality structure, the extraction of a Sociality Trait Construct across the genus *Gorilla*, and the analysis of the effect sex and age have on the personality structure, as well as the validation with behavioural observations.

Inter-rater reliability of the personality factors, analysed using FA$_{\text{Minres,v}}$.

The internal consistency (Cronbach's alpha) of the factors was highest for Neuroticism, .95, and lowest for Tolerance/ Self-Control, .81 (see **TableAPP 8**)

Correlations between personality factors and behaviour for validation

To validate all factors of the personality structure in iWLGs, behavioural data have been used as described in **Table 13**. For all factors of the personality structure generated via FA$_{\text{Minres,v,}}$ significant correlations to predicted behaviour categories could be found (see **Table 16**).

Table 16 explains the correlations found between the four personality factors and observed behaviours.

Table 16 *Correlations between personality factors and behaviour in iWLGs (N= 124)*

Behaviour	Neu$_{iWLG}$	Soc$_{iWLG}$	Dom$_{iWLG}$	T-SC$_{iWLG}$
Agonism^{b}	**-.39****	**-.18***	.10	**-.31****
Activity^{b}	**-.21***	.12	.14	**-.35****
Approach^{b}	-.07	.11	.11	**-.18***
Vigilance^{b}	**-.24****	-.07	.12	**-.21***
Submissive^{b}	-.12	.09	-.04	-.11
Sexual^{b}	-.06	.11	**.20***	-.15
Play^{a}	.04	**.34****	**.28****	**-.26****
Affiliative^{a}	.01	**.38****	**.28****	-.16
Mother-infant Affiliative^{a}	**.19***	.12	.12	.15

Note.
For descriptions of the behaviours, see **Table 13**
^{a} Focal individual coded as either actor or recipient. ^{b} Focal individual coded as actor (behavioural performed).
Column 1: Behaviour Categories: All behaviours were recorded as ad libitum sampling and the frequency of the occurrence of the behaviour was divided by the total number of days the individual was observed between 2013 and 2016.
Column 2-5: Factors: Neu$_{iWLG}$ = Neuroticism, Soc$_{iWLG}$ = Sociability, Dom$_{iWLG}$ = Dominance, T-SC$_{iWLG}$ = Tolerance / Self-Control.
Bold font indicates significant correlations *p< .05, ** p<.01 *** p < .001.

As indicated in **Table 16**, the personality factor Neu$_{iWLG}$ was significantly negatively correlated with agonistic, activity, and vigilance behaviours, suggesting that more neurotic iWLGs tend to engage in these behaviours less often. Neu$_{iWLG}$ is positively correlated with mother-infant affiliative behaviour, indicating that iWLGs higher on Neu$_{iWLG}$ show more affiliative behaviours with their infants. The Soc$_{iWLG}$ factor shows positive correlations with play and affiliative behaviour. Conversely, it has a negative correlation with agonism, suggesting that more sociable individuals engage less in agonistic behaviours. The factor Dom$_{iWLG}$ is significantly positively correlated with sexual behaviour, playing, and affiliative behaviour, suggesting that more dominant individuals tend to engage more in these behaviours. T-SC$_{iWLG}$ is negatively correlated with agonism, activity, vigilance, and playing.

Effects of sex and age differences on personality.

In **Table 17**, the six age categories for iWLGs are categorised as following: infants (both gender), juveniles (both gender), subadults (both gender), blackbacks (males only), young silverbacks (males only), adults (both sexes). The effect on rating scores for NeuiWLG, and SociWLG depended on age and sex and on the interaction.

Table 17 *Age, Sex and Age x Sex Effects on Personality factors of iWLGs*

Factor	**Tested effect**	***b***	***SE_b***	***t***	***p***
Neu$_{iWLG}$	**Age**	-.70	.48	-1.46	**< 0.001*****
	Sex	3.66	3.33	1.10	**< 0.001*****
	Age x Sex	-1.89	.68	-2.80	**.01 ****
SOC$_{iWLG}$	**Age**	-1.60	.47	-3.42	**< 0.001*****
	Sex	-9.65	3.22	2.99	**.06**
	Age x Sex	-2.60	.66	-3.96	**< 0.001*****
Dom$_{iWLG}$	Age	-.04	.52	-.10	.56
	Sex	1.32	3.57	.37	.66
	Age x Sex	-.33	.72	-.45	.87
T-SC$_{iWLG}$	Age	.46	.53	.87	.72
	Sex	1.47	3.64	.40	-.93
	Age x Sex	-.53	.74	-.72	.46

Note.
b = unstandardized linear regression coefficient
SE$_b$ = SE of linear regression coefficient
t = t value
p = p values, bold font indicates significant correlations *p< .05, ** p< .01 *** p < 0.001.
green=increasing, or on females red=decreasing, or on males

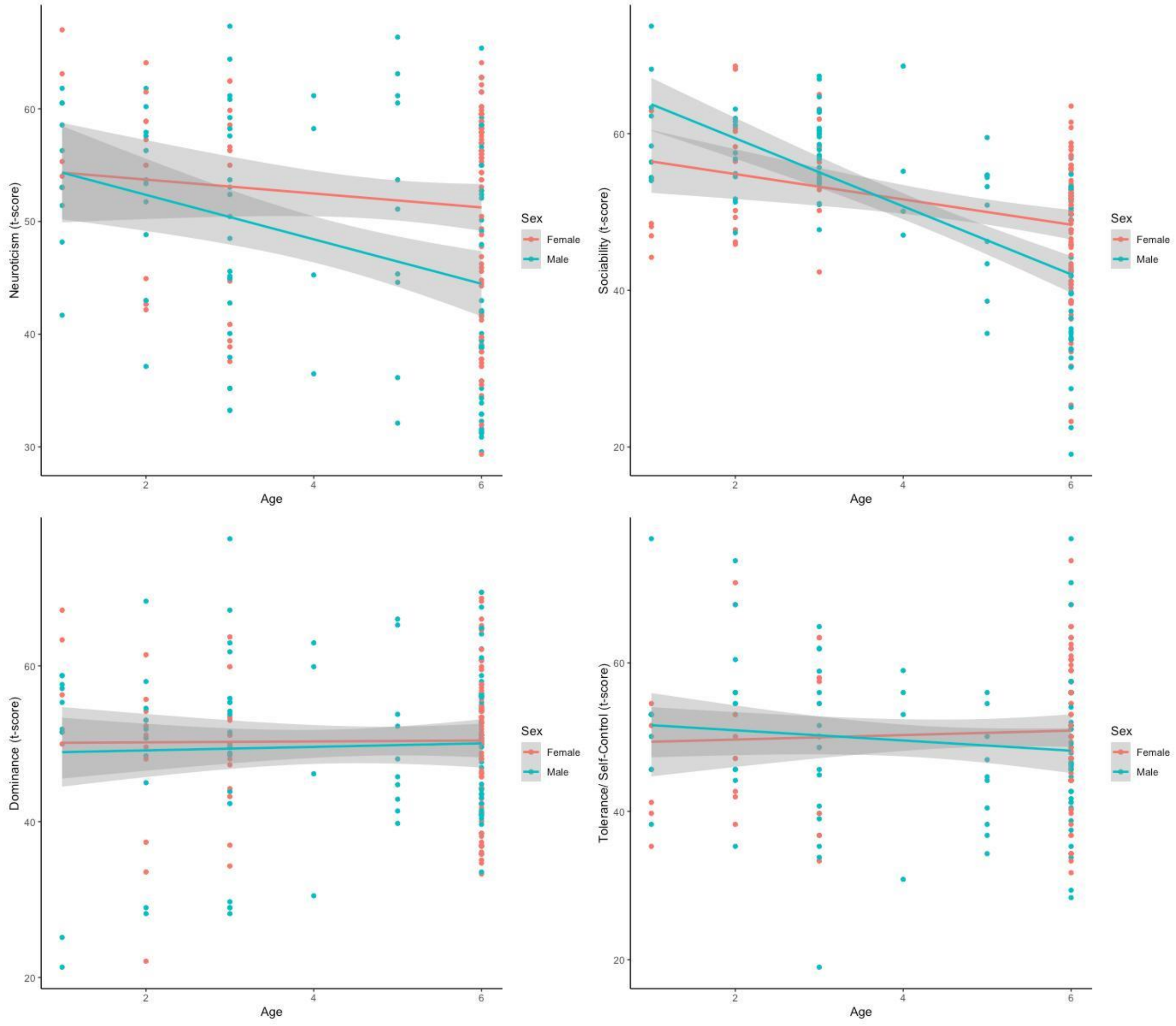


Figure 11 *Age Differences on Personality factors of iWLGs*

Note.
Graphs are shown in the following order of the personality factor of eWLGs: Neu$_{\mathrm{iWLG}}$, Soc$_{\mathrm{iWLG}}$, Dom$_{\mathrm{iWLG}}$, and T-SC$_{\mathrm{iWLG}}$.
Score distribution of female (red) and male (blue) on each of the personality factor presented by iWLG age categories (according to **Table 12**, Chapter 4, see also description above in the text).

Significant effects on age, sex or interaction (Figure 11) are found for the factors Neu$_{\mathrm{iWLG}}$ and Soc$_{\mathrm{iWLG}}$.. The graphical representation of the regression line for females for boh factors Soc$_{\mathrm{iWLG}}$ and Neu$_{\mathrm{iWLG}}$ shows a slight downward trend, indicating that Soc$_{\mathrm{iWLG}}$ decreases marginally with age, whereas males on the other hand show a steeper downward trend in both factors, suggesting a more pronounced decrease with age. However, both genders have similar levels in the factor Neu$_{\mathrm{iWLG}}$ in age category 1, but differ in the factor Soc$_{\mathrm{iWLG}}$, with males higher than females. For the factors Dom_{iWLG}, and $\text{T-SC}_{\text{iWLG}}$, no significant effects could be found. Considerable individual variability in the scores was found for all factors.

Cross-species comparison.

The personality structure of different great ape species was compared to our population of eWLGs (Chapter 4). This included ex situ and in situ bonobos, ex situ orangutans, ex situ and in situ chimpanzees, and humans. Personality structure comparisons and the distribution of individual traits is shown. Correlations between the generated $\text{iWLG,}_{\text{EFA,min,var,4}}$ personality factors (based on unit-weighted scores) and those of eWLGs and all other ex situ or in situ great ape populations (bonobos, chimpanzees, and orangutans), and humans are also shown in **Table 18**. A detailed overview of the variances of the correlation coefficient acquired in comparison with the personality structure generated via $\text{iWLG,}_{\text{EFA,min,var,4}}$ are also within **Table 18**.

Table 18 *Correlation coefficients between iWLG Personality Factors (Unit-Weighted Scores) and eWLGs, iVMGs, in situ bonobos, in situ chimpanzees, ex situ bonobos, ex situ orangutans, ex situ chimpanzees (two structures), and humans*

$\text{iWLG,}_{\text{EFA,min,var,4}}$	**Neu_{iWLG}**	**Soc_{iWLG}**	**Dom_{iWLG}**	**$\text{T-SC}_{\text{iWLG}}$**
eWLGs[a]				
Dominance	.36 (.05, .32)	.18 (.87, .92)	**.98** (-.16, .11)	-.37 (.60, .75)
Openness	.46 (.70, .82)	**.94** (-.13, .15)	.23 (-.52, -.25)	.14 (-.46, -.21)
Conscientiousness	-.90 (-.26, .02)	-.41 (-.17, .11)	-.49 (-.48, -.25)	.19 (-.11, .16)
Agreeableness	.54 (.05, .32)	.89 (.05, .32)	.05 (.05, .32)	.38 (.05, .32)
Neuroticism	.87 (.05, .32)	.32 (.05, .32)	.20 (.05, .32)	-.05 (.05, .32)
Extraversion	-.67 (.05, .32)	.07 (-.11, .16)	-.40 (-.01, .26)	.08 (.32, .54)
iVMGs[b]				
Dominance	-.71 (.36, .57)	-.32 (-.15, .12)	.31 (.52, .69)	-.22 (-.29, -.02)
Openness	.55 (.35, .57)	.68 (.80, .88)	.59 (-.49, -.25)	-.43 (.18, .43)
Sociability	.02 (-.37, -.11)	.64 (.45, .64)	-.45 (.06, .32)	.56 (.86, .92)
Proto-Agr	-.54 (-.95, -.91)	-.27 (-.23, .04)	-.93 (.14, .39)	.21 (.09, .35)
iB[c]				
Unemotionality	**.93** (.29, .52)	.41 (-.17, .01)	.40 (.36, .57)	.16 (-.30, -.03)
Conscientiousness	.64 (-.94, -.90)	.89 (-.32, -.06)	.28 (.36, .57)	.09 (.10, .36)
Aggressiveness	.22 (.06, .32)	.05 ()	.94 (-.16, .11)	-.34 (.46, .65)
Irritability	.15 (-.30, .04)	-.56 (-.17, .01)	.47 (.94, .97)	-.21(-.20, .07)
Activity	.43 (-.23, .05)	.64 (.46, .65)	.67 (.04, .31)	-.21 (.95, .97)
iC[d]				

Dominance	-.31 (.07, .33)	-.31 (.89, .93)	.66 (-.01, .26)	-.31 (.35, .57)
Extraversion	.07 (.78, .87)	.82 (.06, .32)	-.02 (.05, .32)	.19 (-.25, .03)
Neuroticism	.53 (-.07, .02)	.11 (.83, .90)	.67 (-.13, .14)	-.61 (.71, .82)
Openness	.50 (-.84, -.74)	.89 (-.36,- .10)	.39 (.59, .74)	.03 (-.02, .26)
Agreeableness	.51 (-.40, -.14)	.84 (.16, .41)	.29 (.13, .38)	.35 (.81, .89)
Conscientiousness	-.49 (.31, .53)	-.30 (.12, .38)	-.77 (-.37, -.11)	.61 (-.27, .00)
eB[e]				
Assertiveness	-.73 (.29, .52)	-.38 (-.17, .01)	.23 (.36, .57)	-.15 (-.30, -.03)
Conscientiousness	-.55 (-.94, -.90)	-.24 (-.32, -.06)	-.94 (.36, .57)	.39 (.10, .36)
Openness	.36 (.06, .32)	.89 ()	.27 (-.16, .11)	-.06 (.46, .65)
Attentiveness	-.89 (-.30, .04)	-.45 (-.17, .01)	-.57 (.94, .97)	.13 (-.20, .07)
Agreeableness	.48 (-.23, .05)	.89 (.46, .65)	.22 (.04, .31)	.30 (.95, .97)
Extraversion	-.60 (-.09, .18)	.00 (.24, .48)	-.55 (.11, .37)	.23 (.28, .51)
eO[f]				
Extraversion	.00 (.08, .34)	.80 (.95, .97)	.04 (-.10, .17)	-.05 (.47, .65)
Dominance	.32 (.99, .99)	.09 (-.03, .24)	**.98** (-.33, -.06)	-.35 (-.04,- .15)
Neuroticism	.87 (-.03, .24)	.30 (-.08,.19)	.39 (-.72, -.56)	-.16 (-.23, .04)
Agreeableness	.48 (-.23, .05)	.89 (.46, .65)	.22 (.04, .31)	.30 (.95, .97)
Intellect	-.86 (.03, .03)	-.48 (-.28, .01)	-.02 (.74, .84)	-.18 (-.44, -.19)
cC[g]				
Dominance	-.37 (.07, .33)	-.18 (.89, .93)	.68 (-.01, .26)	-.37 (.35, .57)
Extraversion	.11 (.78, .87)	.85 (.06, .32)	-.13 (.05, .32)	.21 (-.25, .03)
Conscientiousness	-.68 (-.07, .02)	-.31 (.83, .90)	-.88 (-.13, .14)	.38 (.71, .82)
Agreeableness	.49 (-.84, -.74)	.76 (-.36,- .10)	.32 (.59, .74)	.26 (-.02, .26)
Neuroticism	.20 (-.40, -.14)	.07 (.16, .41)	.44 (.13, .38)	-.66 (.81, .89)
Openness	.49 (.31, .53)	.87 (.12, .38)	.39 (-.37, -.11)	.02 (-.27, .00)
eC[h]				
Dominance	-.41 (-.72, .56)	-.19 (-.55, -.33)	.65 (.56, .72)	-.37 (-.15, .13)
Extraversion	.06 (.66, .79)	.81 (-.04, .23)	-.21 (.18, .43)	.25 (-.34, -.08)
Conscientiousness	-.81 (-.09, .18)	-.41 (.80, .88)	-.80 (-.13, .15)	.28 (.72, .83)
Agreeableness	.53 (-.72, -.56)	.73 (-.30,-.04)	.26 (.81, .89)	.51 (-.08, .20)
Neuroticism	.22 (-.45, -.21)	-.01 (.01, .28)	.44 (.15, .40)	-**.73** (.74, .84)
Openness	.50 (.21, .45)	.89 (.09, .35)	.39 (-.44, .32)	.03 (-.27, .00)
H[i]				
Openness	-.20 (.22, .47)	.66 (.92, .96)	.11 (-.15, .12)	-.13 (.44, .64)
Agreeableness	.77 (-.95, -.91)	.40 (-.11, .16)	.06 (.01, .36)	-.03 (.35, .57)
Conscientiousness	.22 (-.31, -.05)	.72 (-.16,.12)	.47 (.92, .95)	-.21 (-.24, .03)
Neuroticism	-.05 (-.16, .11)	.34 (-.05, .22)	-.78 (-.43, -.18)	.46 (-.14, .13)
Extraversion	-.93 (.01, .28)	-.51 (.58, .74)	-.50 (.09, .35)	.12 (.06, .75)

Note.
Bold = highest correlation.
Column 1: eWLGs[a] = ex situ gorilla personality structure extracted via $\text{EFA}_{\text{Minres, v}}$ 6 factors, Chapter 3; *iVMGs*[b] = Virunga mountain gorilla (Eckardt et al., 2015); iB[c] = in situ bonobo (Garai et al., 2016); iC[d] = in situ chimpanzee (Weiss et al., 2017) ; eB[e] = ex situ bonobo (Weiss et al., 2015); iO[f] = orangutan (Weiss et al., 2006); eC[g] = chimpanzee (King and Figueredo, 1997); eC[h] = chimpanzee (Weiss et al., 2009); and H[i] = human (Weiss et al., 2022).
Column 2-5: Neu_{iWLG} = Neuroticism, Soc_{iWLG} = Sociability, Dom_{iWLG} = Dominance, $\text{T-SC}_{\text{iWLG}}$ = Tolerance/ Self-Confidence.

Overall, the iWLG personality structure had the highest agreement in Neu$_{\text{iWLG}}$ with in situ bonobos (.93/ Unemotionality); in Soc$_{\text{iWLG}}$ with eWLGs: (.94/ Openness); in Dom$_{\text{iWLG}}$ with eWLGs: (.98/ Dominance) and ex situ orangutans Dominance (.98/ Dominance; in Weiss et al. 2006); and in T-SC$_{\text{iWLG}}$ with the inverse of the factor Neuroticism in ex situ chimpanzees (-.73, Weiss et al., 2009).

Comparison of eWLGs (Chapter 3) vs. iVMGs (Eckardt et al., 2015).

When comparing eWLGs' personality factors (Chapter 3) with iVMGs four factor solution (Eckardt et al., 2015), high agreement was found between the personality structure of eWLG Agreeableness/ Sociability (Agr$_{\text{eWLG}}$) and iVMG Sociability, and the inverse of eWLG Dominance and iVMG Pro-Agreeableness (see **Table 19**).

Table 19 *Correlations between eWLGs and iVMGs Personality Factors Unit-Weighted Scores*

eWLGs[a]	Dominance	Openness	Conscientiousness	Agreeableness/ Sociability	Neuroticism	Extraversion
iVMG[s]						
Dominance	.47 (.36, .57)	-.01 (-.15, .12)	**.61** (.52, .69)	-.16 (-.29, -.02)	-**.77** (-.82, -.70)	.29 (.16, .41)
Openness	.47 (.35, .57)	**.84** (.80, .88)	-.38 (-.49, -.25)	.31 (.18, .43)	.33 (.02, .45)	.51 (.04, .60)
Sociability	-.25 (-.37, -.11)	.56 (.45, .64)	.19 (.06, .32)	**.90** (.86, .92)	-.18 (-.31,- .04)	**.63** (.54, .71)
Proto-Agreeableness	**-.93** (-.95, -.91)	-.01 (-.23, .04)	.27 (.14, .39)	.22 (.09, .35)	-.04 (-.08, .01)	-.11 (-.24, .03)

Note.
Bold = highest correlation
Colum 1: WLGs[a] = ex situ gorilla personality structure extracted via EFA$_{\text{Minres, v}}$ 4 factors, see Chapter 3.
iVMG[b] = Virunga mountain gorilla (Eckardt et al., 2015).

Comparison of the trait loadings for iVMGs showed that five traits loading into eWGL Dominance overlapped with Proto-Agreeableness: (not) *Stingy,* (not) *Aggressive,* (not) *Persistent,* (not) *Jealous,* (not) *Irritable,* and (not) *Manipulative.* For Agreeableness, five traits overlapped with the dimension Sociability in iVMG: S*ympathetic, Affectionate, Friendly, Sociable* and *Gentle*. All of our Openness-traits – with the exception of *Imitative* – were shared with the Openness dimension in iVMGs: *Innovative, Inventive, Inquisitive, Curious, Active, Playful,* (not) *Lazy, and* (not) *Conventional*. For Conscientiousness, six traits loaded onto iVMG Dominant: (not) *Disorganized, Intelligent,* (not) *Distractible,* (not) *Clumsy, Decisive,* and *Sensitive*; and four onto iVMG Openness *Thoughtless,* (not) *Predictable, Erratic,* and *Quitting*. Similar distribution is shown for our additional factor Neuroticism. Four traits loaded onto iVMG Dominance: (not) *Fearful,* (not) *Vulnerable,* (not) *Anxious,* and (not) *Timid*; and four onto iVMG Openness: (not) *Stable,* (not) *Cool, Excitable,* and (not) *Independent*).

The distribution of the traits of the four factors in iWLGs in comparison to great ape species (in situ and ex situ) and humans is shown in **Table 20**.

Table 20 *Overview of trait distribution across the genus Gorilla (eWLG and iVMGs), ape species (in situ: chimpanzees and bonobos; ex situ: bonobos, orangutans, chimpanzees), and humans in relation to the generated personality structure of iWLGs*

	Cross-gorilla comparison					Cross-great ape comparison				
GPQ Traits	iWLG $_4$	eWLG$_6$	eWLG$^{a}_{1994}$	iVMG$^{b}_{4}{}^{b}$	iC^{c}	iB^{d}	eB$_{c}^{e}$	eO^{f}	eC^{g,h}	H^{i,j,k,l,m}
Anxious	+N	+N	----	-D		+U-E	-As	+N	$-D^{h}$	$+N^{i,l}$
Timid	+N	+N	----	-D		-	-As	+N	$-D^{g,h}$	$-E^{i,k,l}$
Depressed	+N	-E	----	-S		-	-E	-E	$-E^{g,h}$	$-E^{j,m}$
Quitting	+N	-C	----	+O		+U-E	nl	----	$-C^{h}$	$-C^{k,m}$
Erratic	+N	-C	----	+O		+U-E	-C	+N	$-C^{g,h}$	$-C^{i,m}$
Disorganized	+N	-C	----	-D		-	-At	-I	$-C^{g,h}$	$-C^{i,m}$
Clumsy	+N	-C	----	-D		+U-E	-At	+I	$-C^{h}$	C^{m}
Lazy	+N	-O	$-E^{a}$	-O		+U-E	-O	-E	$-E^{g,h}$	$-C^{i,m}$
Unperceptive	+N	-C	----	nr		+U-E	-At	nl	$-C^{h}$	nl
Fearful	+N	+N	$+Fef^{a}$	-D		-	-As	+N	$-D^{h}$	$+N^{i,m}$
Imitative	+N	+O	----	-D	-C	-	+O	+E	$+E^{g,h}$	$-O^{j}$
Irritable	+N	+D	$+D^{a}$	-P-A		+Ir	-C	+D	$-C^{g,h}$	$-A^{i,k,m}$
Vulnerable	+N	+N	----	-D		+U-E	-As	+N	$-D^{h}$	$+N^{k,l}$
Unemotional	+N	-E	----	+D		+U-E	+As	+I	$+N^{g,h}$	$-N^{i,k,m}$
Dependent	+N	+A	----	-D	-D	-	-As	-I	$-D^{g,h}$	$+N^{i}/-C^{m}$
Thoughtless	+N	-C	----	+O		-	-At	----	$-C^{h}$	$-C^{k,m}/-A^{i}$
Independent	-N	-N	----	-O		+U-E	nl	-E	$D^{g,h}$	$-N^{i}/+O^{m}$
Playful	+S	+O	$+E^{a}$	+O		-Ir	+O	+E	$+E^{g,h}$	$+E^{i}/+O^{m}$
Inquisitive	+S	+O	----	+O	+O	-	+O	+E	$+O^{g,h}$	$+O^{i,m}$
Curious	+S	+O	$+E^{a}$	+O	+O	-	+O	+E	$+O^{h}$	$+O^{i}$
Friendly	+S	+A	----	+S		+F	+A	+A	$+E^{g,h}$	$+A^{i}/+E^{m}$
Active	+S	+O	$+E^{a}$	+O	+E	+Ac	+O	+E	$+E^{g,h}$	$+E^{i}/+O^{m}$
Sociable	-S	+A	$+E^{a}$	+S	+E	-Ir	+A	+A	$+E^{g,h}$	$+E^{i,k,m}$
Affectionate	+S	+A	----	+S		+F	+A	+A	$+E^{g,h}$	$+A^{i}/+O^{m}$
Inventive	+S	+O	----	+O	+O	+F	+O	+E	$+O^{g,h}$	$+O^{i,m}$
Helpful	+S	+A	----	+D	+A	-	+A	+A	$+A^{g,h}$	$+A^{g,h,k}$
Innovative	+S	+O	----	+O	+O	-	+O	----	$+O^{h}$	$+O^{i,m}$
Sympathetic	+S	+A	$+Und^{a}$	+S	+A	-	+A	+A	$+A^{g,h}$	$+A^{i,m}$
Distractible	+S	-C	----	-D		-	-At	----	$-C^{h}$	C^{m}
Intelligent	+S	+C	----	+D			+At	+I	$+D^{g,h}$	$+O^{i}$
Gentle	+S	+A	$+Und^{a}$	+S		-	+C	-D	$+A^{g,h}$	$+A^{j,m}$
Solitary	+S	-E	$-E^{a}$	-S	-E	-	-E	-E	$-E^{g,h}$	$-E^{i,m}$
Sensitive	+S	+C	----	+D	+A	-U-E	+A	+A	$+A^{g,h}$	$+A^{i}/+N^{m}$
Dominant	+D	+D	$+D^{a}$	+D		-	+As	+D	$+D^{g,h}$	$+E^{i,k}$
Persistent	+D	+D	----	-P-A		-	-C	+D	$+D^{g,h}$	$+J^{i}$
Bullying	+D	+D	----	+D		+Ag	-C	+D	$+D^{g,h}$	$-A^{i,k,m}$
Aggressive	+D	+D	$+D^{a}$	-P-A		+Ag	-C	+D	$-C^{g,h}$	$-A^{i,m}$
Decisive	+D	+C	----	+D	+D	+Agg	+As	+I	$+D^{g,h}$	$+C^{i,m}$
Jealous	+D	+D	----	-P-A		-F	-C	+D	$-C^{g,h}$	$-A^{i,m}/+N^{i}$

Stingy	+D	+D	----	-P-A		-	-C	+D	+D[g,h]	-A[i,k,m]
Defiant	+D	+D	----	-S		+Ac	-C	+D	-C[g,h]	-A[i,m]
Manipulative	+D	+D	----	-P-A		+F	-C	+D	+D[h]	-A[i,m]
Protective	+D	+A	+Und[a]	+D		+Ir	+A	+A	+A[g,h]	+A[i]/+O[m]
Reckless	+D	+D	----	+O	-C	-	-C	+D	-C[g,h]	-C[i,m]
Submissive	-D	-D	----	-D		+U-E	-As	-D	-D[g,h]	-E[k]/+N[i]
Excitable	+D	+N	+D[a]	+O	+N	-	-As	+N	+N[g,h]	+N[i,m]
Impulsive	+D	+D	----	+O		+F	-C	+N	-C[g,h]	+E[i]/+O[m]
Individualistic	+D	nr	----	-S		-	-E	----	-E[h]	-N[i]/+O[m]
Predictable	+SC	+C	----	-O	+C	-	+C	-N	+C[g,h]	+C[i]
Stable	+SC	-N	+Und[a]	-O	-N	-	As	-N	-N[g,h]	-N[i,m]
Cool	+SC	-N	+Und[a]	-O		+U-E	As	-N	-N[h]	-E[i]/-N[m]
Conventional	+SC	-O	----	-O		-	-O	-E	+A[h]	-O[k,m]/-C[i]
Cautious	+SC	-D	----	nl		-	Nl	+N	-D[g,h]	+C[i]/+N[m]
Autistic	nr	nr	----	nl		-	-E	nl	+N[h]	----
Total traits		53								

Note.
'+' = positive loadings; '-' = negative loadings; nr = item is not reliable; nl = no loading; '----' = trait (or included term) not assessed.
A = Agreeableness; Ac = Activity; Ag = Aggressiveness; As = Assertiveness, At = Attentiveness; C = Conscientiousness; D = Dominance; E = Extraversion; F = Friendliness; I = Intellect; Ir = Irritability; N = Neuroticism; O = Openness; P-A (Proto-Agreeableness; S = Sociability; T-SC + Tolerance / Self-Confidence; U-E = Un-emotionality; Und = Understanding.
[a] traits (or synonyms of traits) and classification in eWLGs (Gold & Maple, 1994), 10 traits.
[b] traits and their classification in iVMGs (Eckhardt et al., 2015), 51 traits.
[c] traits and their classification in in situ chimpanzees (Weiss et al., 2017), 24 traits.
[d] traits and their classification in in situ bonobos (Garai et al., 2016), 31 traits.
[e] traits and their classification in ex situ bonobos (Weiss et al., 2015), 51 traits.
[f] traits and their classification in ex situ orang-utans (Weiss et al., 2006), 47 traits.
[g] traits and their classification in ex situ chimpanzees (King and Figueredo, 1997), 40 traits.
[h] traits and their classification in ex situ chimpanzees (Weiss et al., 2009), 54 traits.
[i] traits (or synonyms of traits) and classification in humans (Goldberg, 1990).
[j] traits and their classification in humans (Goldberg, 1990) as described in **Table 1**, Chapter 2 (King and Figueredo, 1997; Weiss et al., 2011).
[k] traits and their classification in humans (McCrae and Costa, 1987).
[l] in humans, more details see John (1990) and Costa and McCrae (1992).
[m] traits and their classification in humans (Weiss et al., 2022), 46 traits.
Column order:
Column 1: all 54 traits according to the HPQ (Weiss et al., 2009; taken from http://extras.springer.com/2011/987-1-4614-0175-9/weiss_chimpanzee_personality.pdf).
Colum 2-8: 2. eWLG$_6$ = eWLGs extracted via EFA$_{\text{Minres, v}}$ 6 factors; 3. eWLG$_{1994}$ = personality structure ex situ gorilla analysed with the Gorilla Behaviour Index[a]; 4. = iVMGs; 5. eB = ex situ bonobo; 6. eO = ex situ orangutan; 7. eC = ex situ chimpanzee; and 8. H = human.

The distribution of the traits within the four factor personality structure of iWLGs maps well to those of in situ bonobos (Garai et al., 2016), and eWLGs and orangutans.

Comparison of evolutionary integrated low-order facets across the *Genus Gorilla*.

In **Table 21-24,** the lower-order facets are colour-coded for comparison of trait clusters across the genus *Gorilla*: iWLGs, eWLGs and iVMGs are all rated with the same personality instrument. The lower order facets are described **Table 11**, Chapter 3 and will be similarly used here (also identical colour codes), to explain the distribution of the traits and the lower-order facets.

Table 21 *Overview of low-order facets in the iWLGs personality structure/ 4 personality factors*

Personality Factors	Definition
Neuroticism	+ Anxious + Timid + Depressed + Quitting + Clumsy + Erratic + Disorganized + Lazy + Fearful + Unperceptive + Imitative + Irritable + Vulnerable + Thoughtless + Dependent +Unemotional– Independent
Sociability	+ Inventive + Playful + Inquisitive + Curious + Friendly + Active + Sociable + Affectionate + Helpful + Innovative + Sympathetic + Distractible + Gentle + Intelligent + Sensitive– Solitary
Dominance	+ Dominant + Persistent + Bullying + Aggressive + Decisive + Stingy + Jealous + Defiant + Reckless + Protective + Excitable + Impulsive + Manipulative + Individualistic - Submissive
Tolerance/ Self-Control	+ Predictable + Stable + Cool + Conventional + Cautious

Table 22 *Overview of low-order facets in the eWLGs personality structure/ 6 personality factors*

Personality Factors	Definition
Dominance	+ Stingy + Bullying + Aggressive + Dominant + Persistent + Jealous - Submissive + Irritable + Reckless + Manipulative + Defiant - Cautious + Impulsive
Openness	+ Innovative + Inventive + Inquisitive + Curious + Active + Playful – Lazy + Conventional + Imitative
Conscientious-ness	- Disorganized – Thoughtless + Intelligent – Distractible – Clumsy – Unperceptive + Decisive + Sensitive + Predictable - Erratic – Quitting
Agreeableness	+ Sympathetic + Affectionate + Friendly + Sociable + Helpful + Gentle + Protective + Dependent
Neuroticism	+ Fearful - Stable + Vulnerable + Anxious - Cool + Excitable + Timid – Independent
Extraversion	- Depressed - Solitary – Unemotional

Table 23 *Overview of low-order facets in the iVMGs personality structure/ 4 personality factors*

Personality Factors	Definition
Dominance	+ Intelligent + Decisive + Protective – Timid – Anxious + Independent + Dominant + Fearful + Sensitive - Distractible + + Helpful + Bullying – Dependent – Disorganized – Submissive – Imitative + Persistent – Clumsy – Vulnerable
Openness	+ Active – Cool + Thoughtless – Unemotional + Playful + Impulsive – Lazy + Curious + Inventive + Excitable + Reckless + Innovative + Inquisitive – Stable – Conventional + Quitting + Erratic – Predictable
Sociability	+ Friendly + Sociable + Affectionate – Solitary – Depressed + Gentle + Sympathetic - Defiant - Individualistic
Proto-Agreeableness	- Jealous - Irritable - Aggressive - Stingy - Manipulative

Note.

Lower-order facets (trait constructs):

SOC = Sociability = traits such as: Sociable and Solitary
ACT = Activity = traits such as: Playful, Active
ALT = Altruism = traits such as: Friendly, Sympathetic, Helpful
ANX = Anxiety = traits such as: Anxious, Depressed, Timid, Fearful, Vulnerable
CNF= Confidence = traits such as: Confident, Independent
EMO = Emotional stability / Self-Control= traits such as: Cool, Stable
NEGAFF = Negative affect = traits such as: (NEGAFF)
SUP = Supportive = trait Protective
CREA = Creativity
EXP = Explorative tendencies

INT = Intelligence
ACH = Achievement
Dominance = DOM = Dominance = Competitive prowess (COM), Emotionality, Risk taking and Resource monopolisation (RR)+ Aggressive (AGG) + Impulsive + Vulnerable

Higher-order dimensions:
Neuroticism = NEU = ANX + CNF = Anxious + Less confident
Intelligent= INT = OPN + CON
Friendliness = FRI = ALT + SOC
Agreeableness = AGR = ALT + DOM
Extraversion = EXT = SOC + ACT
Dominance = DOM = Dominance = Competitive prowess: Emotionality, Risk taking and Resource monopolisation + Aggressive + Impulsive + Vulnerable
Openness = OPN = Creativity + Exploratory tendencies
Conscientiousness = CON = Achievement, Intelligence

Table 24 *Overview of the distribution of the facets across the gorilla sub-species*

iWLGs	**eWLGs**	**iVMGs**
Neuroticism (NEU) Anxious (ANX) Less confident (CON) Negative affect (NEGAFF) Achievement (ACH)	**Neuroticism (NEU)** Anxious (ANX) Emotional Stability (EMO)	**No distinct** **NEU**
Sociability (SOC) Activity (ACT) Creativity (CREA) Explorative tendencies (EXP) Altruistic (ALT) Sociable (SOC) Intelligence (INT) **No distinct** **EXT** **OPN**	**Openness (OPN)** Activity (ACT) Creativity (CREA) Explorative tendencies (EXP) **divided into 2 additional factors:** **Agreeableness/ Sociability (AGR/SOC)** Altruistic (ALT) Sociable (SOC) Supportive facet (SUP) **Extraversion (EXT)** Sociable (SOC) Negative affect (NEGAFF)	**Openness (OPN)** Activity (ACT) Creativity (CREA) Explorative tendencies (EXP) Emotional Stability (EMO) Achievement (ACH) **additional factor:** **Sociability (SOC)** Altruistic (ALT) Sociable (SOC) Negative affect (NEGAFF)
Dominance (DOM) Competitive prowess (COM) Supportive facet (SUP) Aggressive (AGG)	**Dominance (DOM)** Competitive prowess (COM) Aggressive (AGG)	**Dominance (DOM)** Competitive prowess (COM) Supportive facet- (SUP) Anxious (ANX) Less confident (CON) Negative affect (NEGAFF) Intelligence (INT) **additional factor:** **Proto-Agreeableness (PROTO-AGR)** Inverse of Aggressive (AGG)
No distinct **CON** **Tolerance/ Self-Control/ perversion of CON** Emotional Stability (EMO) Might be a perversion of CON	**additional factor:** **Conscientiousness** Intelligence (INT) Achievement (ACH)	**No distinct** **CON**

Note.
Factors are highlighted in bold, these are the following:

iWLGs factors: Neuroticism, Sociability, Dominance; Tolerance/ Self-Control.
eWLGs factors: Dominance, Openness, Conscientiousness, Agreeableness/ Sociability, Neuroticism, Extraversion.
iVMGs: Dominance, Openness, Sociability, Proto-Agreeableness.
in red and cycled in: if there was no distinct factor found.

To summarise, no distinct Neuroticism factor was found in iVMGs, as well as no distinct Conscientiousness factor in the two in situ gorilla populations (iWLGs and iVMGs). The factor Sociability in iWLGs was split into three factors in the eWLGs (Agreeableness/ Sociability, Extraversion and Openness), iWLGs also showed a split into two factors (Openness and Sociability). The Dominance factor is split into two factors in iVMGs (Dominance and Proto-Agreeableness).

Socio-ecological comparison between eWLGs, iWLGs and iVMGs.

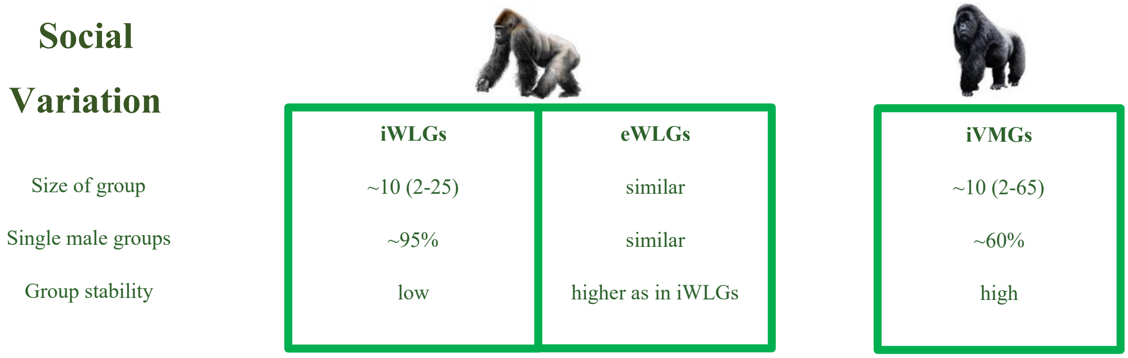
Socio-ecology and predicted correlations with the personality factors were compared with earlier findings in iVMGs (Eckardt et al., 2015; Eckardt personal communication). A social-ecological approach (see below **Figure 12, 13**, and especially the life cycle (**Figure 14**)) will be used to explain the differences of facet combinations in the personality factors between the two sub-species.

Summary of key differences within the compared gorilla populations (iWLG vs eWLGs) and sub-species (iWLG vs iVMG) in respect to their differences in their personality structure:

Ecological Variation	iWLGs	eWLGs	iVMGs
Seasonal fluctuation of food	high	absent to low	absent to low
Diet/ energy	frugivorous	frugivorous	folivorous
Home range size	larger	zoo-dependent	small
Daily travel distances	larger	zoo-dependent	small
Time travelling	longer	zoo-dependent	less time
Time feeding	more time	much less	less time

Figure 12 *Key differences in ecological variation between the compared populations and its relation to their personality structures*

- ⇨ iWLGs feeding ecology: ranging and activity patterns are affected by seasonal resource availability and inter-site habitat (Doran & Sheehy et al., 2009; Salmi et al., 2020; Seiler & Robbins, 2020, Robbins et al., 2022; Yamagiwa et al., 2003) might might result in NEU$_{\mathrm{iWLG.}}$ and T-SC$_{\mathrm{iWLG}}$ in iWLGs.
- ⇨ eWLGs adapted to zoological facilities, environment, and safety, which might result in Neu$_{\mathrm{iWLG.}}$ and a split in three factors of the SOC$_{\mathrm{iWLG}}$ (in OPN$_{\mathrm{eWLG}}$ EXT$_{\mathrm{eWLG}}$ and SOC$_{\mathrm{eWLG}}$) as well as a CON$_{\mathrm{eWLG,}}$ due to environmental and cognitive enrichment.
- ⇨ iVMGs lack a distinct NEU. This might be due to predictable and stable annual environments and social relationships, low competition over food, less time travelling and shorter distances, more time to rest and sleep.

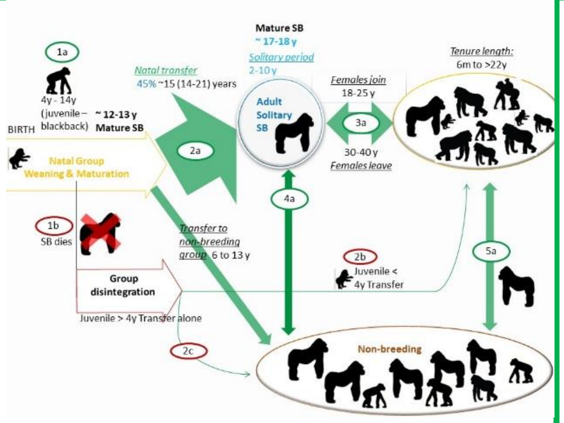
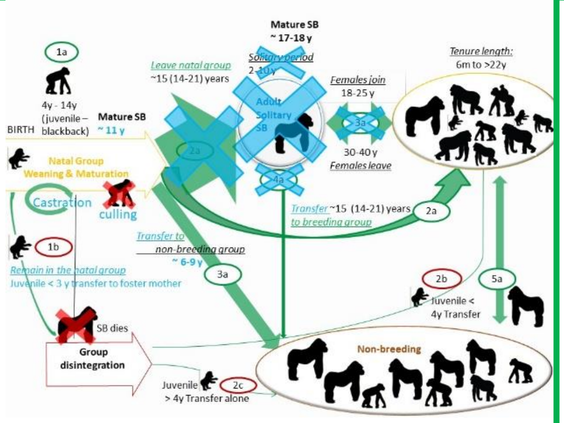
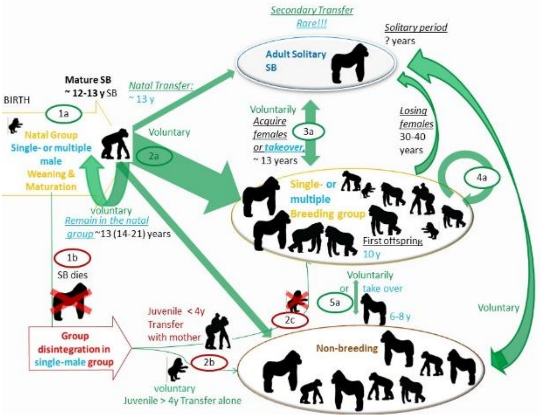


Social Variation

	iWLGs	eWLGs	iVMGs
Size of group	~10 (2-25)	similar	~10 (2-65)
Single male groups	~95%	similar	~60%
Group stability	low	higher as in iWLGs	high

Figure 13 *Key differences in social variation between the compared populations and its relation to their personality structures*

- ⇨ Importance of differences in life cycles and reproduction of female and male gorillas and compared populations (iWLGs, eWLGs and iVMGs) see Chapter 2 for general information and below, how those cycles, gender and age differences in reproduction might lead to differences in the personality structure analysed, above. Social constraints in eWLGs seem to play a key role in shaping differences between in situ and ex situ population.
- ⇨ I use these social units described in Chapter 2 to explain the life cycle (**Figure 14**, below) of males and females, comparing iWLG to eWLG, and to iVMG,.

Life cycle	In situ WLG	Ex situ WLG	In situ VMG
			
Main differences	**Natal group: 95% single male, harems group** Age at becoming **BB: > 11 - 14 y** Age at becoming **young SB: > 14 - 18 y** Age at becoming **SB: > 18 y** **Solitary period: 2 - 10 y** **Age of successful breeders: 18 - 25 y** (Breuer et al., 2009) **Transfer**: **voluntary transfer** **Age of first transfer: > 14 - 21 y (~ 15 y)** 2a: Male natal transfer: **100%, voluntary, going into a solitary SB period** 3a: Male 2^{nd} transfer: SB acquires females and builds a reproductive group 4a, 5a: Transition between non-breeding and solitary silverback status **Group disintegration: SB dies, same cylcle as in iWLG female**	**Natal group: single male, harems group** **> 11 - 14 y** **> 14 - 20 y** **< 20 y but transferred to be breeding males from 12 y +** **Not existent!** **< 12 y** (Breuer et al., 2009, Stoinski et al., 2004a,b, 2013) **Transfer: decided by Studbook authorities** **9 – 11 y** 2a: **No solitary SB period!!!, Involuntary transfer, either directly to breeding group** 3a: **Involuntary transfer, to non-breeding/ bachelor group** 4a: common, involuntary transfer 5a: **Involuntary transfer, between non-breeding/ bachelor group to breeding group or the other way around** **Group disintegration: SB dies, , same cylcle as in iWLG female**	**Natal group: 60 % single- or 40% multi-male breeding group** **> 8 - 12 y** **> 12 - 15 y** **> 15 y** **?,will be investigated according to Eckard et al., 2015** **< 12 y** **Transfer**: **female choice, voluntary transfer,** **8.3 y** 2a: voluntarily, **46 % remain in natal group** 3a: **disperse** from SB to **single- or multi-male breeding group or** by take over 4a: **voluntary dispersal, from single- or multi-male breeding group?** Take over 5a: **Voluntary secondary dispersals**, from **non-breeding group to single- or multi-male breeding group** **Group disintegration: SB dies** 1b: juvenile <3 y, transfer to foster rearing in natal group 3b: male replacement, most common 2c: Juvenil, when <6month, transfer with mother→no inf. 2b: Juvenil, when >4y, no transfer alone to non-breeding group. But maybe transfer alone to breeding group to be adopted by SB male.

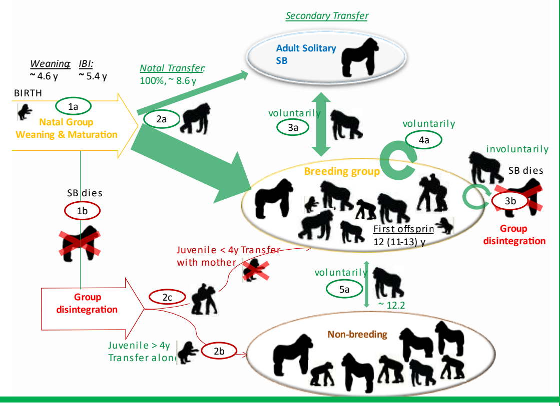
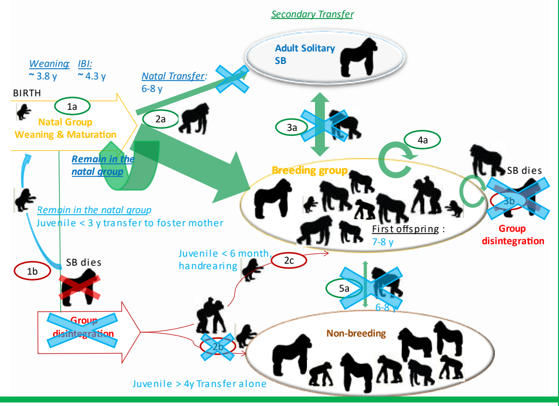
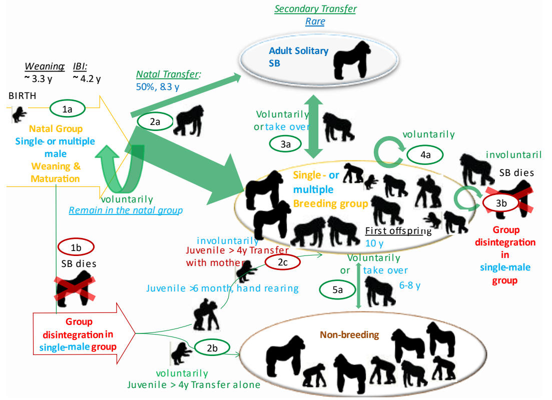
			
Main differences	**Natal group: single male, harems group** Age being infant: **0 - 4 y** Age at becoming juvenile: > **4- 7.5 y** Age at becoming subadult female: **> 7.5 - 10 y** Age becoming adult female: **> 10 y** Weaning age: **4.7 y** Age at first birth: **12.2 (11-13) y** (Breuer et al., 2009) Inter-birth intervals: **5.7 (4.25-8.8) y** Infant survival (to weaning): **55% (48-62%)** **Transfer: female choice, voluntary transfer** Age of first transfer**: 8.6 y** 2a: Female natal transfer: **100%, voluntary transfer** 3a, 4a, 5a: Female 2nd transfer: **common, Involuntary, or voluntary transfer** **Group disintegration: SB dies** 1b: Involuntary transfer 3b: Involuntary transfer 2c: Juvenil, when <4y, transfer with mother ➔ infanticide 2b: Juvenil, when >4y, transfer alone to non-breeding group	**Natal group: single male, harems group** **?, definitive younger as in iWLGs** **?, definitive younger as in iWLGs** **> 6 y** **6-8 y** **3.8 y** **7 - 8 y,** youngest was 5 years (Abello et al., 2017, Meder, 1989) **4.3 y** 50% **Transfer: decided by Studbook authorities** **6 - 8y** 2a**: less common,** females often remain in their natal groups or will be transfered to a breeding group when matured. 3a: Usually, no transfer to or away from a single male 4a: common, involuntary transfer 5a: No transfer to nor out of a bachelor group **Group disintegration: SB dies** 1b: juvenile <3 y, transfer to foster rearing or handrearing in natal group in case of the death of the mother 3b: male replacement, most common 2c: Juvenil, when <6month, transfer with mother, selected groups ➔no infanticide 2b: Juvenil, when >4y, no transfer alone to non-breeding group. But maybe transfer alone to breeding group to be adopted by SB male.	**Natal group: single- or multi-male breeding group** **1 - 3.5 y** **> 3.5- 6 y** **> 6 - 8 y** **> 8 y** **3.3 y** **10.1 y, 46 % in natal group, 54 % in novel breeding group** **4.2 y** **73%** **Transfer: female choice, flexible dispersal patterns** **8.3 y** 2a: Voluntarily, **46 % remain in natal group** 3a: Disperse from SB to single- or multi-male breeding group or by take over 4a: Voluntary dispersal, from single- or multi-male breeding group, or take over 5a: Voluntary dispersals, from non-breeding group to single- or multi-male breeding group **Group disintegration: when the only SB of the group, dies** 1b: Involuntary transfer 3b: Involuntary transfer 2c: Juvenil, when <4y, transfer with mother ➔ infanticide 2b: Juvenil, when >4y, transfer alone to non-breeding group

Figure 14 *Key differences in the life cycle between the compared populations and their relation to personality structures*

Legend:

🦍	🦍	🦍	🦍	🦍	✕	✕
Adult SB	**Young SB**	**Adult female**	**Adult female with infant**	**Infant**	**Not existent or difference in blue**	**Death of SB**

Additional notes:

To eWLGs life cycle:

1) **Female eWLGs: Surplus Females:**

Females undergo various contraceptive methods, such as birth control pills, implants, tubal ligation, hysterectomy, or ovariohysterectomy, as well as artificial insemination and periods of rearing by human caregivers before potential reintroduction to conspecifics.

Additional information to:

Foster rearing in the natal group: Generally, it is highly recommended that juvenile gorillas are nurtured by their biological mothers or a foster mother within their natal group, with human intervention in their upbringing reserved for situations where the survival of the infant is at risk. Decisions regarding the introduction of an infant to a group other than its natal, the possibility of infanticide needs to be addressed. Infants that have been raised by hand are typically introduced to their biological or foster mothers before reaching six months of age.

Hand-rearing/ Nursery reared: In cases where early socialization or reintegration into a gorilla group is not feasible or successful within the EEP, rearing infants alongside conspecifics in the EEP nursery located in Wilhelma, Stuttgart, Germany is advisable. Early contact and socialization conspecifics, preferably adults, are crucial for facilitating the integration of infants into a family-related unit. Newborns should be transferred to the nursery during the first month of life, but no later than four months of age (EAZA BPG, Abelló et al., 2017). Typically, the infants remain in the nursery until they reach three years of age. The integrated nursery within the great ape house in Stuttgart facilitates visual, olfactory, and auditory contact between hand-reared infants and a gorilla family group at the Wilhelma Zoo in Germany. It offers the potential for direct interaction with members of the family group, aiding the acquisition of early social skills. Consequently, the EEP aims to identify suitable zoos with prior expertise in reintroducing hand-reared gorilla juveniles with interactions with other gorilla group members before the age of three.

- Numerous primate studies suggest that early experiences play a pivotal role in social development, emphasizing the detrimental effects of maternal deprivation (W. Mason et al., 1968; Meder, 1989). Gorillas raised by humans, especially with limited interaction with conspecifics during early development, may experience varying degrees of social deprivation, negatively affecting their social and sexual behaviours (Beck & Power, 1988).
- It is advisable to consider all available alternatives prior to making a final decision to hand-rear a newborn gorilla. Additionally, it is imperative to contemplate the prospects of the juvenile prior to concluding to rear it in human care, encompassing its genetic worth to the EEP breeding program and the probability of a possible successful reintroduction. In cases of uncertainty, euthanasia may be contemplated, provided it is permissible under the applicable legislation and has been consented to by the proprietor, the authorised veterinarian, and the EEP coordinator. As per the guidelines of the Ape TAG, the use of euthanasia is deemed acceptable by organisations (zoo) in cases where keeping the gorilla under conditions that diminish their long-term welfare is the only alternative (Abelló et al., 2017). However, this decision must be approved by the EEP coordinator/ species committee. This standpoint is reflected in the EAZA Culling position statement available at www.eaza.net/assets/uploads/Position-Statements. So far, to my knowledge this decision has never been taken.

Reproduction. Studbook records indicate that female eWLGs can give birth very early (from age of 5 years) and at advanced ages, with the oldest recorded birth occurring at 41 years, 9 months, and 9 days. Several females have given birth after the age of 35, and some have had their first offspring when they were slightly over 32 years old. Certain females did not give birth until they surpassed 25 years of age, highlighting variations in reproductive patterns (EAZA BPG, Abelló et al., 2017).

Scientific evidence supports the presence of menopause-like characteristics in older female gorillas, akin to those observed in human females, including changes in cycle duration, reduced levels of oestrogen and progesterone, and a shortened follicular phase (Atsalis & Margulis, 2008).

In cases of recurring maternal neglect, a review of the current husbandry management of gorillas is advisable, exploring potential transfers within the EEP in consultation with the species committee. The EAZA's BPG prevents mating or contraception of female gorillas, particularly until they have observed a model for maternal behaviour.

In summary, female **eWLGs** in zoological facilities exhibit accelerated **IBI** and faster maturation. Additionally, the introduction of a new SB following the death of the previous one often prevents group disintegration, leading to rarer cases of natal transfer rates.

2) Male eWLGs

Additional information to surplus of males:

There exists a tendency towards a higher proportion of males in relation to females born as maternal age increases (M. Robbins et al, 1995). The disparity between the intended sex ratio in individual institutions and the actual sex ratio in the EEP population has been an important factor contributing to "surplus" males. To reduce this “issue” various potential strategies for addressing this excess have been proposed (Stoinski et al., 2004 a,b, 2013, Létang et al., 2021, Abello et al., 2017). These include maintaining male individuals in **solitary** conditions or in **groups consisting only of bachelor males** (Vermeer et al., 2014). In addition to the ethical and legal challenges associated with proposed solutions (see below), the task of locating enough zoological institutions prepared to maintain bachelor groups for an extended period has proven to be arduous. Hence, it is essential to investigate the feasibility of mitigating a surplus by implementing measures such as restricting the birth rate of males.

(1) **Reducing the group size**: The recommended size per group for eWLGs is one adult male with two or a maximum of three reproductive females and their offspring. Minimising the total number of reproductive females per male increases the variety of genes by enabling more males in different groups to reproduce (Abelló et al., 2017) and reduces the number of surplus males.

(2) The majority of zoological institutions that will begin to add gorillas into their collection are inclined to collect exclusively males at the beginning, given that females are hardly available. It is common practice to house surplus male gorillas in so-called **bachelor groups**. Therefore, it is recommended that zoos commencing with the keeping of gorillas construct an enclosure that is appropriate for such a group setting.

(3) Another way to deal with the surplus males is, at least in the European region (European studbook), to **castrate** young gorilla males (as of now, 15 males have been castrated). The United States (the AZA group) disagrees with this invasive procedure which affects the hormonal system of the gorilla males irrevocably (Stoinski et al., 2013). They have reduced the group size over decades and build bachelor groups so that the overall group size is smaller than in Europe (Abelló et al., 2017). If a male gorilla infant of low genetic value to the breeding program needs to be hand-reared, castration may be a viable option to enable future cohabitation in a social group with mixed sexes according to Létang and colleagues (2021).

So far, out of the eWLGs study group from Apenheul and Artis, 15 males have been castrated.

(4) Ex situ **culling**, also known as euthanasia or selective killing, is a controversial and ethically complex practice that involves intentionally ending the life of animals, often with the goal of managing population sizes in captivity (EAZA, 2015). This practice has been considered in various animal populations, including gorillas, to maintain long-term population viability (in respect to the issue of surplus individuals and limited resources or space available), and for reasons to maintain welfare and natural and normal behaviours (EAZA, 2015, p. 2). See more information above at the female cycle. Ex situ culling of gorillas has generated significant debate within the conservation and animal welfare communities.

(5) The practice of **sex-selective abortion** encounters legal and ethical challenges in several jurisdictions and nations. Additionally, the current state of artificial insemination procedures using female-selected semen seems to lack the necessary advancement for use in gorillas. The operations will also have a significant effect on the welfare of the animals involved (Vermeer & Devreese, 2015).

EAZA support the idea of reintroducing gorillas into their natural habitat instead of culling them. Gorillas have been successfully returned to their natural environment through rewilding initiatives. For instance, the Aspinall Foundation has reintroduced more than 70 gorillas into the wild in the last three decades (according to Aspinall, 2021).

To summarise, the decision about castration or other management measures for male gorillas in zoos requires careful evaluation of biological factors, public perception, and ethical considerations (see also EAZA statement on gorilla management, 2021). Conservation efforts remain crucial to protect these endangered animals. In Chapter 6, the One Welfare Plan will be discussed, and further options will be highlighted. The surplus of males remains an issue in several ex situ housed species, not only within WLGs. More research needs to be done on effects and conservation possibilities.

To iVMGs life cycle:

1) **Female iVMG**

Research suggests that multi-male **iVMG** groups exhibit a considerable variability in their mating systems. These groups exhibit specific **behavioural** characteristics, including philopatry in multi-male groups, natal dispersion from multi-male groups, and dispersal from one-male groups. This adaptability is evident in the flexible dispersal patterns of VMG females between groups with varying compositions, involving transitions between polygynandrous and polygynous mating systems. Age and parity are significant factors influencing female reproductive success (Robbins et al., 2006).

A later age of maturation rather than the physical development may partially explain why iWLG populations lack multi-male groups, as a male's tenure may not last long enough for his male progeny to attain maturity (Breuer et al., 2009).

2) **Male iVMGs**

Research suggests that multi-male **iVMG** groups exhibit a considerable variability in their mating systems. These groups exhibit specific **behavioural** characteristics, including philopatry in multi-male groups, natal dispersion from multi-male groups, and dispersal from one-male groups. This adaptability is evident in the flexible dispersal patterns of VMG females between groups with varying compositions, involving transitions between polygynandrous and polygynous mating systems.

Shared sociality trait constructs across genus *Gorillas’* personality structures.

Using fuzzy intersection analysis, the membership of the traits between the personality factors of iWLGs, eWLGs and iVMGs was compared. The extracted sociality construct gives a fuzzy set of social traits generated for the genus *Gorilla* (see **Table 29)**. Results on the fuzzy set interaction across great apes will be shown and discussed in Chapter 5.4. The generated constructs built appropriate upper-order social personality dimensions, as earlier described in Macaques (Adams et al., 2015).

First, the cut-off points for the traits within each intersect was generated via permutation test (see **TableAPP 9**. The analyses was done according Adams and colleagues (Adams et al., 2015) on macaque species. The generation of the cut-off point includes data of all great apes including ex situ bonobos (Weiss et al. 2016), humans (Weiss 2022), ex situ orangutans (Weiss et al., 2011), iVMGs (Eckardt et al., 2015), ex situ chimpanzees (Weiss et al., 2009), and eWLGs and iWLGs from this study. Results will be further discussed in Chapter 5.4.

The cut-off points with a zero loading had to be excluded as they might have not represented within the questionnaire of some of the included great apes species. They are faced in bold. For the rest of the traits the cut-off point estimates the minimum

The sociality trait constructs for great apes' personality structures.

Below, **Table *25*** shows the results of the upper-order of the generated social constructs ($\mathrm{DOM}_{\mathrm{soc}}$, $\mathrm{EXT}_{\mathrm{soc}}$, $\mathrm{NEU}_{\mathrm{soc}}$, $\mathrm{OPN}_{\mathrm{soc}}$, $\mathrm{AGR}_{\mathrm{soc}}$, and $\mathrm{CON}_{\mathrm{soc}}$). A trait was loaded into the dimension with the highest overall loading, and the in **TableAPP 9** represented cut-off point determined whether the trait remained in the dimension or needed to be deleted. When a trait was represented in different factors, it remained in the upper-order (higher level) factor (from $\mathrm{DOM}_{\mathrm{soc}}$ to $\mathrm{CON}_{\mathrm{soc}}$), when the value of the trait was the same or the trait loaded into the dimension with the highest absolute loading.

Table 25 *Sociality personality construct analysed via fuzzy set analysis*

DOM$_{Soc}$	Dom.	Jeal.	Aggress.	Stingy	Bully.	Irritable	Reckl.	Manip.	Def.
	.88	.73	-.71	-.68	-.57	.52	-.50	. 49	.47
	Persis.	Excit.	Prot.	Caut.					
	-.47	-.37	.30	-.28					
SOC$_{Soc}$	Affec.	Friendly	Social	Symp.	Gentle	Solitary	Depend.	Helpful	Stable
	.74	.70	.69	.63	.57	-.46	.40	.29	.29
CON$_{soc}$	Pred.	Thought.	Impul.	Sens.	Conv.				
	-.48	-.46	-.37	.35	.19				
NEU$_{soc}$	Fearful	Anxious	Vuln.	Timid	Subm.	Indep.	Quit.		
	.62	.58	-.53	.50	.47	-.46	.28		
OPN$_{soc}$	Curious	Inventive	Active	Inquis.	Innov.	Playful	Imitative		
	.73	.70	.68	.68	.62	.62	.45		
Proto-AGR$_{soc}$	Erratic	Dec.							
	-.45	-.20							

Note.

Dimensions are listed as following: DOM$_{soc}$ = Dominance, SOC$_{soc}$ = Sociability, CON$_{soc}$ = Conscientiousness, NEU$_{soc}$ = Neuroticism, OPN$_{soc}$ = Openness, Proto-AGR$_{soc}$ = Agreeableness.

Traits are listed to compare the membership between the personality dimensions (fuzzy sets). E.g., in AGR, the traits are shortcuts of the original trait, thus here the traits standing for: Helpful, Friendly, Gentle.

'-' = negative loadings.

Table 25 represents the traits within the factors generated with the fuzzyset analyses shared between the three gorilla populations (eWLG, iWLG and iVMG).

4.5 Discussion

The difference matters – the iWLG personality in comparison to eWLGs and iVMGs.

The primary objective was to investigate the personality structure of iWLGs by employing the GPQ approach involving raters and gorillas from five field sites. I used distinct methodological approaches (principal component analysis vs. factor analysis) and various rotation methods, as also performed for eWLGs, see Chapter 3. Different factoring rotations yield high dimensional agreement (Eckardt, Stoinski, et al., 2016; Morton, Lee, Buchanan-Smith, et al., 2013; Weiss et al., 2009), even when comparing across methods (Weiss et al., 2007). The data reduction and the identification of the personality structure resulted in a four-factor personality structure: namely Neuroticism (Neu$_{\text{iWLG}}$), Sociability (SOC$_{\text{iWLG}}$), Dominance (Dom$_{\text{iWLG}}$), and Tolerance/ Self-Control (T-SC$_{\text{iWLG}}$) in iWLGs.

Neuroticism (Neu$_{\text{iWLG}}$).

Neuroticism encompasses a 'blended' higher-order factor. This factor comprises of Conscientiousness, including the low-order facet of achievement (ACH), and Neuroticism, encompassing the low-order facets that denote feelings of anxiety, diminished confidence, and the presence of negative affect (NEGAFF).

High factor agreement was found to be the inverse of the factor Conscientiousness in our eWLGs. Fair agreement was shown in the same factor in other ex situ great apes: chimpanzees (Weiss et al., 2009), to the inverse of Intellect in orangutans (Weiss et al., 2006), and to the inverse of bonobos Attentiveness factor (Weiss et al., 2015). In respect to Neuroticism in the iWLGs factor, fair agreement was found with Neuroticism in eWLGs (Chapter 4), with orangutan Neuroticism (Weiss et al., 2006), with in situ bonobo Unemotionality (Garai et al., 2016), and with the inverse of the Extraversion factor in humans (Weiss, 2022). Neither Neuroticism nor Conscientiousness existed as separate factors in iVMGs but they were distinctly separate factors in eWLGs.

The differences in Neuroticism and Conscientiousness factors between various in situ and ex situ populations may result through differences in feeding ecology (see **Table 1**, Chapter 2 for differences in ecology for iWLGs and iVMGs and the explanation in Chapter 2 for the eWLGs).

The combination of the Conscientiousness and Neuroticism facet in iWLGs shows the capacity of iWLGs to effectively use a varied array of habitats, resulting in a wide geographical distribution and dispersal pattern (Tutin & Fernandez, 1984) facilitated by a great **plasticity** of their **folivore-frugivore diet**. Fluctuating food availability throughout the year results in a relatively uncertain and unpredictable environment that impacts their behaviour, such as the need to adapt to longer daily travel distances during the fruiting season (Bermejo, 2004; Doran-Sheehy et al., 2004; Goldsmith, 1999; Remis, 1997, Seiler et al., 2018). Therefore, uncertainty in food availability may drive variabilities within personality structure between the subspecies and ex situ or in situ conditions. The typical daily range of iWLGs expands during periods of fruiting (Rogers et al., 2004) and they experience a heightened vulnerability from their lower altitude home ranges that expose them to human interaction and the risks associated with that. In contrast, iVMGs inhabit higher elevations, benefitting from year-round food availability (Seiler et al., 2018). This flexibility in iWLG to react to changes of resources requires considerable planning, logistical knowledge and time (Masi et al., 2009), and can impact their survival and reproduction, especially for females with dependent young (see life cycles, **Figure 14**). The differences in life history, slower physical growth and higher mortality rate in iWLGs compared to iVMGs (Manguette, Breuer, et al., 2020), and their dispersal patterns result in this "neurotic" in situ personality differences.

In contrast, iVMGs do not show clear Neuroticism nor Conscientiousness. This might be due to their relatively predictable and stable annual environment where competition for food resources is low and relatively evenly distributed across habitat types (Eckardt et al., 2015; McNeilage, 2001; Watts, 1994). They also spend less time from their day travelling as distances are shorter (6.5 % vs in iWLGs 12%), and the logistical knowledge of the habitat might be less important compared to iWLGs (e.g. due to steep slopes, no food in same area, avoidance). Similar findings have been observed in in situ bonobos. Research has shown that competition within bonobos is generally lower compared to other species of great apes due to their feeding ecology (Garai et al., 2016).

Another possible factor impacting personality structure in iWLGs is their social organisation which is a **single-male/harem structure** which is in contrast to the philopatric, multi-male structure of iVMGs. In situ WLGs groups face risk **of disintegration** following the **death of the leading silver back (SB) male** (see **Figure 14**) causing a less stable group with increased vulnerability to various threats, including infanticide, poaching, and predator encounters. In the case of iVMGs multi-male groups, these risks are decreased as the group can remain stabilised through other males in the group, at least in 40% of the groups (M. Robbins et al., 2016).

Young iWLG **SB males undergo a solitary period,** and those individuals might suffer from social isolation which can impact their mental and emotional wellbeing, overall health and survival in situ. **Human activities** (i.e. poaching) are a risk factor to solitary SB survival as well as habitat loss and fragmentation due to deforestation, mining and other activities which can impact the **availability of suitable habitats**, forcing them to move to suboptimal areas with increased exposure to dangers. This counts for both subspecies, but male natal dispersal in iVMGs is 50%, instead of 100 % in iWLGs (Stoinski et al., 2009). Habitat loss can also lead whole groups to travel longer in iWLGs. Even when predation risk is relatively rare for adult gorillas, this can still occur in more vulnerable solitary gorillas (Klailova et al., 2013). In contrast, **iVMGs live in relatively protected areas** and face no predation risk, apart from the humans (M. Robbins et al., 2004). Due to many of these factors, iVMG near Karisoke NP are the only subspecies growing in numbers.

A wide range of circumstances have the capacity to initiate or intensify neurotic tendencies in non-human animals, as shown by the research conducted by Mason (1991). The manifestation of neurotic behaviours in animal populations may be impacted by a wide range of environmental factors (social and ecological constraints). Gorillas who show neurotic tendencies may express heightened levels of aggression, especially when they encounter perceived dangers or changes in their environment. The possible increase in aggressive behaviour may be associated with changes in the availability of fruit, leading to heightened competition within groups and with other groups. Behavioural adaptations, such as increased aggressiveness, might potentially function as indications of elevated levels of anxiety within this population (Dallaire et al., 2006). Our findings may provide valuable insights into the observed association between shown agonistic behaviour and vigilant behaviour. Moreover, it is important to highlight that animals exhibiting neurotic tendencies may display behaviours such as heightened anxiety levels, tension and hyperactivity (Mason, 1991). One interesting finding arising from this study is the tendency individuals/ populations of those with higher degrees of neuroticism to have reduced levels of activity. These behavioural patterns may have the potential to limit their ability to move and search for food, therefore influencing their chances of survival and reproductive success.

Unlike iWLGs, the presence of Consciousness in eWLGs might be linked to the many methods used in their confined settings to stimulate their environment. Prominent strategies include task complexity adjustments, medical training sessions, and the provision of enrichment activities specifically designed to enhance cognitive abilities, promote proficient problem-solving skills and reduce boredom. This observed factor of Conscientiousness in eWLGs might account for the similarity in outcomes seen among ex situ chimpanzees and bonobos (Weiss et al., 2015, 2017). This observation could potentially bear significance in the broader context of non-human primate cognition and bear relevance within the larger framework of ex situ animal management.

Concurrently, the emergence of a distinct Neuroticism factor within eWLGs like in iWLGs merits scrutiny. This phenomenon could potentially be ascribed to the intricate interplay of artificial natural selection characteristic of social-ecological differences. However, confinement possesses the ability to begin or enhance neurotic tendencies in non-human organisms (Mason, 1991). The expression of neurotic behaviour in ex situ populations may be influenced by several environmental and social variables, such as exposure to an environment that they cannot change or control, causing anxiety (some of the eWLG gorillas have been transported up to 9 times). Additionally, the regular changes of people (e.g., visitors, caretakers etc.) as well as the complete shift of surroundings and social companions during transportation between zoos could generate unpredictability leading to increased neurotic tendencies. However, it is worth mentioning that gorillas in ex situ settings are free from the pressures of being preyed upon, have the provision of meticulous veterinary attention when required, and a consistent nutritional supply that adheres to established dietary guidelines for ex situ gorillas (Abelló et al., 2017). One might anticipate that these factors would alleviate the stressors experienced by animals in zoos; however, they may not be sufficiently counteracted to prevent the development of this personality trait. The implications of these behavioural inclinations carry far-reaching consequences, demanding meticulous scrutiny and intervention within both ex situ and natural settings. Detecting and comprehending neurotic tendencies within these species holds considerable importance in safeguarding their wellbeing and augmenting the efficacy of ongoing conservation endeavours (Mason, 1991, 2010).

Sex differences observed in Neuroticism in iWLGs may be ascribed to the distinct life cycles encountered by male and female gorillas. Comprehensive insights into these disparities can be found in the life cycles, for females and males respectively. Dispersal pattern in females can lead to risks in life history, reproduction, and fitness. The solitary phase observed in males, accompanied by the concomitant obligation for the dominant male to provide safeguarding and guidance to the collective unit, may be key in males to a healthier and longer life.

Sociability ($\mathrm{Soc_{iWLG}}$).

Overall, the finding of a Sociability factor highlights the importance of social systems and underpins the emergence and maintenance of primate personality structures. Social tendencies are necessary for species living in complex social systems that rely on social bonding, social learning, and cooperation (Gosling & John, 1999; M. Robbins et al., 2016; van Schaik, 2016). The capacity to form and maintain social relationships seems to have significant effects on an individual's fitness in both ecological and evolutionary contexts (Wolf & Weissing, 2012). Previous studies have shown that sociable individuals have a greater chance of surviving (Archie et al., 2014) and have a higher rate of reproduction (Parish, 1996), both for themselves and their offspring (Silk, 2003, 2009). For animals that live in groups, their degree of sociability is often the deciding factor in how they will fare (Perry, 1997) and this seems to impact their personality structure.

Findings reveal that Sociability is the most consistently extracted dimension in animal studies – as reported in 69 studies across 12 different species – and contributes to harmonious social relationships and low levels of conflict (Gosling & John, 1999). A review of non-human primate personality including 17 independent studies and species also showed that Sociability is a homologous personality dimension across diverse species (Freeman & Gosling, 2010). Gosling and John (1999) describe prosocial dispositions and include characteristics such as sympathetic, cooperative tendencies, and friendliness in an Agreeableness/Sociability dimension.

The iWLGs' $\mathrm{SOC_{iWLG}}$ factor resembles a blended factor, including Extraversion and Openness factors, and comprises lower-order facets, such as SOC, ALT, a typical OPN (EXP +CREA), and typical EXT (ACT), plus Intelligence (INT). The incorporation of human AGR traits (Friendly, Helpful, and Affectionate) in $\mathrm{SOC_{iWLG}}$ factor may reflect the mild nature of gorilla interactions and the distribution of their social compounds. The factor is similar to the description of the human "ultra-social" tendency (Dachner et al., 2009), which describes human nature as showing an exceptionally high degree of social complexity, cooperation, and reliance on intricate social interactions that characterise human societies, as well as those of other great apes species, including gorillas.

The factors showed great agreement to OPN, EXT, AGR, SOC and CON factors across the great ape comparison, such as fair agreement to the in situ and ex situ chimpanzee factors Openness and Extraversion (King & Figueredo, 1997; Weiss et al., 2009, 2017); to ex situ bonobo Openness (in Weiss et al., 2015), and to the ex situ orangutan Extraversion factor (Weiss et al. 2006). Fairly agreement was shown to the facets in ex situ orangutans' Agreeableness factor (Weiss et al., 2006), and in situ bonobos' factor Conscientiousness (Garai et al., 2016).

Surprisingly, only a moderate agreement was found with the two distinct factors - Sociability (ALT, SOC, and NEGAFF) and Openness (facets are: ACT, ACH, EXP, CREA, and EMO) in iVMGs. In eWLGs the Sociability factor is evenly divided into three distinct factors, such as Openness (ACT, EXP, and CREA), Agreeableness/Sociability (ALT, SOC, and SUP), and Extraversion (SOC and NEGAFF). Differences might result from social system and diverse life cycle patterns between the species and population. Those have been intensively described above within this Chapter.

Disparities in maternal care and social interactions can lead to variations in social organizational aspects such as group size, composition, and cohesiveness (M. Robbins et al., 2016). Maternal investment plays a crucial role in shaping social dynamics, offspring survival, dispersion patterns, and social interactions within different gorilla subspecies populations (M. Robbins et al., 2016). These observations underscore the profound influence of maternal behaviour on the development of intricate social structures in gorillas and social interactions, which may also contribute to the emergence of distinct personality factors among gorilla subspecies.

As shown in **Figure 14**, iWLG females show a slower life history than iVMGs, characterized by older age at first birth (12.2vs 10.1 years), longer weaning periods (6 vs. 3.3 years), longer inter-birth intervals (5.7 vs. 4.2 years), and lower infant survival (55 % vs 73%) (Breuer et al., 2009; M. Robbins et al., 2007; Yamagiwa & Kahekwa, 2001). I briefly add additional differences between the two in situ subspecies which might help shape the factor Sociability. Unlike many primates, iWLGs exhibit natal dispersal in both sexes upon reaching maturity and beyond (Forcina et al., 2019; Manguette, Breuer, et., 2020). This dispersal behavior is further augmented by frequent secondary dispersal in female iWLGs, contributing to higher dispersal rates compared to iVMGs (Yamagiwa et al., 2003, Manguette, Breuer, et al., 2020, Manguette, Robbins, et al., 2020). Moreover, social groupings differ between the two subspecies, with iWLGs typically residing in single-male/harem groups characterized by lower group cohesiveness (M.Robbins et al., 2017). In contrast, iVMGs exhibit male philopatry and multi-male group dynamics, leading to distinct social hierarchies (Yamagiwa et al., 2003). The robust social connection between female and male iWLGs fosters group cohesion, reduces tension, and provides female support during intergroup conflicts. Conversely, iVMGs demonstrate more defined hierarchies, with less variability observed in both female and male social dynamics (Yamagiwa et al., 2003). As such, the amalgamated Sociability trait could be an outcome of natural and artificial influences stemming from human activities impacting these factors as well as sexual selection. Variations in social organization, dispersal patterns, and group dynamics, highlighting the complex interplay between genetic, environmental, and social factors in shaping the social behaviour of gorilla populations and thus their personality. The correlations with this factor indicate that more sociable individuals tend to engage in increased play, exhibit more affiliative behaviours, and display fewer agonistic behaviours, aligning well with the manifestation of their innate social dynamics.

A detailed description of the personality structure of the eWLGs with the three distinct factors - Agreeableness/Sociability, Openness and Extraversion - and their phylogenetic relationship to other species was presented in Chapter 3. Ex situ WLGs live in controlled environmental conditions and social and ecological constraints, where breeding decisions are made by Studbook holders based on genetic management plans and pairings are selected to maximise genetic diversity and minimise the risk of infanticide. Further birth control is implemented at both the female and male levels. As a result, group WLG composition within an ex situ setting is less adaptable compared to in situ settings, relying on transfer decisions dictated by the ex situ management plan. The range of social choices and opportunities for social learning are curtailed within controlled environments, potentially diverging significantly from their inherent natural social systems. Constrained space alters social dynamics, and the regulated conditions of captivity can shape their behaviours and interactions, giving rise to distinctive personality traits. It's important not to overlook the influence of human interactions, which can serve as either social or constrained stimuli, particularly during the hand-rearing process. The artificial setting of captivity may therefore contribute to the manifestation of personality traits that are more pronounced and distinguishable.

For more explanation on social differences, see the life cycle (**Figure 14**).

Dominance ($\mathrm{Dom}_{\mathrm{iWLG}}$).

The $\mathrm{Dom}_{\mathrm{iWLG}}$ factor in iWLG comprises lower-order facets, such as competitive prowess (COM), and a supportive (SUP) and aggressive facet (AGG). A comparative analysis reveals similarities with the extracted $\mathrm{Dom}_{\mathrm{iWLG}}$ factor have been found with Dominance in the eWLGs (Chapter 3) as well as in ex situ orangutans (Weiss et al., 2006), to Aggressiveness within in situ bonobos (Garai et al., 2016), to the inverse of Conscientiousness in ex situ bonobos (Weiss et al., 2015), and to the inverse of the Proto-Agreeableness dimension in iVMGs (Eckardt et al., 2015). Fair agreement was found for Conscientiousness in ex situ chimpanzees (King & Figueredo, 1997; Weiss et al., 2009), and Neuroticism in humans (Weiss, 2022).

Unlike iWLGs, iVMGs have two distinct factors: Dominance (with low order facets such as: COM, SUP, ANX, CON, NEGAFF, INT) and Proto-Agreeableness (an inverse of the aggressiveness facet (AGG) (Eckardt et al., 2015). High negative agreement was found to their Proto-Agreeableness, but not to iVMGs' Dominance factor. This is consistent with Eckardt and colleagues' (2015) description of the Proto-Agreeableness factor in iVMGs, which noted similarities with, for example, Dominance in ex situ orangutans and with the inverse of human Agreeableness factors. On the other hand, the Dominance factor is linked to the strength of dominance in leading males and high-ranking females but not to aggressiveness. Time staring at other gorillas was associated with Dominance in iVMGs but no significant relationship between Dominance and aggressive behaviour displayed by iVMGs could be found (Eckardt et al., 2015).

The Dominance dimension plays a crucial role in social dynamics, as observed in various primate species. For instance, dominance rank in baboons correlates with the Dominance dimension (Sapolsky & Ray, 1989), and it is central to chimpanzee personality (King & Figueredo, 1997). Social dominance is hypothesized to result from a combination of aggressiveness and emotional stability, rather than solely relying on aggressiveness (Budaev, 2000).

In iWLGs, intergroup encounters often involve non-physical conflicts (57%), with instances of physical aggression being less frequent (Bradley et al., 2004; Doran & McNeilage, 1998; Parnell, 2002; Stokes, 2004). These encounters are characterized by peaceful interactions, particularly during feeding in swamp clearings ("bais"). In contrast, physical aggression were predominantly instigated by solitary males and young, dominant silverbacks, likely owing to their increased motivation to attract potential mates or by SB to reducing the risks of infanticide and protecting females and their offspring. Also, iWLGS males intervene in female agonistic interactions.

In chimpanzees, infanticide and cannibalism were positively correlated with ratings on Aggression (Buirski & Plutchik, 1991). Conversely, iVMGs exhibit a wider range of encounters, including displays and fights that may lead to fatalities (Morrison et al., 2019; Morrison, Dunn, et al., 2020; Morrison, Hirwa, et al., 2020)). However, this is mainly due to increased iVMG density in shared forest spaces contributes to higher rates of infanticide and fighting. However, male aggression also varies within groups (Watts, 2006) and primarily serves to defend the group and their territory from other males (Watts, 2012). In general, affiliative behaviour far outweighs aggression in gorillas (Harcourt & Stewart, 1987; Watts, 1992, 1996).

However, positive correlations between the factor Dom$_{\text{iWLG}}$ and playing, affiliative and sexual behaviour were found. Play fighting – a highly malleable and adaptable behaviour – is commonly employed in animal societies to gather information about the potential roles of conspecifics as rivals or social partners. This competitive/cooperative interaction helps to assess a performer's readiness to engage in an interaction and, at the same time, their own willingness to tolerate vulnerability (Palagi, 2006). Nonetheless, play sessions might sometimes evolve into overt anger, culminating in screaming and/or bared teeth by a participant or a violent engagement (Forcina et al., 2019). The sensitivity of play to the quality of group interactions reflects the fundamental nature of social networks (Mancini & Palagi, 2009). WLG intergroup confrontations display striking parallels to those reported among bonobos. While bonobos keep a strong incentive to play well into maturity, chimpanzees participate in progressively less play fighting as they mature (Palagi & Cordoni, 2012). Gorillas may also use these intergroup encounters to assess possible mating and transfer possibilities. Relatively little research has examined how intra- and intergroup relationships and individual personality moderate aggressiveness and play. In summary, the factor of Dom_{iWLG} might be explained by these frequent and fluid encounters and the explained social system of gorillas.

Feeding competition does not affect female reproductive success in iWLGs (Stokes, 2004), which may explain why agonistic behaviour in feeding context was not associated with the factor Dominance. In addition, agonistic interactions between females and adult males are generally low compared to primate species known for high levels of aggression, such as rhesus macaques or chimpanzees (Watts, 1994). Female gorillas build strong bonds with the protecting and defending males in the group, and thus female mating choices and transfer decisions may not only depend on the males' skills and ability to protect the group but also on their supportive behaviour (Harcourt & Stewart, 2007). However, in the context of mating and courtship, gorilla males tend to be aggressive towards females in estrus (Sicotte, 2002). This can explain the correlation found in this behaviour and the personality factor. The agonistic interactions between females for food and access to the SB male can explain why we did not find sex and age differences, as agonistic interactions seem to outweigh between sexes.

Differences on the protective/supportive facet included in situ might reflect their need to navigate complex, potentially hazardous environments, threats from human activities, territorial disputes, predators, and the challenge of finding food and sleeping sites. In eWLGs, the protective facet of Dominance might not be as prominent due to the controlled and safe nature of their artificial habitats. There are no dangerous intergroup encounters, food scarcity, little risk for infanticide, and they are safe from predators. This lack of exposure to natural threats, limited resources, and intense mating competition in captivity may also lower the level of agonistic behaviour within breeding groups leading to a decrease in aggressive behaviour.

Tolerance/ Self-Control ($\text{T-SC}_{\text{iWLG}}$).

The iWLG's T-SC factor encompasses traits like Predictable, Stable, Cool, Conventional, and Cautious, which represent emotional stability (EMO) in the compared lower-order facets While modest agreement was found with the Neuroticism factor in ex situ chimpanzees (Weiss et al., 2009), the T-SC factor in iWLGs exhibited the lowest overall consistency across compared great ape studies. Nonetheless, this factor effectively captures anecdotal attributes associated with gentleness, peacefulness, and emotional stability in gorillas (Eckardt et al., 2015; Parker & Mitchell, 1999).

Gorillas reside in a flexible, multilevel society (Forcina et al., 2019; Morrison et al., 2019) , similar to other gregarious species (Adams et al., 2015). The dynamics of such a social structure necessitate a high degree of social tolerance among individuals (van Schaik & van Hooff, 1983). Individuals must consistently engage in a relaxed and non-aggressive way to maintain cohesive social groups. The degree of social tolerance within a group signifies the balance between competition among group members for resources and the need for cooperation (interdependency). This cooperation within gorilla groups often comes into play during intergroup encounters or for safeguarding against predators/threats (Schülke & Ostner, 2012). Behavioural flexibility in gorillas ranges from tolerance to aggression, influenced by various factors such as food availability, intra- and intergroup encounters, power dynamics, and social relationships. Examples of these are food availability (resource availability in time and space, the value of the resources, seasonality), intra-group encounter (gender, rank, reproductive condition, mating partners quality), intergroup encounter (power balance) between the two groups, mating resources, relatedness and familiarisation of the group members (Morrison, Dunn, et al., 2020; Morrison, Hirwa, et al., 2020). Emotionality encompasses the range and intensity of emotional responses exhibited by an individual. Therefore, tolerance can refer to an individual's capacity to manage and respond to various stressors, challenges, and social interactions with a level of equanimity and flexibility which are attributes that iWLGs need to survive in their unpredictable environments.

Studies on social tolerance have linked it to factors like group size, with higher social tolerance being linked to larger sizes (Dardenne et al., 2013; D'Eath & Keeling, 2003). Social learning is also enabled by social tolerance (Forss et al., 2016; Wild et al., 2020), as well as domestication where domesticated species show higher levels of social tolerance than their in situ counterparts. In macaque subspecies, differences in aggression and tolerance have been used to classify levels of social tolerance (Balasubramaniam et al., 2018; Thierry, 2007) Differences in aggression and tolerance have been used to classify social styles in macaque subspecies, with direct correlations to personality differences (Adams et al., 2015).

Research by Forcina et al. (2019) highlights the dynamic social structure of iWLGs, characterized by frequent exchanges between groups and peaceful coexistence among members. According to Morrison, Dunn, et al., (2020), a pattern of avoidance across iWLG groups was consistent with an awareness of the "ownership" about the core areas and higher avoidance to their neighbours, as closer they were to their home range centre. Gorillas also avoided the home ranges of larger groups, which is consistent with more robust defensive reactions to groups higher in dominance (Morrison, Dunn, et al., 2020; Morrison, Hirwa, et al., 2020). It is indicated that groups may be territorial, defending core sections of their home ranges against neighbours, and that their behaviour resembles patterns seen throughout human development with core regions of resident dominance and wider zones of mutual tolerance. It has also been shown that gorillas consider former social relationships (after they split to disperse) when outside core areas, as then the territorial defence of the showed more affiliative and less aggression. In core areas aggressiveness tends to be higher (Morrison, Dunn, et al., 2020).

In contrast to iVMGs, intergroup encounters in iWLGs tend to last several hours (Sicotte, 1993), with one or both groups engaging in agonistic behaviours (Mirville et al., 2018; M. Robbins & Sawyer, 2007; Sicotte, 1993). Those interactions have the potential to escalate into physical confrontations leading to injuries or fatalities and increased level of stress (Caillaud et al., 2014; Eckardt et al., 2015; Eckardt, Stoinski, et al., 2016; Rosenbaum, Maldonado-Chaparro, et al., 2016; Watts, 1989). It has been found that intergroup aggression escalates when groups were matched in terms of group size (Mirville et al., 2018). The transfer of females between groups may be facilitated by intergroup interactions, with intergroup antagonism primarily motivated by male competition for the retention or recruitment of females (Mirville et al., 2018; M. Robbins & Sawyer, 2007; Sicotte, 1993).

The evolution of personality traits such as increased tolerance and reduced emotional reactivity might have contributed to the development of this emotional stability-like personality factor. Greater levels of tolerance and reduced emotional reactivity in gorillas might provide them with enhanced abilities to effectively handle stressors, navigate social interactions, and manage conflicts both within and between groups. Tolerant gorillas may display a more composed emotional response, akin to emotional stability in humans. While the term "self-domestication" has been primarily used in the context of human evolution, the underlying principles of reduced aggression and enhanced prosocial behaviours, such as friendliness (Hare, 2018) can potentially be applied to gorillas as well.

In this study, Tolerant/Self-Controlled with reduced emotional reactivity showed significantly less agonism, vigilance, and activity, and they approached other individuals less frequently. Our findings highlight that these individuals might form and maintain social bonds more successfully as well as navigate group dynamics and manage conflicts better. These traits can therefore be positively selected over time and lead to reduced aggression. This finding might underpin human evolutionary routes in respect to the increase in collaboration and communication, which came from an increase of in-group bonding, tolerance, and cooperation.

Consequently, the development of an emotional stability-like personality factor could be influenced by the socio-ecological context in which gorillas live. Tolerance/Self-Control and increased prosocial behaviour could be essential for: a) maintaining stability within groups by reducing emotional reactivity, such as conflicts, b) increasing peaceful social dynamics as gorillas with increased tolerance are more likely to form and maintain alliances, share resources, and engage in cooperative behaviours leading to success within the group, c) offering advantages in food availability, group cohesion, and survival, as increased resource sharing suggests that tolerant gorillas were more amenable during feeding in the presence of individuals within close proximity, and d) reduced emotional reactivity which might translate to lower levels of anxiety, less aggression in response to challenges, and a greater capacity to adapt to changing circumstances, thus coping with novelty.

While tolerance may be a key factor in mediating interactions within iWLG groups, its necessity may diminish in captivity. Furthermore, adapting to novelty and rapid change to artificial environments appears to be an inherent aspect of personality in eWLGs, it is plausible that within the eWLG population these traits could expedite changes in their personality structure. Consequently, I encountered difficulty in generating this specific factor.

This study underscores the role of tolerance as a mechanism for facilitating cooperative interactions and minimising resource-related conflicts. Gorillas with higher tolerance levels exhibit more flexible and accommodating behaviours, promoting an environment where sharing is more likely to occur. This connection between tolerance, sharing (habitat outside the core), and reduced ownership-related behaviours provides insights into the broader implications of tolerance for the social dynamics and behaviours of gorillas. Gorillas that displayed greater tolerance towards other individuals showed less aggression. A future interest could be to explore whether gorillas with higher tolerance levels are less likely to exhibit strong "ownership behaviours", such as displaying aggression or guarding, over specific resources and whether these individuals will be more flexible in the presence of others near their resources.

In summary, tolerance plays a vital role in facilitating cooperative interactions and reducing resource-related conflicts among gorillas. Understanding the implications of tolerance for gorilla social dynamics sheds light on the mechanisms underlying their behaviors and social structures.

Shared social personality traits across genus Gorilla.

Utilizing fuzzy set analysis, common social personality traits were identified across two in situ subspecies – iWLGs and iVMGs – and the ex situ WLG population.

The recognition of collective social personality constructs, including - Dominance, Sociability, Conscientiousness, Neuroticism, Openness and Proto-Agreeableness -, suggests that certain aspects of social behaviour and engagement in social contexts are consistent across these populations. This discovery implies that the expression of these social traits in gorillas may be deeply ingrained in evolutionary processes, likely influenced by the ecological and social factors encountered throughout gorillas' evolutionary history.

Gorillas, irrespective of subspecies, exhibit core social traits and behaviours that may be attributed to their shared ancestral lineage and socio-ecological circumstances. For example, gorillas demonstrate intricate social traits, such as friendliness, helpfulness, sociableness, or aggressiveness. These shared social personality components likely play vital roles in fostering social cohesion, resolving conflicts, and forming alliances within gorilla communities.

The prevalence of this common social personality trait construct may stem from a combination of genetic predispositions and environmental influences. Natural selection could have favoured individuals possessing certain social traits conducive to group living and cooperation, thereby leading to the development of a shared social personality construct across different gorilla subspecies.

4.6 Limitations and Future Directions

In addition to the limitations and future directions already mentioned in Chapter 3.6, I will include some here, which seem to update to this chapter's analysis.

4.6.1 Limitations

Limitations of the cross comparison to the iVMGs:

When comparing the two field studies, the iVMG has been monitored consistently for over 55 years plus, providing a complete record of life history. As a result, individual knowledge may be compromised. On the other hand, the information on gorillas visiting Mbeli Bai relies on the duration of their stays at the Bai, which typically represents a very small fraction of their overall time spent there. Consequently, knowledge about the activities of individuals outside the Bai area is limited, potentially affecting the assessment of the 54 traits, as these are less visible. Unlike the iVMG, which are closely observed in all aspects of gorilla behaviour, from feeding and breeding to sleeping, the understanding of gorillas in Mbeli Bai remains incomplete.

Artificial vs. natural environment. Ex situ environments frequently lack the intricacy and diversity found in natural ecosystems (e.g. space restriction), which might restrict the array of natural behaviours and experiences accessible to animals housed in artificial environments and impact on their welfare. However, in in situ field conditions, research involves logistical challenges, such as difficult terrain, weather conditions, and the need for long-term observation but more challenging is the inaccessibility of the animals. Some behaviours and interactions may occur in areas that are not easily accessible to researchers, leading to gaps in data collection. Habituation of groups takes long but observations on the Bai might misses out behaviours as iWLGs are mainly coming to feed there.

The eWLGs are also easier to observe within ex situ conditions in respect to in situ environments. This can lead to overrepresentation of certain observed behaviours in eWLGs, whereas there will be a lack of observation in in situ conditions. See also limitations in Chapter 3.6 and 5.6 on eWLGs.

The life cycle shows that eWLGs have a faster maturation in both sexes than iWLGs. The age difference within the eWLGs should also be considered when running sex and age differences on the eWLG structure to adapt to the early life stages. Therefore, an updated sex-age category and a reanalysis of the effect of sex and age on the personality structure is advised.

Modified activity patterns. Discrepancies in daily routines, transfers between facilities and the availability of resources (nutrition) can affect activity patterns and overall wellbeing and health. Whereas natural fluctuations in activity patterns, influenced by seasons and resource availability, offer a more dynamic view of iWLGs wellbeing and behaviours.

4.6.2 Future directions

Selecting individuals according to their personality traits for certain conservation, breeding or translocation purposes:

WLGs with traits such as high boldness or low neuroticism are more likely to adapt successfully to new environments. By identifying and selecting these individuals for **translocation**, the likelihood of successful acclimatisation and survival can be enhanced.

By integrating personality assessments into the study of **leadership** and **group-changing behaviours**, conservation efforts can develop more effective management and conservation strategies tailored to individual animals' traits. For instance, social personality relevant traits for **leading** males can be assessed as it is still unclear, why some of the iWLG males keep their females in their group for 30 years plus and others are being left by females. Assessing whether exhibiting higher levels of dominance, tolerance, protectiveness, sociability, confidence or boldness are leading to a preferred leadership skills to protect, stabilise, lead to better resources and improve infant survival are crucial for basing females' decisions on to either stay or leave. As shown in the iWLGs life cycles, females often transfer multiple times between breeding groups. This approach can enhance the success of breeding programs, translocations, and overall conservation efforts while addressing the inherent limitations through rigorous and collaborative research methodologies. For more future directions for iWLGs and eWLGs see Chapter 5.6.

4.7 Conclusion

My comparative research (see **Figure 15**) comparing ex situ WLGs and in situ WLGs and VMGs personality structure has contributed to a better understanding of the phylogenetic and socio-ecological influences, revealing evolutionary patterns and communalities across the three populations (eWLG, iWLG and iVMG). This study can provide insights into how unique environmental and socio-ecological challenges faced by each gorilla population can influence the development of their personality structure.

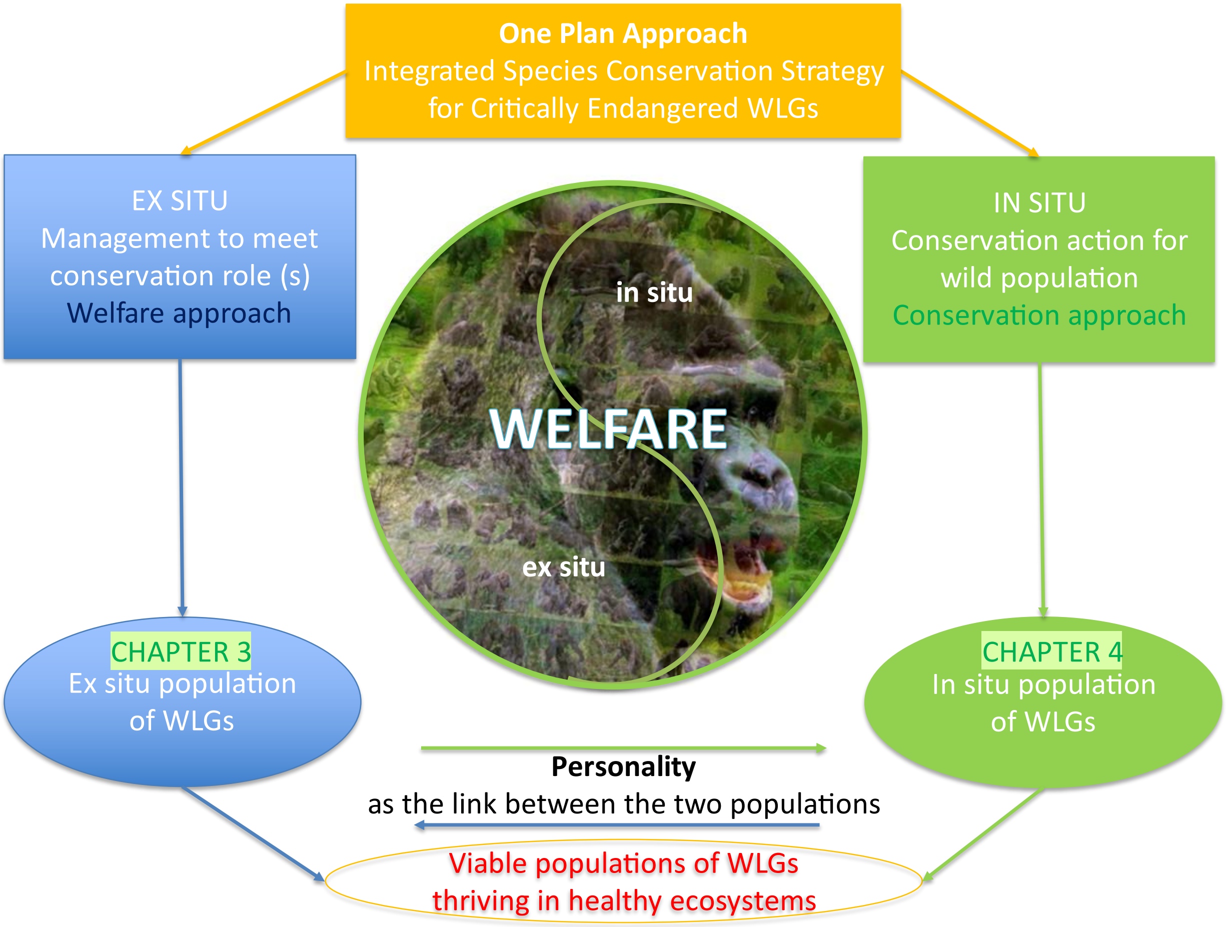


Figure 15 *Road Map Including Chapter 4*

The results of Eckardt et al., (2015) are supported by the present study, as they emphasise the importance of including personality factors as potential predictors of how animals respond to their surroundings and navigate their social interactions. The combined insights contribute to a deeper understanding of the adaptive strategies that gorillas employ to thrive in their natural, artificial and social environments. The significant impact of socio-ecological influences, such as social dynamics or ecological effects, and adaptation on the development of personality structure in relation to the three populations was examined for each of the four personality factors found in iWLGs: Neuroticism, Sociability, Dominance and Tolerance/Self-Confidence.

The present study demonstrates that the condition of ex situ settings, functioning as a controlled and artificial environment, has a significant influence on the formation and expression of personality traits, thereby affecting associated behavioural patterns. In line with the findings presented in Chapter 3, six distinct personality factors were identified for eWLGs, forming the foundation for the subsequent comparison with the iWLG population. Consequently, the phenomenon of confinement might potentially induce alterations in response to selection pressure, resulting in the segregation of personality factors that enhance adaptability to the constraints of confinement within just a few generations. I demonstrated that understanding social-ecological dynamics is crucial for understanding the development of personality factors and I connected these differences to gorillas' specific social structure, particularly to the life cycles of females and males in their different settings. These personality differences have significant impact on the management of eWLGs.

In Chapter 5, I discuss the implications of social wellbeing on eWLGs. The personality structure of eWLGs show similarities with that of iWLGs, however, two additional factors have been found - Opn$_{\text{eWLG}}$ and Ext$_{\text{eWLG}}$|. IWLGs show a blended factor of Sociability (includes Opn and Ext and Soc) and they lack a separate Con$_{\text{eWLG}}$ factor. One possible reason for this is that limited exposure to natural surroundings and social intergroup encounters, in addition to the artificial changes in their life cycles, might lead to reduced opportunities to express natural behaviours and develop personality changes. The exposure of daily human interactions including keepers, visitors and researchers may also shape their socialisation in the form of adaption to a "new" social component and lead to the spread of personality factors into three distinct factors instead as shown in iWLGs' Sociability factor. Similarly, the lack of predation and the natural challenges related to food scarcity and survival pressure is limited in ex situ conditions, which might have altered the personality structure related to risk aversion and foraging behaviour.

These results demonstrate that the emergence of differences in gorilla personality may be attributed to the complex interaction between their socio-ecological conditions and specific adaptations. The covarions seen in gorilla populations may serve as indicators of adaptive responses to the challenges and alternatives from their respective socio-ecological systems as they strive for survival. The complexity in social interactions can shape an individual's behaviour and personality over time. For instance, iWLGs may exhibit increased levels of tolerance due to their regular and ongoing interactions with other gorillas within their natural environment.

The presence of socio-ecological complexity may give rise to gene-environment interactions, whereby certain genetic predispositions provide greater advantages in specific habitats or social circumstances. It is also plausible that gorillas exhibiting certain personality qualities might have greater success in acquiring resources, such as food or mates, and show enhanced tolerance or cooperation with conspecifics as a result of their individual personalities (e.g. female gorillas may prefer males who display higher levels of protectiveness, cooperation, and gentleness). This selection based on specific qualities might potentially result in covariations, since gorillas with complementing characteristics engage in cooperative behaviours.

Chapter 5

A Multi-dimensional Approach to Happiness and Wellbeing in Ex Situ Western Lowland Gorillas

Picture 25 *Mosaic picture of positive close social emotional experiences in Western lowland gorillas“animals, like man, manifestly feel pleasure and pain, happiness and misery.”* Charles Darwin (1871)

5.1 Abstract

Understanding the link between positive animal welfare and the social components of emotion, personality and happiness in ex situ animals is key to improving ex situ management strategies and attempts to increase subjective wellbeing. Sharing positive emotions and happiness with others can be crucial for optimal individual wellbeing and social functioning, and the evolution of altruism can be summarised as “Survival of the Nicest” in humans. Today, new multidimensional welfare approaches attempt to assess and improve animal welfare in captivity and stimulate positive aspects that make an animal’s life a “good life.” Positive welfare is a fundamental consideration in conservation efforts and part of the multi-population One Plan Approach (OPA), which is a holistic strategy for wildlife conservation that emphasises multidisciplinary, comprehensive, and collective enforcements within the ethical guideline principles to prioritise the wellbeing of individual animals within ex situ management and breeding strategies.

Based on the expression of social positive emotion (rewarding goal-directed social engagements, which are said to be pleasurable and to underlie proximate evolutionary causation), this chapter discusses the inter-relationships between the positive aspect of close relationships, friendship, personality, and happiness, and how they contribute to the overall positive wellbeing of ex situ Western lowland gorillas (eWLGs).

To underpin the evolutionary basis of happiness, my data confirms that all personality factors are reliable predictors of subjective wellbeing (SWB). Ratings of SWB as a measure of happiness were gathered from 189 ex situ (607 ratings, 84 raters, 30 zoos) and 189 in situ Western lowland gorillas (eWLGs, 400 ratings, 25 raters, 5 African field sites). In a subset of 24 eWLGs, the SWB ratings were validated with observed behaviour. Strong correlations were found between SWB, observed state-dependent behavioural responses (mood), emotions, and personality factors. They exhibited homophily in their partner preferences signifying dyads of similar personality and SWB. Agr$_{\text{eWLG}}$ and SWB were found to predict friendship in eWLGs. These findings indicate that personality and SWB might be important for finding and maintaining friendships. Having more friends has advantages for fitness, survival, survival of offspring, amongst other benefits. I highlight the evolutionary significance of pleasurable experiences in individual gorillas and underpin the concept of homophily, longevity and social happiness. Additionally, as great apes are social animals with diverse social structures, and with humans leading the primate lineage as the "super-caregiving" species, I tested whether

inherited social personality trait constructs evolved from a common ancestor and are shared across great apes and humans to underpin that sociability is key to personality. I argue that personality variances and covariances are interwoven with their social style, as shown in macaque species previously described by Adams and colleagues (2015). These findings suggest that the enhancement and cultivation of positive social engagements can act as an upwards spiral to positive welfare and increase the quality of life for captive animals, in this case, gorillas.

5.2 Introduction

This chapter discusses and assesses the diverse concepts of animal welfare and how it relates to subjective wellbeing (SWB) and happiness in both in situ and Ex Situ Western lowland gorillas (iWLGs and eWLGs). One of the main goals within my thesis is to integrate the ex situ and in situ goals of the One Plan Approach (OPA). On all levels, whether we look at the breeding programs, translocation, or conservation program, promoting animal welfare is a critical goal, and this operates on the **individuals' level** – the personal level.

Positive welfare/ positive psychology

In human psychology, positive psychology is a relatively new research area. After the second world war, psychology became a science concentrated on repairing damage within a disease model of functioning, with almost exclusive attention paid to pathology at the expense of positive values. With the impetus of Seligman in 2000, where he believes that it is better "to amplify strength rather than repair the weaknesses", the field of Positive Psychology (Seligman & Csikszentmihalyi, 2000, page 8) arose. To assess happiness, the emergent research fields around positive psychology are concentrated on subjective valued experiences like positive wellbeing, quality of life, personality, life satisfaction, purpose and meaning in life, optimism, health, positive early life development, and positive environment. On the individual level, research is focused on positive individual behavioural traits, such as joy, curiosity, friendship, originality, and responsibility, just to mention a few. In humans, some frameworks are used to assess how to foster and cultivate positive emotions (feelings, cognition, and behaviours), increase happiness and quality of life (Lyubomirsky, King, et al., 2005; Lyubomirsky, Sheldon, et al., 2005; Weiss et al., 2016) in an upwards-spiral of positive emotion (Fredrickson & Joiner, 2002).

Since there is no single definition of happiness; SWB is used interchangeably for happiness by most researchers (Costa & McCrae, 1980; King et al., 2005; King & Landau, 2003; Pederson et al., 2005; Robinson et al., 2017; Robinson, Waran, et al., 2016; Weiss, Adams, & King, 2011; Weiss et al., 2008, 2009), whereas others use happiness more in the broader sense of positive affect or satisfaction with life (P. Steel et al., 2008).

There are two common conceptions of happiness in human psychology: *hedonic*[1] and *eudaimonic*[2]. Pursuing enjoyment and pleasure leads to hedonic happiness (transient), whereas seeking meaning and purpose in life leads to eudaimonic happiness (enduring, Aristotle, translated 1962). Both types of happiness are considered attainable and beneficial to an individual's wellbeing. Aristotle argued that besides pleasure (i.e. positive emotions and feelings) being part of the good life, a happy life is one in which one acts consistently with their virtues[3]. Following Aristotle, most researchers concur that both hedonic and eudaimonic happiness contribute to an individual's overall sense of wellbeing, although in different ways. According to Aristotle (translated 1962), happiness might be the combination of hedonic (pleasurable), and eudaimonic (a life well-lived) component. Therefore, pleasure is not synonymous with happiness. Although it is related, it includes the hedonic brain circuits and traits, which predispose happiness in individuals (Kringelbach & Berridge, 2010). Thus, the hedonic concept boosts pleasant feelings and joy, and helps to regulate emotions by reducing negative emotions, tension, sadness, and can therefore be viewed as short term happiness (**Figure** 21, Level 1 on the timescale). In contrast, the eudaimonic concept boosts what leads to a larger sense of personally-relevant values and life satisfaction (**Figure 21**, Level 4 on the timescale) – a purpose and meaning in life – and that those activities lead to more effective wellbeing over time. The eudaimonic perspective on human happiness and flourishing (doing well) is advocated by psychological theories such as Maslow's Hierarchy of Needs (1943) which places self-actualization as the highest life objective. However, Maslow's theory has led psychologists to concentrate on the self rather than the social for decades. The revised model by Tay & Diener (2011), on the other hand, seeks to strike a balance between the pursuit of happiness as the end objective and the achievement of both personal and social goals along the way. "Maslow got right that there are universal human needs beyond the physiological needs that everyone recognizes. But it turns out people are inherently social. We are called the social

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[1] Making one's primary life purpose to achieve the maximum of pleasure is the fundamental concept of the Hedonic happiness theory, which was advocated by a Greek philosopher named Aristippus (435-366 BCE) and Epicurus (341-270 BCE).

[2] The notion of eudaimonia (living well, doing well), like that of hedonia, was first suggested by Aristotle in the fourth century B.C., in the Nicomachean Ethics (Aristotle, translated 1962).

animal now" says Diener (2011). This is consistent with Lieberman's arguments in his book "Social" (2013), which explains why we are so deeply social. People are at their most positive when they are happy; they become more sociable, cooperative, and even ethical (Diener, 2009).

The next section discusses how animal welfare has been conceptualised over time, and that recent research in positive human psychology has influenced animal welfare thinking.

Applying positive psychology in animals (non-human primates)

Positive welfare in animals: moving beyond the "five freedoms" towards a "life worth living," optimal life or happier life.

Definitions of animal welfare are as multifaceted as are the diverse disciplines involved – that is ethology, psychology, ethics, personality, and biology (Mellor, 2016). As an analogue to human positive psychology, we can change our attention from "repairing damage", by minimizing negative welfare states, such as hunger, pain, suffering, stress and distress (Boissy et al., 2007; Burman et al., 2009; Harding et al., 2004; Lawrence, 1987; Stiedl et al., 2004) and using new approaches to welfare that focus on stimulating positive welfare aspects of an animal's life (Balcombe, 2009; Boissy et al., 2007; D. Fraser & Duncan, 1998; Green & Mellor, 2011; Mellor, 2012, 2015a, 2015c, 2015b, 2016; Mellor et al., 2020; Mellor & Beausoleil, 2015, 2015; Mellor & Stafford, 2001; Mendl & Paul, 2004; Spruijt et al., 2001; Yeates, 2011; Yeates & Main, 2008). These modern attempts to improve and assess animal welfare need to be multidisciplinary, and are grouped around three orientations (D. Fraser, 2008; Yeates, 2010; Yeates & Main, 2008): (1) to minimize unpleasant "affective states" and to maximize animal's subjective positive emotional experiences (e.g., Boissy et al., 2007; Duncan, 1993; Mellor, 2012, 2015b; Mellor & Stafford, 2001); (2) to ensure good physical health and biological functioning (Broom, 1986; Broom & Johnson, 1993; A. F. Fraser et al., 1997); and (3) to improve the conditions in which an animal can live in ways that are natural for its species (Bracke & Hopster, 2006; Veasey, 2017). However, positive welfare cannot be defined as the absence of all negatives. Positive welfare includes survival-critical negative effects, and it is the balance between them, where the positive must outweigh the negative (Fredrickson & Losada, 2005; Mellor, 2015c; van der Harst, Baars, et al., 2003; van der Harst et al., 2005; van der Harst, Fermont, et al., 2003; Yeates & Main, 2009), that is crucial. This will result in "a good life" (Edgar et al., 2013; Mellor, 2016), a life worth living (Green & Mellor, 2011; Mellor, 2016), an optimal life (Brando & Buchanan-Smith, 2018; Veasey, 2017), with the attention on psychological wellbeing, or even, as this thesis argues, lead to a "happier and healthier life".

Currently, those directions are interlinked in the widely accepted **"Five Domains Model"** (Mellor et al., 2020; Mellor & Beausoleil, 2015). Another approach is the **Hierarchy of Needs** (WAZA, welfare strategies, 2015), or, for example, the hierarchy of dog needs inspired by Maslow's Hierarchy of (human) Needs (Maslow, 1943), which places an emphasis in a dog's strengths, optimism, and free will/choice. Michaels (2015) highlights that a social animal is far less likely to exhibit abnormal behaviour when their biological requirements, safety needs, and belonging needs are addressed. In Chapter 6, I crafted the "One Welfare Plan"), merging the Five Domain Model with Maslow's Hierarchy of Human Needs, then tailored it for animals (Maslow, 1943; Mellor, 2016; Mellor et al., 2020), surpassing the confines of the OPA. I have proposed that for social animals such as WLGs, sociability is the key to overall welfare, happiness and conservation success.

Positive welfare in eWLGs.

Like many animals, eWLGs live in social groups (see Chapter 2, Chapter 3, and Chapter 4). Measuring individual behaviour and interactions within groups can contribute to our understanding of the evolutionary role of sociality on personality (as already demonstrated in Chapter 3 and Chapter 4 on the genus of gorillas), happiness and how it relates to increased wellbeing on the hedonic (short-lived) level, and eudaimonic (longer-lived) level. Studies of both iWLGs and eWLGs are critical in respect to the OPA (Chapter 1). In situ WLGs live in multilevel societies and have a great capacity to choose their group companions. In ex situ conditions, the management (housing and husbandry decisions) of most gorillas is determined by humans and are most likely socially constrained to conspecifics and other groups (see Chapter 2 and Chapter 4 for differences in socio-ecology, e.g. life cycles, and Chapter 3 and Chapter 4 on the personality structure). The generated personality structure of eWLGs was addressed in Chapter 3 and serves as the foundation of this chapter. Information on individuals' characteristics can be of great importance for promoting wellbeing and breeding, translocation or conservation, for example, by identifying breeding pairs, or group companions, to increasing group cohesion, and ensuring successful introductions (Gold & Maple, 1994; Herrelko et al., 2020; Kuhar et al., 2006; Tetley & O'Hara, 2012).

This chapter aims to interlink and quantify potential indicators of an individual's positive wellbeing to validate them as a means of providing scientifically recognized measures of positive animal welfare in ex situ settings, using eWLGs as the case species. To achieve this, I utilise multiple reliable and predictable welfare measurements at different timescales within a gorilla's life. Starting from short-lived positive emotions (hedonic concept, Level 1), to state-dependant behavioural response (mood, Level 2), zoo records (group composition, translocations, rate of birth, survival rate, etc., Level 3), which give information on breeding circumstances and life history, and finally personality and SWB measures (Level 4), on a long-term scale representative in a gorilla's life as they are expected to be consistent in context and time (see below **Figure 16, Figure 17**, and **Figure 18** within this chapter). Measuring SWB allows assessment of happiness on the eudaimonic level. Therefore, as suggested above from Aristotle's, Happiness via the eudaimonic concept of Happiness can be addressed here with the Subjective Wellbeing questionnaire (SWB). It allows assessment of life satisfaction outcomes. The chapter goal is to provide new findings on how to promote an optimal life, a life worth living for eWLGs and give recommendations for management challenges (Chapter 6). This novel approach integrates the OPA to link the ex situ population in terms of the multi-faceted welfare approach within the OWA (One Welfare Approach) and combines the in situ population (measured at the species level) by addressing ex situ and in situ personality structures.

Research into the field of **positive emotions, rewarding, short-term affective experiences** (see **Figure 16**, Level 1) and recently on longer-term, persistent, positive affective states (Level 2), such **as mood (state-dependent behavioural responses (s-dbr), or optimism)**, **zoo records** (Level 3) **personality, and SWB** in animals (Level 4) represents a new direction for enhancing our knowledge of animal welfare relationships and are combined within this chapter (K. Baker & Pullen, 2013; Balcombe, 2009; Boissy et al., 2007; Burgdorf & Panksepp, 2006; Herrelko et al., 2012; Mellor, 2015a, 2016, 2016; Mendl & Paul, 2004; Powell & Gartner, 2011; Schino et al., 2016a, 2016b; Watters & Powell, 2012; Yeates, 2010; Yeates & Main, 2008).

In Figure 16, I depict the four operating levels of the multi-disciplinary/ multi-dimensional approach and how they are interlinked to work towards the goal of the OPA, even more, the OWP (see **Chapter 6** for more information) and to minimise the potential negative impact of ex situ/ in situ conditions. Therefore, the overall goal is to establish a genetic healthy ex- and in situ populations by maximising the wellbeing of individuals and populations. As welfare is not an exclusive "gorilla" concern - it is a global welfare concern- the OWP challenges the focus on animal species within the "Reserve the Red" issue (IUCN, 2024). Therefore, welfare, on the level of the individual, promotes the survival of the population, it challenges a global health and welfare issue, and includes humans as we embrace an ethical responsibility and the capacity to take action and improve the welfare of gorillas, in this special case.

Overview of the multi-dimensional approach, using four welfare measures to assess happiness/SWB on different time spans within the life of a gorilla: with focus on sociability.

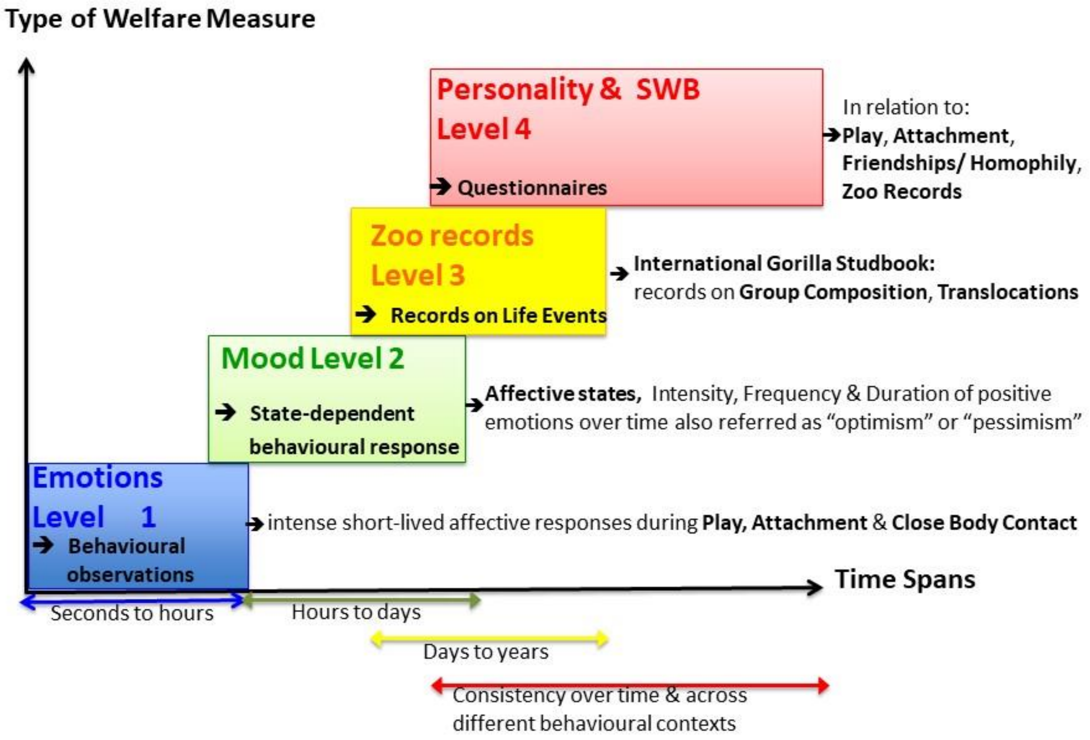

Figure 16 *Measures of positive welfare, showing the timescales of the four indicators, and a summary of the measures recorded*

Notes:
Operational Level:

1. **Emotions** are defined as **intense short-lived** (seconds to hours) **affective responses to internal or external events** (Burgdorf & Panksepp, 2006; Dantzer, 1989), which are associated with specific body changes and facial expressions (universal, see (Ekman, 1999). Socially rewarding experiences, like play, attachment and close social contact (Balcombe, 2009; Boissy et al., 2007; Mellor, 2015a, 2015b, 2016; Mellor & Beausoleil, 2015; Špinka, 2012; Yeates & Main, 2009) will be assessed using behavioural observations (see definitions in Ethogram, ***TableAPP 2***).
2. **Mood** lasts much longer than emotions (Mendl et al., 2010). Positive mood is linked to "optimism," negative mood to pessimism, and mood states may last hours or days. However, long-term disturbances, such as depression and bipolar disorders can last months to years. Optimistic mood will be measured via intensity, frequency, and duration of positive social experiences, **measured via state-dependent behavioural responses over a longer period of time** (Harding et al., 2004; Scheier & Carver, 1992).

3. **Zoo records** (i.e., on the status of health, birth, rearing, number of transportations between zoos, and death) are recorded daily in zoological facilities. Life-time reproductive success will be assessed using the **International Gorilla Studbook** (Wilms & Bender, 2017) which contains detailed information on the current gorilla population, and yearly birth (Holtkötter & Scharpf, 2005; Louvet, 2003), deaths and transferal rates. Group constellations will be used to assess group structure.
4. **Personality** and **SWB** are consistent over time and across different behavioural contexts and ecological situations (within an individual) (Weiss et al., 2006). Personality predisposes emotional, cognitive, and behavioural tendencies, certain types of moods, zoo record outcomes and happiness (Weiss, Adams, Widdig, et al., 2011; Weiss et al., 2006, 2008). These dispositions (differences) result from the combined influences of genetic, epigenetic and environmental effects (Sih et al., 2015). **Personality and SWB will be rated using questionnaires** (King & Landau, 2003; Schaefer & Steklis, 2014). A comparison of ex situ and WLGs will be used to explain social-ecological differences within the model of personality. Happiness is subjective!

In the following section, I discuss the fundamental background of emotions, my first welfare measure (**Figure 16**).

Emotion: level 1; the hedonic concept, a relation to positive animal welfare.

As in human psychology, most research is conducted on animal sentience in respect to the negative aspect of welfare, like pain, suffering, stress, and distress (Burman et al., 2009; Forkman et al., 2007; Harding et al., 2004; Lawrence, 1987; Stiedl et al., 2004). Exploring positive emotions in animals, which encompass rewarding short-term affective experiences as well as state-dependent behavioural responses like mood, signifies a novel avenue for advancing our understanding of animal welfare (Balcombe, 2009; Boissy et al., 2007; Burgdorf & Panksepp, 2006; Mellor, 2014, 2015a, 2015c; Mendl & Paul, 2004; Yeates, 2010; Yeates & Main, 2008). This leads to improved life conditions and satisfaction (see above SWB) and is linked to greater health (e.g. in humans, to a lower risk of heart disease than pessimists), longevity, personality, and social factors.

Evolution of emotion.

Expressions of emotion or affective states are strongly influenced by the organism's body and mind (i.e. brain, muscles, viscera, heart, immune response, etc.), environment (social and ecological) and experiences within it and are promising indicators to measure animal wellbeing (de Waal, 2011; Mellor, 2015c). The expressions of emotion are signal states that have value (Cabanac, 1992; Revelle & Scherer, 2009) and Darwin (1872) considered emotional expressions to be hereditary and evolved. He outlined clear parallels and antecedents between human effects and the effect of animals and our hominid ancestors, and the use of the term "emotion" in the context of animals was for several decades considered unscientific (e.g., "scientifically unwieldy" according to Seligman et al., 2005, p. 7) as it implicated anthropomorphic assumptions of human-like subjective experience. Contemporary studies changed this view again and argued for a strong link between human and animal emotion (Bekoff, 2001; de Waal, 2011; Mellor, 2012; Panksepp, 2005, 2011, 2015). In a framework on affective consciousness, Panksepp (2005) conceived emotion action-oriented systems, such as SEEKING, FEAR, RAGE-ASSERTIVENESS, BONDING, CARE-PLAY, and LUST and outlined their neuropsychological foundation (neural circuits) and emotional substance-specific behaviours. He described two relevant social systems in response to engagements, such as pro-social and affiliative emotions and behaviours (social bond, attachment, sexuality, maternal care, other joyful and pleasurable social possibilities). The first of these was the BONDING system with positive (via pro-social and affiliative behaviour induced system) and negative affect (attempt to avoid separation or isolation, when reunited). The second are the CARE (nurturance), PLAY (joy of play) and LUST (pleasure in sexuality and appetitive eroticism) system.

The expression of emotion (e.g., pleasure and pain) is usually triggered by encountering either aversive or attractive biologically appropriate external stimuli (de Waal, 2011). Emotions are defined as an intense but short-lived affective response to an event, which is associated with specific body changes (Dantzer, 1989; de Waal & Ferrari, 2010; Reefmann et al., 2009). Therefore, stimuli that are encountered by a subject can either be evaluated as a fitness decreasing threat/hazard (e.g. injury, disease, death; traditionally termed “punishers” in learning theory and affective neuroscience (Jean-Richard-Dit-Bressel et al., 2018)) or a fitness-increasing resource (e.g. food, water, shelter, mates, play; termed a “reward”) (Dawkins, 1998) with a more intense reaction (Boissy et al., 2007) than toward a positive encounter. Thus, emotional reactions to positive stimuli can vary more individually and are more labile, and their expression can be more subtle (Boissy et al., 2007).

Social positive emotion

Emotions play a significant part within the communication system and in social interactions. The ability to interpret the emotional signals of others and to respond to them discriminatively is a prerequisite for social interactions, which are a complex interplay between sender and receiver, each with their own goals (Bradbury et al., 1998). Emotions underlie a social fundament and social connections. Emotion also affects behaviours, conformity in responses, and moods of others – one example being their positive impact on cooperation and group performance via the contagious nature of positive emotion through social connections

(Fredrickson, 2003). Furthermore, emotions help develop trust and harmonious relationships within groups (Walter & Bruch, 2008). Researchers have been interested in understanding the evolutionary origins of emotions to optimise their expression and increase wellbeing and happiness (de Waal, 2011; Fredrickson & Joiner, 2002; Panksepp, 2005), and it has been found that optimists live up to 19% longer than pessimists (Seligman & Csikszentmihalyi, 2000). Frederickson suggests that putting significant effort into optimizing friendships increases wellbeing and health (the Broaden-and-build theory: Fredrickson, 2003, 2004).

Social welfare: Positive animal-to-animal interactions

Among the best predictors of positive emotional states in animals are the behavioural components of positively valanced social engagements, such as play, breeding, and affiliative behaviours, including grooming, hugging, touching, mouth to mouth greeting, and kissing (Abelló et al., 2010; Balcombe, 2009; Boissy et al., 2007; D. Fraser & Duncan, 1998; Mellor, 2015c; Yeates, 2010). In humans, positive bidirectional relationships between positive emotion and positive aspects of close relationships have been found to lead to an upward spiral of wellbeing and to contribute to an overall positive wellbeing (Fredrickson, 1998; Ramsey & Gentzler, 2015). The expression of social positive behaviours, which are multi-modal interactions, drive individuals towards each other, help maintain friendly contact behaviour and lead individuals to connect and stay together, often in close proximity (Reinhardt, 2009). Social interactions include rewarding goal-directed behaviours, such as feeling positive emotions during pleasurable experiences like when we are with friends or during play (Balcombe, 2009; Mellor, 2015a, 2015b). Social connections also foster positive emotions via touch or close proximity (Fredrickson, 2001) and enhance emotional experiences like empathy (Waal, 2009; Koski & Sterck, 2010) as seen in contagious yawning (Campbell & de Waal, 2014) and the infectiousness of laughter (Davila Ross et al., 2008)), sympathy (Liebal et al., 2014) homophily (Massen & Koski, 2014; Morton et al., 2015) and conformity within groups, populations and species (in humans: (van Schaik, 2012; von Rohr et al., 2012; Walter & Bruch, 2008); Expressing higher levels of positive emotions increases the likelihood of building new friendships or creating new groups (in humans: (Fredrickson & Joiner, 2002), of engaging in diverse social and physical activities, and increasing social dimensions in space and location (de Waal, 2009; Harker & Keltner, 2001) and this is most effective with compatible conspecifics (Reinhardt, 2009). Furthermore, positive emotions help to develop trust and harmonious relationships, strengthen social bonds, evoke mutual affection, and increase social engagements, such as cooperation (Fischer & Manstead, 2008; Klein, 2014). Pleasure is said to be “useful” (Cabanac, 1971), “life-driving” (Kringelbach & Berridge, 2010) and rewards adaptive behaviour as it is a vehicle used by nature to facilitate evolutionary benefits. Thus, pleasure is the “blessing of adaptation” (Balcombe, 2009) and it can serve as a proximate fitness-factor (Eibl, 2010). Social positive emotions are therefore crucial for interactions and a developmental process - from grooming to complex social communication systems. From a survival perspective, they are an evolutionary strategy with empathy as its peak (Waal, 2009) and altruism as the key to the “Survival of the Nicest” in humans (Klein, 2014). Already Darwin's evolutionary thinking (1871), where he argued for "the greater strength of the social or maternal instincts than that of any other instinct or motive," (p. 87) with sympathy as the strongest instinct underpinning the concept of “survival of the friendliest” (Hare & Woods, 2020), "survival of the kindest" and humans as the "super-caregiving" species at the top of the primate lineage (Dachner et al., 2009).

“Happiness” – a personality thing” (Weiss et al., 2008). Understanding that the experience of positive emotions and "happiness" is intricately linked to an individual's personality (Weiss et al., 2008), means we are compelled to acknowledge that an animal's emotional sensitivity and temperament play pivotal roles in his/her overall wellbeing. Determining whether an animal possesses a predisposition to experience positive emotions provides a solid foundation for investigating sustained positive emotional states in animals. The terminology and concepts employed to describe these enduring emotional states vary in the level of structure they offer, ranging from optimism and "individual differences" to the broader notion of personality.

Subjective Wellbeing. Happiness-Questionnaire. Sociability is key to Happiness.

In humans, numerous studies have identified a relationship between the Five Factor Model (FFM) and SWB (Diener, 2000a; González Gutiérrez et al., 2005; Jovanovic, 2011; McCrae & Costa, 1991; P. Steel et al., 2008; Weiss et al., 2008). For instance, people with higher level of extraversion seem more cheerful and tend to be happier in comparison to introverts (Lucas & Baird, 2004). Extroverts tend to flourish if their actions are accomplished socially, whereas introverts prefer to do things alone (McCrae & Costa, 1991). Further, in humans, social behaviours related to Agreeableness increase wellbeing; such as behaviour directed towards family or altruistic behaviours (Headey, 2008). Overall increased life-satisfaction seems part of humans' personality and is also subject to sociality. In short, in humans, happier means healthier (e.g., lower risk of diseases, such as heart diseases, cancer, stroke, diabetes and depression which lead to a longer life) and this correlates with social emotional wellbeing (being more optimistic, enthusiastic, balanced and socially engaged) and personality (Veenhoven, 2008).

Following the evidence from humans, in animals too sociality is key to improving life circumstances. Social enrichment is one of the best ways to promote subjective wellbeing as it works as a catalyst of pleasurable experiences (Balcombe, 2009; Boissy et al., 2007; Mellor, 2015a, 2016). It is of utmost importance to provide environments that promote and support natural behaviour in ex situ animals, including providing a rich source of social positive relationships, starting with mother-infant bonding, and allowing friendships to develop so individuals can spend time with those who make their lives most rewarding.

Social happiness, as aptly expressed by Christopher McCandless in "Into the Wild" by Jon Krakauer (1997, p. 189)- "Happiness is only real when shared". This quote highlights the importance of social support in enhancing happiness. Social factors play a pivotal role in the pursuit of happiness among humans (Kringelbach & Berridge, 2010). Research suggests that individuals who report higher levels of happiness tend to have larger social circles and greater social support compared to those who experience lower levels of happiness (Baldassare et al., 1984). Furthermore, individuals who report higher levels of happiness are more inclined to marry and maintain more intimate and satisfying long-term relationships, leading to the expansion of their social networks (Fredrickson, 2003). This interplay between happiness and sociality suggests a reciprocal relationship: happier individuals may engage in more social activities, both formal and informal (Rohrer et al., 2018) or conversely, their heightened social engagement may create more opportunities for them to cultivate stronger and more profound connections with others.

Model on state-dependent feedback to explain the evolutionary role of sociality on personality. Sociality is the key to personality.

As shown in Chapter 3and Chapter 4, the social nature of animals shapes their personalities. Here, I argue, that sociability is also key to understanding animal personality, wellbeing, and happiness. To extend an existing model on state-dependent feedback loops (see Sih et al., 2105), I visualise the model and explain the evolutionary role of sociability on personality, and highlight that sociability is the key to personality. Within the following section, I give examples from **Table 17** to better understand how personality and happiness relate to sociability on the proximate and ultimate level.

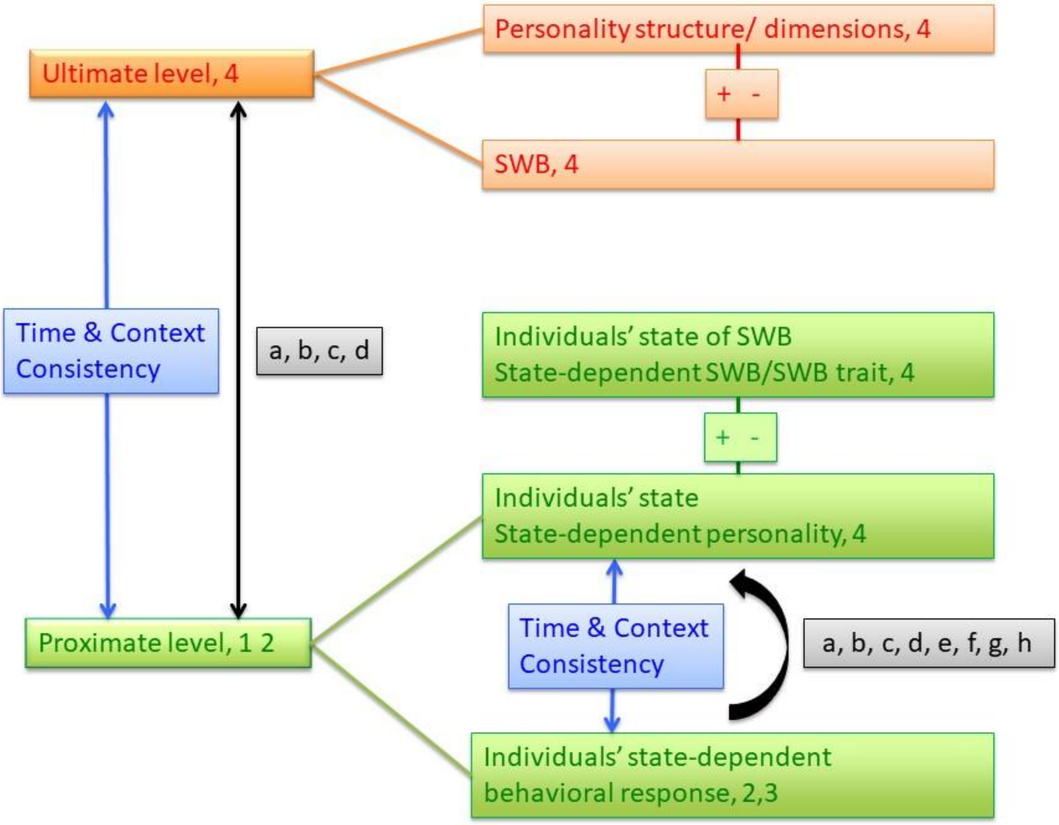

Figure 17 *Extended model on state-dependent feedback loops based on Sih et al. (2015) and adapted to the thesis*

Note.
Orange = Ultimate level (4). Including SWB = Subjective Wellbeing (4b). Certain personality dimensions (4a) are reliable predictors of SWB (4b) as successfully shown in other non-human primate species and animals (Robinson et al., 2017; Robinson, Waran, et al., 2016; Weiss et al., 2008, 2009; Weiss, King, et al., 2011).

Green = Proximate level, individuals' state (2), including individuals' state of personality (2a) and SWB (2c), and its state-dependent behavioural responses (2b).

Black lines and arrows are **feedback loops** (positive and negative) and **allow fine-tuning to any circumstances**: Feedback loops help to explain individual **plasticity**. Thus, they give information on the flexible reaction of an individual to any external (social or ecological) as well as internal changes and lead with the help of feedback loops to maintain state variations. The expression of the state-dependent behaviour is therefore influenced in return. Multiple feedback loops can act simultaneously.
a = among-individual (state-behaviour). Influence the personality structure of different populations/species or societies. E.g., a comparison of the personality structure of gorilla populations and subspecies with that of different great ape species and humans can help shed light on the phylogenetic relationships of those species.
b = extrinsic state variables include external features, such as an expression of a social partner, other species, or environmental changes.
c = the direct influence of different selective scenarios on the state or state-dependent behaviours of each individual, such as social niche specialization. They also act at the population level.
d = sex and age effect on personality.
e = intrinsic state variables: contain any internal feature, such as hormonal responses, risk-reward relationships, or individual experiences.
f = co-development feedback loop (e.g., between genes and environment during ontogeny, sensitive time windows)
g = feedback loop describes the relationship between the expression of behaviour and SWB (vice versa). Including intrinsic state variables, such as the expression of hormones during socio-positive experiences, i.e., pleasure.
h = joint evolution feedback loop: individuals differ systematically in their state and the way in which they adjust their behavioural tendencies (state-dependent behaviours, such as emotional, cognitive, etc.) in an adaptive way to the variation in state.

Blue lines and arrows = **individual consistency**, based on consistent individual reactions in time and context.
On the ultimate level, consistent differences in the personality structure of different species lead to species differences.
On the proximate level, individuals, which are consistent in their state over time show also more consistency in their state-dependent behavioural response in respect to diverse behavioural conditions and ecological circumstances. Stable states can emerge via already inherently stable states (features that are cost and time intensive to change) or stabilized states (due to positive feedback between state and behaviour).

Proximate level (2, green, in **Figure 17)**: "Proximate level" refers to personality on the level of the individual. At this level, variations between individuals are evident in various state-dependent behavioural responses, such as emotional and cognitive (Weiss, Adams, & Johnson, 2011). An individual's state (2) is based on genetical (gene variant and expression), epigenetical (i.e., development induced, such as weaning or rearing), physical (body composition), physiological (immune system, hormones, health) and neuro-psychological (cognitive ability) differences (Weiss & Adams, 2010; Wolf & Weissing, 2010).

Correlations between personality states (2b,c) can co-vary or impact the variability of each other (interdependencies, such as correlations of state-dependent behaviours (2b): aggressiveness and exploration), as these all underlie phenotypic plasticity (Penke et al., 2007; Réale et al., 2007; Sih et al., 2015; Wolf & McNamara, 2012; Wolf & Weissing, 2010). In addition, multiple states can be affected simultaneously (Dingemanse & Wolf, 2013; Sih et al., 2015).

State-behavioural feedbacks of intrinsic (e.g., social roles or experiences, sensitivity to risk–reward and life-history trade-offs) and extrinsic state variables (b, **Figure 17,** e.g. any social interaction with social partners or other species (also parasites) and ecological influences) are used to explain the evolution of personality and the relationship between flexible, state-dependent behaviour responses (2b, **Figure 17**) and state variables (a, **Figure 17,** Furthermore, phylogenetic mechanisms and adaptation shape genetic dispositions, which in turn (c, via the feedback loop) influence individual differences in state (2) and thus the structure of the personality (for more details see (Weiss & Adams, 2010). Therefore, a wider range of correlated individual states (intrinsic states, e), states of other individuals (extrinsic states, b), as well as patterns that are sensitive to the ontogeny of an individual are included (f). Further, this model also tolerates specific reactions later in life (e.g., via sensitive time windows, f). Also, individuals differ systematically in their state and the way in which they adjust their behavioural tendencies adaptively to the variation in state (h; in **Figure 17**) (Sih et al., 2015).

Beyond that, the phenotypic selection approach allows the evaluation of all kinds of different selective scenarios (c, **Figure 17**, Bergmüller & Taborsky, 2010; Krause et al., 2010; Réale & Dingemanse, 2010) in relation to extrinsic (b) and intrinsic state (e) variables and shows how these are linked back (feedback, black arrows) to personality variations (on the level of the population, state or the state-dependent behaviour of the individual). For instance, in relation to extrinsic states, social niche specialization (individuals maximise their fitness by selecting different behavioural strategies that minimise conflict) has been described as a critical factor in the evolution of individual variation (Bergmüller & Taborsky, 2010; Carter et al., 2014; Montiglio et al., 2013). In humans, the knowledge of personality is used to find people for specific "social niches" (Odling-Smee et al., 2003), such as for professions (e.g., leaders need to have higher levels of assertiveness, and clinicians need to be more empathetic). Having appropriate "friends" can help in different life situations (Massen & Koski, 2014). Therefore, similarity in personality (known as “homophily”) should result in more predictable interactions and can increase wellbeing in animals. Similar personalities build stronger bonds and friendships as well as spend more time in close proximity (Ebenau et al., 2019; Massen & Koski, 2014; Morton et al., 2015; Weinstein & Capitanio, 2008) (**Figure 17).** Furthermore, the model allows additional selective scenarios, such as frequency-dependent selection theories (e.g., social responsiveness, (Wolf et al., 2011), spatio-temporal variation, and others, to be explained (Nettle, 2006). In addition, those inter-linked relationships have a strong impact on the survival of the individual and the species (a, **Figure 17).**

On the other hand, individual variations are consistent (blue arrows, **Figure 17**) over time (or parts of the ontogeny) and across diverse behavioural conditions (e.g. anti-predator (attack and avoidance) and foraging behaviour (exploration)) and ecological circumstances (Freeman & Gosling, 2010; Gosling, 2001; Sih et al., 2004; Weiss, Adams, & Johnson, 2011; Wolf & Weissing, 2010) (see **Figure 17**, green lines). Individuals who are consistent in their state over time also show more consistency in their state-dependent behavioural responses with respect to diverse behavioural conditions and ecological circumstances (Sih et al., 2015). Stable states can emerge via already inherently stable states (features that are costly and time-intensive to change) or stabilized states (due to positive feedback between state and behaviour) (Sih et al., 2015). Personality states (2; traits/ trait combinations/constructs/ facets/ dimensions), which increase "pro-social personality" tendencies, can be favoured.

Therefore, individuals’ personality has a strong impact on a wide range of factors influencing social group living and vice versa (social context in return, via state dependent behaviours (2b), social-positive interactions (a), intrinsic (e) and extrinsic state variables (b)). In addition, individuals’ personality responses in social contexts are affected via social conformity and facilitation (Aplin et al., 2015; Planas-Sitjà & Deneubourg, 2018). As a result, an indirect fitness increase, such as higher social rank and reproductive success, was found in individuals with stronger collaborations (Gilby et al., 2013). Consequently, individual variations are associated with different life-history strategies (Réale et al., 2009; Stamps, 2007; Wolf et al., 2007), survival (Biro & Stamps, 2008; Weiss et al., 2013), reproduction (e.g. mate choice, Bergmüller & Taborsky, 2010; Seyfarth et al., 2012; Wolf et al., 2008) and fitness success (Biro & Stamps, 2008; Dingemanse et al., 2004a; Réale et al., 2000).

Ultimate level (1, orange, in **Figure 17**): Personality on the level of the population (society or species). A cross-species comparison in respect to the survival of the species.

Consistent personality structure variations within a population or species. Different primate species exhibit varying social structures that underlie distinct social organizations. The evolution of stable societies in these species is influenced by adaptive and phylogenetic constraints (Chapman & Rothman, 2009; Shultz et al., 2011). For example, a study comparing social dimensions within five different macaque species focusing on their personality structures revealed interspecific differences in social style, encompassing various social personality domains from despotic to egalitarian (Adams et al., 2015).

The variation in personalities also has implications for the evolution of populations, the survival of the group (across populations and species), general group dynamics, and long-term persistency (e.g., Bremner-Harrison et al., 2004; Dall et al., 2012). Therefore, consistent personality structures among different primate species within evolutionary and socio-ecological time scales can be compared (a, **Figure 17**, model on state-dependent feedback to explain the evolutionary role of sociality on personality). These consistent personality differences can be employed to elucidate phylogenetic relationships among various primate species and facilitate cross-species comparisons (e.g., Weiss, Adams, Widdig, et al., 2011). Furthermore, personality structure comparisons between species have been employed to address questions regarding how sex and age differences have contributed to the evolution of species-specific traits (Weiss & King, 2015). Sexual selection (d) (Schmitt et al., 2008), social factors or life events (such as status competition or cooperation; Brandt & Henry, 2012; De Waal, 2000; King et al., 2008; Srivastava et al., 2003; Wood & Eagly, 2002), as well as sex differences in human cultural norms or social inequality, are all hypothesized to contribute to sex differences in personality (Weiss & King (2015) and other researchers have demonstrated, similar to studies of human personality, that personality can change over time.

Impact of personality on sociability and vice versa. Sociability was identified as key to personality (Adams et al., 2015; Gartland et al., 2022). An individual's personality has a strong impact on a wide range of factors influencing social group living and vice versa (social context in return, via state dependent behaviour responses e.g., via social-positive interactions (2b), intrinsic (e) and extrinsic state variables (b). Personality is related to a number of social outcomes, including grouping tendencies (Cote et al., 2011; Kralj-Fišer et al., 2007), reconciliation (Webb et al., 2017), social role (Bergmüller & Taborsky, 2010; Montiglio et al., 2013), social network (Best et al., 2015; Blumstein et al., 2018; Croft et al., 2009; Krause et al., 2010; López, 2020; Pike et al., 2008; Sih et al., 2009), collective behaviour (MacGregor et al., 2020; Nagy et al., 2013), affiliative relationships (Weinstein & Capitanio, 2008; grooming: Blaszczyk 2017), number of friends (Massen & Koski, 2014; Morton et al., 2015) and proximity to nearest conspecific (Sibbald et al., 2005). Similarity in personality has been found to be an indicator for positive regrouping success in female rhesus macaques pair formation (Weinstein & Capitanio, 2008). Additionally, similar personalities build stronger bonds and friendships, and result in spending more time in closer proximity (Massen & Koski, 2014; Morton et al., 2015; Weinstein & Capitanio, 2008). Having appropriate "friends" can help in different life-situations (Massen & Koski, 2014) and are a source of positive wellbeing (Mellor, 2015a, 2016; Mellor et al., 2020). An indirect fitness increase, such as higher social rank and reproductive success was found in chimpanzees with stronger collaborations (Gilby et al., 2013; Weiss et al., 2023). Consequently, individual variations are associated with different "social" life-history strategies (Réale et al., 2009; Stamps, 2007; Wolf et al., 2007), survival (Biro & Stamps, 2008; Weiss et al., 2013) reproduction (e.g. mate choice, Bergmüller & Taborsky, 2010; Seyfarth et al., 2012; Wolf et al., 2008) and fitness success. It is important to note that sociability has been shown as one of the key dimensions that can influence an individual's personality (Gartland et al., 2022).

It is imperative to acknowledge that ex situ animals deserve the right to lead a life characterized by a sense of wellbeing that is considered "worth living." Such an enhanced quality of life not only aligns with prolonged and healthier lifespans but also correlates with improved overall fitness and survival prospects. As shown above, sociability is key to personality and happiness, and fostering increased positive wellbeing can be closely intertwined with social interactions.

Interlinking social positive emotion, mood, personality, and happiness

In humans, numerous studies have identified a relationship between the Five Factor Model (FFM) and SWB (DeNeve & Cooper, 1998; Diener, 2000b; González Gutiérrez et al., 2005; Jovanovic, 2011; McCrae & Costa, 1991, 1991; P. Steel et al., 2008; Weiss et al., 2008). For instance, people with higher levels of extraversion seem more cheerful and happy in comparison to introverts (Lucas & Baird, 2004). Extroverts tend to flourish if their actions are accomplished socially compared to introverts who prefer to do things alone (McCrae & Costa, 1991). Further, in humans, social behaviours related to Agreeableness increased wellbeing such as acting eudaimonically (McCrae & Costa, 1991; Steger et al., 2008); or performing altruistic behaviours directed towards family (Headey, 2008). Additionally, happier humans tend to be healthier (e.g., lower risk of diseases, such as heart diseases, cancer, strokes, diabetes, and depression which lead to a longer life) and this correlates with social emotional wellbeing (being more optimistic, enthusiast, balanced and socially engaged) and personality. Thus, overall increased life-satisfaction seems part of human personality and is subject to sociality.

Studies on chimpanzees, orang-utans, rhesus macaques and capuchin monkeys have demonstrated that human raters can assess personality and SWB of these species with high levels of reliability and validity (Freeman & Gosling, 2010; King & Landau, 2003; Robinson, Waran, et al., 2016; Weiss, Adams, Widdig, et al., 2011; Weiss et al., 2006). Additionally, in capuchin monkeys, a welfare questionnaire was utilised, in combination with SWB and personality, and was found to be a valid and reliable measurement tool (Robinson, Waran, et al., 2016). This might be explained by phylogenetic generalisations from human to non-human primates using “empathic accuracy” (Ickes, 1993) or our ability to describe another’s feelings (King & Landau, 2003). Humans can reliably assess the SWB of another person (Pavot & Diener, 1993) and so it requires only a moderate inductive generalisation to accept that humans may also reliably assess the SWB of non-human primates (King & Landau, 2003; Weiss, Adams, & King, 2011; Weiss et al., 2006, 2008; Weiss, King, et al., 2011).

Adapting positive psychology for ex situ gorillas

The behaviours of a subset of eWLGs (N=24) were coded to examine the triangulation between subjective pleasurable experiences (on the hedonic component), with emotions (Level 1), s-dbr (e.g., mood/optimism Level 2 which is measured by state-dependent behavioural responses, e.g., via play and proximity) with "social happiness" (the trait rating on SWB = the eudaimonic component) and personality ratings (Level 4). Zoo records (Level 3) are used measure the impact on happiness. The link between these factors and increased SWB will be discussed. The overall goal is to improve welfare strategies in eWLGs and iWLGs within the framework of the OPA.

Individuals scoring higher in positive social engagements are assumed to live a more pleasurable life with higher levels of rewarding or satisfying experiences (in humans Fredrickson, 2001) and so should score higher in happiness. However, a systematic experimental investigation of the relationship between positive social interactions, happiness, and animal welfare in primates is still lacking. I therefore address whether play behaviour differing between individuals informs us of their emotional wellbeing, and whether more playful gorillas score higher in happiness (SWB scores). I predicted that happier individuals show higher levels of positive aspects of close relationships (proximity as a measure for close contact) (as seen in humans, Seligman & Csikszentmihalyi, 2000).

I also explored whether certain personality dimensions are reliable predictors of subjective wellbeing. I highlighted the importance of using personality ratings to understand SWB in non-human primates as a source of reliable data that can be used to improve ex situ management strategies and to shed light on sociable happiness in animals in general.

Understanding that personality is fundamental to improving the expression of positive emotion, pro-social activities, homophily, and longevity in nonhuman primates as personality differences have been shown to have an impact on the management of ex situ animal welfare (Gartner & Weiss, 2013a; Gold & Maple, 1994; Kuhar, 2008; Robinson, Waran, et al., 2016; Stoinski, Kuhar, et al., 2004; Weiss, Adams, & King, 2011; Weiss et al., 2012; Wielebnowski, 1999).

I predict that there will be a bidirectional relationship between the expression of positive experienced behaviours, emotions (Level 1, **Figure 17** and **Figure 21**), mood (Level 2), and social relationships (Level 3). Individuals high in SWB (Level 4) will have more social interactions, and homophily in personality will lead to stronger friendships (level 4). Increased

SWB will also be associated with lower levels of stress or anxiety as measured by personality and behaviour. Additionally, higher socio-positive engagements, optimism, scores in certain personality factors – such as Agreeableness/ Sociability, Openness and Extraversion – and correlated SWB will be associated with enhanced reproductive success and status of wellbeing. Reproductive success has a strong impact on the survival of a species and on the survival considering the origin of personality via sexual selection. A comparison of eWLGs to the iWLGs was conducted in Chapter 4 to discuss the impact of ex situ conditions.

I predict that gorillas with similar personalities would preferentially spend more time together than with those who are measured less similar. Finding "matching partners" (e.g. in humans, dating agencies use information on personality to find a suitable partner, McCrae & Löckenhoff, 2010) in this case, friends, can have a strong effect on subjective wellbeing. I thus anticipate a link between the ability to express positive emotions through play and close proximity with persistent personality traits and happiness. Additionally, I analysed personality differences and SWB in respect to breeding success.

5.3 Methods and Materials

Multiple indicators are recommended for assessing animals' welfare to provide a comprehensive understanding of individual responses and interactions with their surroundings, as described above (Balcombe, 2009; Boissy et al., 2007; Edgar et al., 2013; Howell & Cheyne, 2019; Mellor, 2015a, 2015b, 2015c; Mellor & Beausoleil, 2015; Mendl & Paul, 2004; Novak & Suomi, 1988; Spruijt et al., 2001; Yeates, 2011; Yeates & Main, 2008). Therefore, this chapter outlines the **methodologies** used to assess **four welfare measures—emotion, mood, zoo records, and personality and subjective wellbeing (SWB)—within a multi-dimensional approach** (**Figure 17**, **Figure 19**, and **Figure 21**, within this chapter). Each welfare measure is described in subsequent sections, with an explanation of its selection based on existing literature and a detailed description of the corresponding assessment methods.

A consistent methodology was employed throughout data collection (Chapter 3 and Chapter 4, including SWB) and analysis to ensure comparability and integration of personality and behavioural data, forming a coherent framework. The aim is to improve the consistency of observations within both ex situ and in situ gorilla populations and to enable more robust comparisons, particularly in relation to welfare, breeding and conservation efforts for this endangered species within the goals of the One Plan Approach (see Chapter 1).

Keeping ex situ populations, such as gorillas, is widely recognized as a challenging task due to their perceived complexity. Therefore, the establishment of precise and dependable techniques for assessing their welfare could be beneficial for numerous other animals in human care, particularly when employing a social-ecological comparison to their in situ conspecifics.

5.3.1 Level 1 and 2: Positive Emotions and Mood (State-Dependent Behavioural Responses)

Why and how positive welfare relates to the social emotions and emotional states of gorillas was measured. These measurements formed the first (emotion) and second (mood) levels of the four assessment tools used within the lifespan of gorillas and are described below.

Research into the field of **positive emotions or feelings encompassing both rewarding, short-term affective experiences** and **longer-term (persistent) positive affective states**, such as **mood** in animals, represents a novel avenue for expanding our understanding of animal welfare relationships (Balcombe, 2009; Boissy et al., 2007; Mellor, 2015a, 2015b, 2015c, 2015c, 2016; Mendl & Paul, 2004; Spruijt et al., 2001; Yeates & Main, 2008). It is important to note that affective states are characterised by their valence, which refers to their positive or negative value, spanning from mild to highly positive/negative (pleasure vs displeasure). These states differ in terms of their associated arousal (from low to high), duration (short to longer-term), or level of activity or vitality (from low to high) (Fredrickson, 1998; Russell, 2003). Positive social interactions have been identified as promising indicators of good animal wellbeing and serve as fertile grounds for studying positive emotions and emotional states (Balcombe, 2009; Boissy et al., 2007; Mellor, 2015a, 2015b, 2016, 2020; Mellor & Beausoleil, 2015; Mendl & Paul, 2004; Špinka, 2012; Spruijt et al., 2001; Yeates, 2011; Yeates & Main, 2008). It is suggested that enhancing and cultivating positive emotions improves health, increases reproductive success, and can lead to a better quality of life (Fredrickson, 1998; Fredrickson & Branigan, 2005; Lyubomirsky, King, et al., 2005). Therefore, particular emphasis has been placed on the following positive affective states: play, attachment (e.g. caregiver-infant behaviours), and other close positive behaviour (e.g. touch, grooming, etc.)

5.3.1.1 Play

One parameter often considered one of the most promising indicators of positive emotion and welfare is play behaviour (Boissy et al., 2007; Fagen, 1981; Held & Špinka, 2011; Mintline et al., 2013; Oliveira et al., 2010; Vinke & Schoemaker, 2012; Watters et al., 2021). Play appears to have a crucial role in the behavioural development of young animals (Markus & Croft, 1995; Palagi, 2006, 2008), and young mammals devote a significant amount of time and energy to play (Pellegrini & Smith, 2005; Pereira & Fairbanks, 1993). Various functions of play have been proposed, including the acquisition and development of skills needed in adulthood, such as exploring the environment, establishing boundaries, aiding in socialization, and developing locomotor skills (Ahloy-Dallaire, 2015; Ahloy-Dallaire et al., 2018; Fagen, 1981; Panksepp & Beatty, 1980; Špinka et al., 2001). Play can also serve as valuable training for flexibility – both kinematically and emotionally – in responding to unexpected events (Boissy et al., 2007; S. G. Brown, 1988; Pellegrini et al., 2007; Špinka et al., 2001). While play behaviour is recognizable, its great variability, discernibility, and flexibility make it challenging to define (Burghardt, 2005; Held & Špinka, 2011; Norscia & Palagi, 2011; Špinka et al., 2001). Although there is no exclusive definition for play, common characteristics have been identified. Burghardt (2005) provided a comprehensive framework consisting of seven criteria that are commonly employed in play: (1) the behaviour is lacking complete functionality in its form or context, (2) it is spontaneous in nature, voluntary in participation, and provides pleasure and rewards, (3) play behaviour differs structurally or temporally from the serious performance of ethotypic behaviour, (4) it is repetitive but not stereotyped, (5) it typically occurs when the animal is in a relaxed state, such as being well-fed, healthy, and free from stress (6) engaging in play is intrinsically rewarding and pleasant for the animal involved and yields positive experiences, hence strengthening the associated behaviour (7) The act of play often manifests itself throughout the early stages of an animal's existence and may undergo transformations in its structure as the individual progresses in development. The act of engaging in play may fulfil significant developmental roles in the processes of learning and socialisation.

As mentioned above, there are several reasons why play can be seen as an indicator of positive wellbeing.

First, play indicates the absence of fitness threats (Held & Špinka, 2011) and several factors can facilitate, inhibit, or modulate play behaviour. Severe stress, illness, and hazardous environmental conditions are associated with a reduction in play behaviour (Fagen, 1981; Mintline et al., 2013; Thompson, 1996). As play correlates with welfare, its absence has the potential to indicate situations where animal welfare may be compromised (D. Fraser & Duncan, 1998; Held & Špinka, 2011; Špinka et al., 2001; Yeates & Main, 2008). Additionally, play is considered a motivational affective state (D. Fraser & Duncan, 1998), and motivational behaviours are considered key for positive welfare (Jensen & Toates, 1993). Play has been found to not occur when an animal is under severe stress and is most often displayed under relaxed conditions when all the primary needs of the animal are met (Fagen, 1981; Oliveira et al., 2010; Pellegrini et al., 2007; Thompson, 1996; Vinke & Schoemaker, 2012). Lack of play can serve as an indicator for inadequate welfare and its expression for the existence of favourable welfare (Burghardt, 2005; Fagen, 1981; Held & Špinka, 2011; Martin & Caro, 1985; Oliveira et al., 2010).

Secondly, play appears to be intrinsically rewarding (Balcombe, 2009; Bekoff, 1972; Boissy et al., 2007; D. Fraser & Duncan, 1998; Goodall, 1995; Held & Špinka, 2011; Špinka et al., 2001; Thompson, 1996; Vanderschuren, 2010; Yeates & Main, 2008) and is indicative of pleasurable emotional experiences mediated by opioids (Burghardt, 2005; Held & Špinka, 2011; Panksepp, 2005; Vanderschuren, 2010; Vinke & Schoemaker, 2012). Play also contributes to long-term brain development, such as increase in brain size (relative to body size) in species like chickens (Henriksen et al., 2017; Iwaniuk et al., 2001; Racicot et al., 2021) and increases in cerebellum size and structure during short-term play (Henriksen et al., 2017). Young animals also appear to enjoy play, exhibiting a state of pleasure during play behaviour (Balcombe, 2009; Bateson, 2014; Bekoff, 2001; Burgdorf & Panksepp, 2006; Calcagnetti & Schechter, 1992; D. Fraser & Duncan, 1998; Held & Špinka, 2011; Špinka et al., 2001; Yeates & Main, 2008). Several arguments support the rewarding nature of play: animals actively seek out play partners and solicit play behaviour (Boissy et al., 2007; Fagen, 1981), the opportunity for play can be used as a reward in preference experiences (Boissy et al., 2007; Martin & Caro, 1985), and after a period of inhibited play, there is often a rebound in play behaviour under more favourable circumstances (Bekoff, 1972; Boissy et al., 2007; Thompson, 1996).

Thirdly, play can bring immediate psychological benefits, such as stress reduction (Fagen & Fagen, 2004; Norscia & Palagi, 2011; Palagi, 2006), limited aggression and increased tolerance around food (Palagi et al., 2004), and long-term fitness and health benefits including the development of strength, motor coordination, physical resistance, learning of novel environmental information, and acquisition of social skills (Bekoff & Byers, 1998; Burghardt, 2005; Fagen, 1981, 1981; Oliveira et al., 2010; Špinka et al., 2001). Furthermore, different sub-types of play may equip animals with the necessary skills to adapt to forthcoming environments that could potentially elicit adverse emotional states (Marks et al., 2017; Pellis & Pellis, 2011; Špinka et al., 2001). Play can therefore have immediate and long-term benefits that can improve current and future welfare in addition to reflecting it (Held & Špinka, 2011).

Fourthly, play also is socially contagious (Bekoff, 2001; Fagen, 1981). Merely observing animals engaged in play can stimulate others to engage (Bekoff, 2001; Chaloupková et al., 2007; Held & Špinka, 2011), and through this spread of play, the pleasurable effect and its beneficial consequences can also be transferred (Špinka, 2012) and so have the potential to spread good welfare within groups (Held & Špinka, 2011).

Play behaviour is a strong candidate for indicating positive emotions and good welfare as it serves as a foundational element of motivational behaviour that is considered one of the key behaviours for promoting positive welfare. I focused on the investigation of play behaviours by means of studying the link between positive emotions, play behaviour and animal welfare through testing the proposed aspects of play. I focused on individual flexibility and variability of playfulness and linked the inherently rewarding and enjoyable nature of play to personality differences and life satisfaction (SWB) in two groups of eWLGs using behavioural observations. The rewarding nature of play was examined by studying the active solicitation of play and assessing the observers' subjective feeling of the expressed emotion using a defined emotions of positive to negative valence (see Chapter 3.2.1.1.5). For details on the coding of play behaviours and their categories, see Ethogram (Ethogram, ***TableAPP 2***).

Although play behaviour shows promise as an indicator of positive emotions and good welfare, there have been some criticisms of its use. Held & Špinka, (2011) note that play may also increase in the form of a "displacement" play, when the animal exhibits play as a means of managing or alleviating stress, anxiety, or unpleasant affective states This behaviour is often seen as a strategy for alleviating stress or as a method of redirecting attention away from unfavourable conditions (such as in form of social- or environmental stressor or general limitations in confinement). Therefore, it is advisable not to rely solely on play behaviours but to investigate other aspects of an individual's engagement and additional positive markers of welfare, such as attachment and close positive social behaviours.

5.3.1.2 Attachment: Positive Socio-emotional Parent-infant Relationship

Bonding is a complex social behaviour that plays a vital role in the wellbeing and subjective emotional experience of individuals (Carter, Goldizen, et al., 2012; Clay & De Waal, 2013; Maestripieri, 2001). It involves the interaction of multiple cognitive systems and is influenced by a variety of hormones. Extensive research has explored the role of hormones in affiliative bonding (Kikusui et al., 2008; Maestripieri, 1999, 2001; Maestripieri et al., 2009; Pryce, 1996; Saltzman & Maestripieri, 2011).

Given the positive valence of bonding, an additional focus is laid on observations in positive social-emotional experiences with a conspecific caregiver (i.e., mother, foster caretaker, father, or another caregiving gorilla within the group). These interactions are important for positive and secure development and for long-term mental health (Mogi et al., 2011). The mother-infant relationship attachment bond is unique among the various types of bonds within a social group, and it was previously believed to develop solely during the postpartum period but is now recognized to also form at later developmental stages (Maestripieri, 2001).

To address this, Silk, Cheney, and Seyfarth (2013) proposed indices to quantify dyadic social interactions that focused on assessing the variety of behaviours exchanged or the tone of the connection between individuals, providing indirect measures of bonding. The close bond between a mother and her infant is crucial for the offspring's survival and significantly impacts their cognitive, socio-emotional, and behavioural development (Tyler et al., 2006). Studies in humans and non-human primates have shown that this bond strongly influences an infant's sociality (Clay & De Waal, 2013). Individuals reared by their mothers exhibit lower levels of stress and greater communication skills when faced with a new environment or social partner compared to hand-reared individuals (e.g., in rodents: Mogi et al., 2011).

In addition to facilitating the development of social skills, a mother's emotional stability is essential for the survival and healthy growth of her infant (Bard, 2009; Bard & Hopkins, 2018). This close emotional attachment benefits not only the newborn – providing comfort, security, and feeding – but also the mother (Mellor, 2014). Studies have demonstrated that oxytocin, a hormone commonly known as the "bonding hormone," activates brain regions associated with reward when rats engage in nursing behaviour. This activation contributes to the positive emotions and bonding experienced by a mother towards her newborn offspring (Anestis, 2010; Mogi et al., 2011).

Maternal behaviour in primates is associated with a “positive perception of the individual's own internal state,” indicating a connection with subjective wellbeing (Ohl & Putman, 2014, p.43). The mother not only assists in the learning of social skills but also establishes an emotionally stable foundation vital for the infant's survival and proper development (Mellor, 2014). More than just assisting in the learning process of social skills, the mother sets an emotionally stable background for her infant(s) vital for its survival and proper development (Bard, 2009).

I investigate whether the quantity of bonding between parents and infants has an influence on their wellbeing (Mellor, 2015a, 2015c, 2016; Mellor & Beausoleil, 2015; Špinka, 2012), and whether an infant is a source of pleasure for the caregiver and other group members. I put a special focus on the mother-infant relationship (see Ethogram, ***TableAPP 2*** for details on the coded behaviours).

5.3.1.3 Additional Close Social Positive Behaviour

Close socio-positive engagements (Mellor, 2016) such as grooming, touching, kissing, or proximity are deemed to be directly correlated with positive welfare, reproductive success, and longevity in several animal species (Brent et al., 2011; Cameron et al., 2009; Lea et al., 2010;

Silk, 2003; Waugh & Fredrickson, 2006). Social connections foster positive emotions (McCall et al., 2010) and enhance empathy (Koski & Sterck, 2010) (e.g., contagious yawning, Liebal et al., 2014), sympathy (Campbell & de Waal, 2014) and homophily (Massen & Koski, 2014; Morton, Lee, Buchanan-Smith, et al., 2013). Positive emotions help to develop trust and harmonious relationships via similarity and conformity within groups (van de Waal et al., 2013). The measure of proximity can give us information on the relationship of the individual in the social network and in the case of an infant, it is a good measure of the strength of the relationship to their caregivers. A correlation between the reproductive success of the females and their social engagement would support previous findings (Mogi et al., 2011).

5.3.1.3.1 Proximity

Proximity is often used to analyse the social connectedness between individuals. The significance of interactions among non-human primates and maintaining proximity to other group members gives a good understanding on the social network of an individual. Proximity is often a measure of strong bonds (Silk, 2007). Friendship has been shown to provide several benefits such as social support and coalitions, fostering good emotions, decreasing feelings of loneliness, promoting higher self-esteem, improving coping strategies, reducing stress levels, instilling a sense of purpose, and influencing lifespan and infant survival (Brent, 2015; Seyfarth & Cheney, 2012; Silk, 2003). In capuchin monkeys a positive correlation has been found between the personality factor "sociability" and centrality of the social network (Morton, Lee, Buchanan-Smith, et al., 2013). A correlation has also been observed in chimpanzees between the quality of social relationships and the degree of similarity in personality traits (Massen & Koski, 2014) as well as in other animals and humans. Therefore, Chapter 6 investigates whether personality and ratings on the SWB correlate with proximity measured within our eWLGs sample, as having friends is known to be one of the best predictors of positive welfare (e.g., Massen, 2018).

5.3.1.3.2 Other Affective Social Positive Behaviour

In addition to proximity, as a proxy for positive social interaction, direct affective social positive behaviours, such as touching, kissing, or grooming, were coded (see Ethogram,

TableAPP 2) and this allows corroboration of proximity as a measure of increased social bonds.

5.3.2 Level 2: Mood - State-Dependent Behavioural Responses (s-dbr)

Emotions impact our behaviour, and steady positive emotional (pleasurable) experiences over a longer time scale can contribute to a global persistent affective state of positive mood/optimism. As described earlier, this can lead to an improvement of life conditions and satisfaction (referred to as SWB or happiness) and is linked to greater health, longevity, personality, and social factors. For example, optimists have a lower risk of heart disease than pessimists (Boehm et al., 2020). Within this context, special attention is given to play, attachment-related behaviour, such as mother-infant interactions, and additional close social positive behaviour as described above and identified as promising indicators of good animal welfare.

An understanding of the behaviour of animals in their natural habitat can be used to enhance the manifestation of natural behaviours ex situ. This practice can be beneficial in terms of increasing the chances of survival of primates that are kept as part of a breeding program and can also aid in enhancing public education. The notion that any animal welfare model within the zoo community must incorporate in situ-type behaviour has been deeply embedded since the 1950s with Hedger’s first declaration of that importance (Watters et al., 2021).

The concept that animal welfare is based on natural living proposes that animals exhibiting natural behaviours are experiencing a state of positive welfare (see D. Fraser, 2008). However, this model has been criticized primarily due to the argument that the frequency of displayed natural or in situ-type behaviours does not necessarily imply positive welfare, unless welfare is defined as the expression of natural behaviour (Hutchins, 2006; Veasey et al., 1996). This theory can be subjected to additional scrutiny as it appears to have originated from circular logic (Watters et al., 2021). It is imperative to classify a behaviour as a "need" prior to recognising its value to the individual (Howell & Cheyne, 2019). To address this, it is necessary to consider whether nature embodies a predetermined set of behaviours that ex situ management must adhere to avoid compromising the wellbeing of the animals under their supervision. The precise replication of nature by zoos is deemed impossible according to

Hutchins (2006) and so raises the question of how can we measure the extent to which ex situ settings offer conditions for adequate welfare.

To address this, I did not use a direct comparison of the activity budgets. It has been found that allocation of time to various activities among in situ conspecific groups varies in response to diverse environmental factors (Sih et al., 2015), distribution of resources (King & Landau, 2003), and group size (Schaefer & Steklis, 2014), and so the use of time budgets as a comparative diagnostic tool is complicated (Lyubomirsky, King, et al., 2005). Instead, I used the behaviours assessed in gorillas (N=24) to validate the personality structure and the subjective wellbeing questionnaire to compare the ex-and in situ personality structure of WLGs based on a wider socio-ecological comparison as shown in Chapter 2 and Chapter 4**.**

5.3.3 Level 3: Zoo Records

International Gorilla Studbook - reproductive, physical and health indicators

This section highlights the need for the International Gorilla Studbook (Wilms & Bender, 2017) to collect data on gorilla zoo records in respect to Level 3 of the four welfare measures implemented throughout the lifespan of gorillas in my multi-dimensional methodology (**Figure 21**).

In 2018, the International Union for Conservation of Nature Species Survival Commission (IUCN SSC) released its "Guidelines on the Use of Ex situ Management for Species Conservation". These guidelines aim to assist conservationists in assessing the potential benefits of ex situ management as a component of the comprehensive conservation strategy for a specific taxonomic group. In accordance with the IUCN SS Conservation Planning Specialist Group (IUCN SS CPSG), within Europe, the EAZA (European Association of Zoos and Aquaria) has introduced a new Population Management Structure in 2018. Outside Europe, AZA (American Zoological Association), WAZA (World Association of Zoos and Aquaria), BIAZA (British and Irish Association of Zoos and Aquaria) or other bodies are working independently within their regions under the guidelines of the IUCN SS CPSG.

The adapted management structure by EAZA is a comprehensive and all-encompassing assessment of EAZA's previous population management structures, considering the current range of population management activities, the requirements of EAZA members, and the changes and opportunities within the wider conservation community under the OPA. The EAZA community underwent a transitional phase to effectively execute the new Population Management framework, with a focus on three key foundations, namely: 1) Regional Collection plans (RCPs), 2) EAZA Ex situ programme application, and 3) Long-term management plans (LTMPs). Therefore, the EAZA Ex situ Programme Structure has been designed to enhance the precision of Taxon Advisory Groups (TAG) in their production of RCPs. This is achieved by enabling TAGs to more accurately assess the suitability of conservation and non-conservation roles for each taxon, and by facilitating a more detailed investigation of the genetic and demographic goals that are most appropriate for the assigned roles and situational circumstances of each taxon through LTMPs. While the development of (non)-breeding and transfer recommendations has historically been prioritised, there is a growing emphasis on other aspects that require attention. These include the collaborative development of strategies for socio-behavioural management, education, veterinary issues, banking, data gathering, and research. TAGs determine which species should be managed under an EAZA Ex situ Programme (EEP) and to establish the specific direct, indirect, and non-conservation roles of each EEP for the taxa under its authority. The RCP is the repository for this information. The authorities possess specialised knowledge and a strong passion for the group of species that is the focus of their respective TAG. Individuals employed by universities or international conservation organisations serve as TAG consultants, providing guidance on topics such as welfare, nutrition, health, and conservation. The coordination of the production of EAZA Best Practise Guidelines (BPG) for the managed taxa under the TAG's purview is a significant responsibility of the TAGs. The members of TAG are individuals who possess expertise in the field of zoology and aquarium management and are employed by institutions that are members of the European Association of Zoos and Aquaria (EAZA).

EAZA Housing and conditions of eWLGs – a historical background on the Gorilla EEP.

For the eWLGs, Kirchshofer of the Frankfurt Zoo in Germany published the first International Studbook in 1970. The EEP was founded in 1985 by zoological institutions in continental Europe. In 1992, institutions from the British Isles and Ireland also became members to the EEP. Since then, significant advancements have been achieved in the management of eWLGs. To guarantee the long-term sustainability of their ex situ populations, institutions from various locations (**Australia, Africa, Asia, and South America**) with smaller and non-self-sustaining populations **have also joined the EEP**.

As of December 31st in 2017, a total of 878 (407.470.1) eWLGs were reported to be present **across 138 institutions** within the EEP (Gorilla Studbook, 2017). Since 1991, the ex situ-born animal population has exceeded the in situ-born population due to a rise in births and deaths among the latter (EAZA BPG, , p.109).

The EEP eWLG population exhibits a high degree of genetic robustness (EAZA BPG, Abelló et al., 2017, p.109). The population's genetic variability has exceeded 98% due to the contributions of 97 founders. By implementing effective management strategies, it is possible to sustain a genetic variation of 90% for a period of approximately five hundred years (EAZA BPG, Abelló et al., 2017, p.109). The selection of breeding pairs is determined by mean kinship and the practice of breeding with genetically predominant individuals is restricted or potentially circumvented. By implementing this approach, it may be feasible to further enhance the genetic composition of WLGs' overall population (EAZA BPG, Abelló et al., 2017, p.113).

Daily records are maintained in zoological facilities regarding the health status, birth, rearing, transportation between zoos, and mortality of animals housed therein, commonly referred to as "social zoo records". Internationally, a collaborative partner Species360 serves as the governing body responsible for overseeing the Zoological Information Management System (ZIMS), an internationally used web-based database system designed to store and manage animal information for more than 1100 zoological institutions throughout the globe. ZIMS incorporates advanced internet-based technologies, data storage capabilities, and veterinary care monitoring features, facilitating instantaneous worldwide access to ex situ husbandry (zoo) and health records and is the foundation for the International Studbook. Species360 allows for joint endeavours in husbandry, healthcare, and population control within AZA, WAZA, EAZA and BIAZA and more.

5.3.4 Level 4: Subjective Wellbeing (SWB) Questionnaire and Personality

It has been proven in chimpanzees, orangutans, rhesus macaques, and capuchin monkeys that human raters can assess personality and SWB with high levels of reliability and validity (Freeman & Gosling, 2010; King & Landau, 2003; Robinson, Waran, et al., 2016; Weiss et al., 2006; Weiss, King, et al., 2011). Additionally in capuchin monkeys a welfare questionnaire was tested in combination to SWB and personality and was found to be a valid and reliable resource (Robinson, Waran, et al., 2016). This might be explained by phylogenetic generalizations from human to non-human primates using "empathic accuracy" (Ickes, 1993) or our ability to describe another person's feelings (King & Landau, 2003). It is proven that humans can reliably assess the SWB of another person (Pavot & Diener, 1993) and it requires only a moderate inductive generalization to accept that humans can also reliably assess the SWB of non-human primates (King & Landau, 2003; Weiss et al., 2006, 2008; Weiss, King, et al., 2011).

In the context of non-human animals, SWB has historically been evaluated based on the absence of abnormal behaviours and the presence of normal, species-typical behaviour in chimpanzees (King & Landau, 2003). Contemporary SWB assessments now encompass all three aspects of human happiness, as well as incorporating questions addressing the perception of SWB in animals. First, a dual-component framework encompassing both affective (comprising positive affect, negative affect, and the balance between the two). Second, a social component to overall happiness, this factor is of relevance in my study as it is about pleasurable social interactions. Third, a cognitive dimension related to life satisfaction in humans. The third factor, the amount of perceived autonomy an individual has over important life events has been identified as critical in human SWB studies due to confinement. The last factor asked how happy the rater would be if he or she were the target animal for a week (King & Landau, 2003; Weiss et al., 2006, 2008; Weiss, King, et al., 2011).

As for personality, about 50% of human happiness is influenced by genes, 10% is the result of uncontrollable factors such as birthplace and parental influence, but 40% is under the individual's control (Lyubomirsky, Sheldon, et al., 2005). Thus, while we have some control over our level of pleasure and satisfaction, over half of it is determined by circumstances beyond our control.

The measurement of SWB leads to an understanding of the enduring happiness dimension also known as eudaimonic happiness. Therefore, measuring individual emotional reaction and interactions within the group can contribute to our understanding of the evolutionary role of sociality on personality (as already shown in Chapter 4 on the genus *Gorilla*) and its impact on the eudemonic (enduring) dimensions.

5.3.5 Data Collection

Ex situ WLGs

5.3.5.1 Level 1 and 2: Emotion and State-Dependent Behaviour Response (sdb-r, Mood)

As previously stated, positive welfare encompasses survival-critical negative effects and is contingent upon achieving a balance between them, whereby the positive outweighs the negative. This perspective is supported by Mellor, (2015a, 2016, 2020), van der Harst (2003, 2005) Yeates & Main, (2008). Therefore, I included a full spectrum of positive, neutral, and negative behaviours into the data collection. Taking stress as an example, ex situ animals need to cope with their artificial surroundings and this mechanism may involve a certain degree of stress to trigger a response to an event. However, if the resulting actions are successful and lead to a positive outcome, the animal gains mastery over its environment, as per the findings of Boissy et al. (2007). As per the recommendations of Mason & Latham (2004) and Novak & Suomi, (1988), stress-related behaviours should not be considered as the only indicator of poor welfare since the lack of such behaviours may not necessarily indicate a desirable condition. Additionally, a full spectrum of gorillas behaviours is needed to validate the personality structure (Chapter 3), the SWB ratings additionally to assess positive welfare (this chapter), and to gain a better understanding of the social-ecological comparison to in situ gorillas (Chapter 4). The data collection is described in Chapter 3 and the ethogram (***TableAPP 2***) presents an overview of all observed behaviours collected on two main study groups of eWLGs (N=24).

The behaviours collected to validate SWB are described in **5.3.5.3.** Additional behaviours on observed **subjective impression on gorillas' emotional states are included in this chapters analysis on SWB, (description see below).**

Additional coding of the observer's subjective impression on gorillas' emotion and mood states

During behavioural coding, gorillas' emotions and moods (state-dependent behavioural responses, s-dbr) were systematically recorded according to the Ethogram of emotions and s-dbr, ***TableAPP 2***. The observer documented their subjective impressions of the gorillas' emotions and systematically coded the transition from one emotion to another and therefore changed them whenever the observer perceived a change in the gorilla's emotion. It will be investigated whether there is a relation between some of the coded emotions with s-dbr. For instance, is there a transition of the emotion when a change of s-dbr occurs, e.g. is a transition from walking, which might be associated with the perceived emotion neutral, to play (as a s-dbr) associated with perceived emotion, e.g. joy. This change was meticulously noted. Inter-observer reliability tests to ensure consistency across different observers were conducted prior to coding as mentioned for emotion and s-dbr coding.

This detailed recording allowed for a comprehensive investigation into the relationship between the coded perceived emotions (observer's subjective impression) and mood (s-dbr, performed behaviours of eWLGs). EWLGs' corresponding behavioural outcomes (including their change of valence, e.g. from positive to negative) can be addressed. This approach to coding provides valuable insights into how gorillas' emotional states influence their behaviours. By linking specific behaviours to perceived emotional states, researcher can better understand the emotional lives of e eWLGs and how these affect their overall wellbeing. This method also facilitates the identification of patterns and triggers for emotional changes, which is crucial for improving welfare practices both in situ and ex situ. Furthermore, understanding these dynamics can inform the development of more nuanced and effective conservation and management strategies that consider the emotional wellbeing of the animals.

5.3.5.2 Level 3: Zoo Records

Life events, veterinary and health output-related animal welfare indicators on a population and individual level (G. Mason & Veasey, 2010; Veasey, 2017), serve here as the **third assessment tool** within the thesis. The evaluation of lifetime reproductive success is conducted by YP using the International Gorilla Studbook (Wilms & Bender, 2017), which comprises comprehensive data on the present gorilla population, as well as annual statistics on birth, mortality, and relocation rates. The relationship of group structure (determined from the international Studbook on a fixed date: 31.12.2017) and measures of wellbeing is explored with the help of a regression model. Therefore, demographic information for each gorilla was obtained from the International Gorilla Studbook (2017) and additionally from the JRDavisGorillaStudBook (online database) for a total of 2,300 individual gorillas. Information extracted includes the number of infants born and survived (until age of 5 years), rearing (hand or mother), ex-or in situ born, age, sex, group composition, and transportation between zoos. However, only those eWLGs (N=203), were SWB and personality ratings are present, the Regression models were used to test the effect of group composition and homophily.

5.3.5.3 Level 4: Subjective Wellbeing Questionnaire (SWB)

The assessment of SWB in gorillas was developed by Weiss et al. (2006) and King & Landau (2003) and contained four questions displaying a 7-point Likert scale, with 1 representing either total absence or negligible amounts and 7 being extremely large amounts of the trait. For example, "Estimate the extent to which social interactions with other gorillas are satisfying, enjoyable experiences as opposed to being a source of fright, distress, frustration, or some other negative experience. It is not the number of social interactions that should be estimated, but the extent to which social interactions that do occur are a positive experience for the gorilla. Use as many social interactions that you can recall as a basis for your judgement." This rating form was used to assess ex-and in situ WLGs' SWB (Chapter 4 and 5).

Ex situ:

All gorillas who were included in the eWLG personality rating (see Chapter 3) were also included in the ratings for SWB.

Study Sites and Subjects is described in Chapter 3.4

Raters is described in Chapter 3.4

In situ WLGs:

All gorillas who were included in the iWLG personality rating (see **Chapter 4**) were included in the ratings for SWB**.**

Study Sites and Subjects is described in Chapter 4.4

Raters is described in Chapter 4.4

5.3.6 Data Analyses

5.3.6.1 SWB in eWLG

Missing data. Once 14 individuals were deleted from the full data set, 189 individuals remained for the SWB analyses. A total of 617 SWB questionnaires were collected, of which 603 were fully completed and we did not replace missing traits.

Inter-rater reliability is described in Chapter 3.4

Dimension identification is described in Chapter 3.4

The mean of all four subjective wellbeing traits were used to extract the correct number of components via PCA.

Behavioural validation of the SWB

As with personality scores, SWB scores need to be validated by behaviours to ensure ratings truly predict certain types of behaviours rather than being a measurement of anthropomorphic traits.

Validation of the GPQ in Chapter 3 and as basis of this Chapter 5, a wide range of gorilla specific behaviours was collected over a period of time and for different contextual/conceptual backgrounds to validate rating scores of the GPQ and SWB. Within-individual temporal stability (repeated behaviours over time, 6 coding spread over a three month period) as well as contextualised consistency within their ex situ environment allow the identification of individual behavioural differences, also called behaviour types or behavioural traits. It is generally accepted that coded behaviours can not only be used to identify the existence of a particular personality dimension (i.e. high level or low level) but also the expression of a personality trait (Weiss et al., 2009).

The goal is to combine measures to predict positive welfare outcomes. According to Boissy et al. (2007) and Novak & Suomi (1988), an animal's behaviour may be evaluated to establish whether it exhibits a desired behavioural profile, which includes many affiliative behaviours that indicate a happy emotional state. Robinson and colleagues (2016) found that capuchins

(*Cebus apella*) who exhibited personality traits of “Sociability” and “Attentiveness” were linked to elevated welfare scores. Their study revealed that individuals who scored as more sociable had higher welfare rankings compared to those who were not as sociable, suggesting that animals with improved welfare exhibit a greater prevalence of specific personality traits. This observation may provide a potential avenue for quantifying elevated levels of affiliative behaviours. Affiliative behaviours like play (as discussed earlier) are typically observed only when an animal's basic physiological needs have been satisfied. Therefore, the coded social positive emotional interactions, such as play, parental-infant behaviour, and close positive affective engagement in addition to long-term zoo records have been assessed to provide evidence of convergent validity between ratings on personality and the SWB (see Chapters 3 and 5).

As explained in detail in chapter 5.3.4., the goal within this chapter is to address a multi-dimensional approach, an additional coding of the observers’ subjective impression on gorilla’s emotion and positive and negative moods states (s-dbr) have been included into this chapter.

The validation of the SWB rating have been done multi-faceted. See below in zoo records additionally analyses on “friendship” and group composition, which are conducted via regression models.

First, I tested for correlations using bivariate correlations, two-tailed Pearson’s r for normal distributed data and Spearman’s rank for non-normally distributed data, between the observed emotions, s-dbr, SWB and personality factors. The issues of mitigating the risk of Type I errors was addressed in (Chapter 3.3). Therefore, coded emotions, data on positive and negative affect, another level of proximity (contact-resting with body contact instead of close proximity), and other behaviors, such as mother-infant behaviours were used to address the research questions without repeating behaviors multiple times. I also used single behaviours instead of building categories. Only play and proximity behavior were used repetitively, but combined for other distances, in terms of proximity or whithin play, other categories have been choosen.

In addition, I used regression models to test the effect on group composition (based on data from Studbook) and friendship (based on proximity, measured via s-dbr). The rated personality and SWB scores of the extracted personality structure (**see Chapter 3),** and individual SWB ratings were used. This approach accounted for non-independence by including random effects to model the data structure properly, incorporating sex and age differences.

The extraction of sociality trait constructs for the cross-great apes' personality structures is described in Chapter 3.4. R script is in Supplementary materials.

Zoo records: International Studbook:

I gathered information on group composition, transfers between zoological facilities and breeding success from the International Studbook (Wilms & Bender, 2017) and conducted the following tests:

The estimation method was maximum likelihood estimation (MLE) and analyses included all gorillas from the ex situ dataset (N=189 gorillas). SPSS was used to run the analysis. The analysis made use of multilevel modelling with the gorilla characteristics included as fixed effects and the zoo specific effects included as random intercepts.

Effect of group composition on SWB

Within the Regression model, the effects of the following gorilla characteristics on happiness were tested:

- Age
- Sex
- Age and sex interaction
- Group size and composition (number of unrelated gorillas, parents, siblings, infants etc.- including the total number, yes/no dummies, and ratios)
- Whether the gorilla has been transferred from in situ conditions, number of transfers from ex situ conditions etc.
- Rearing
- Breeding group

The dependent variables were:

- Mean of moods

Testing for social preferences

Based on the same analyses described in Massen and Koski (2014), the difference between each personality factor score and of SWB (this is a novel approach) was calculated for all dyads in each location (N=24 gorillas, from two groups (see description of locations and group members in Chapter 3. Resulting in 136 dyads). Therefore, the similarity in personality for each pair was calculated by measuring the absolute difference between the personality scores of both gorillas.

The percentage of **time** that each dyad spent in social proximity (based on observed behavioural data, described in Chapter 3) was calculated and each dyad was ranked for both personality similarity and time spent in proximity, and the relationship tested using Spearman's ρ.

Homophily: Similarity in personality using proximity/friendship.

The analysis made use of multilevel modelling (MLE) with the gorilla characteristics included as fixed effects and the zoo specific effects as well as each gorilla's specific effects (for the two gorillas included in the dyed) included as random intercepts.

The analysis included the information gathered from the ex situ Studbook dataset. The dataset was constructed so that each pair of gorillas belonged to the same zoo and group, and thus could interact creating a dyad. Dyads consisting of all mothers and infants (maternal kinship) were excluded from the analysis.

A Regression model was used in SPSS to analyse the effect of the following gorilla characteristics on friendship:

- Age difference
- Sex difference (whether gorillas are same or different sex)
- Degree of relatedness
- Differences in the personality structure on each of the six personality factors (extracted using EFA, Chapter 3)
- Happiness variables (one overall mean of the SWB traits)
- Interactions between the relatedness and the happiness variables
- Interactions between relatedness and the differences in the personality traits

The dependent variables were Ln(sociability)- the natural logarithm was used for the distribution of the sociability to resemble more a normal distribution.

- The unit of analysis was gorilla dyads (a couple) as opposed to an individual as in the previous analyses

5.3.6.2 SWB in iWLG

Study Sites and Subjects is described in Chapter 4.4.

Raters is described in Chapter 4.4.

Missing data. Once 14 individuals were deleted from the full data set, 189 individuals remained for the SWB analyses. A total of 617 SWB questionnaires were collected, of which 603 were fully completed and we did not replace missing traits.

Inter-rater reliability is described in Chapter 4.4.

Dimension identification is described in Chapter 4.4

The mean of all four subjective wellbeing traits were used to extract the correct number of components via PCA.

Behaviour correlations with personality and SWB. is described in Chapter 4.4.

5.4 Results

5.4.1 Ex Situ WLGs

Missing data. No missing data were shown in 603 SWB questionnaires, see above data collection for more information.

Inter-rater reliabilities for SWB traits. None of the traits were rejected based on the ICCs 0 criterion (references in Chapter 3). The trait reliability ICC (3,1) of the SWB traits reached from .44 (Goals) to .49 (BeGorilla), respectively and therefore, all four traits have been reliable. The ICC (3,k) represents values ranging from .72 (Mood) to .76 (BeGorilla), respectively of a total of 603 ratings from 84 raters.

Extraction of the SWB structure

A PCA extracted a single component (adjusted eigenvalue 2.66). The mean score for all four SWB traits (M_{Mood}=4.90, SD_{Mood}=.95; M_{SocInt}=4.55, $SD_{SoclInt=}$1.06; M_{Goals}=4.87, SD_{Goals}=1.02; $M_{BeGorilla}$=4.63, $SD_{Begorilla}$=1.10) was calculated per individual (SWB_{Mean}=4.74, SD_M=1.03).

The SWB factors correlated in **Table 26** have been highly correlated, therefore I constructed the mean per gorilla of SWB = $SWB_{Mean.}$

Table 26 *Correlation between the SWB factors*

	Mood	**Soc_{Int}**	**Goals**	**$Be_{Gorilla}{}^a$**
Mood		.70	.60	.80
Soc_{Int}	.70		.60	.70
Goals	.60	.60		.70
$Be_{Gorilla}{}^a$	.80	.70	.70	

Note.
Column 1: Moods= the extent to which the gorilla is in a positive mood, Soc_{Int} = the extent to which social interactions are satisfying to the gorilla, Goals = the extent to which the gorilla is successful in achieving its goals, $Be_{Gorilla}$= the extent to which the rater would like to be a particular gorilla.
Factors: ^{a} = normally distributed.

Correlation between SWB and Personality

To test for correlations between SWB_{Mean} and personality factors generated in Chapter 3 for eWLGs a spearman test was conducted (see **Table 27**).

Table 27 *Correlation between Personality and* $\textit{SWB}_{\textit{Mean}}$ *(N = 189) in eWLGs*

Happiness	$\textbf{Dom}_{\textbf{eWLG}}$	$\textbf{Opn}_{\textbf{eWLG}}^{\textbf{a}}$	$\textbf{Con}_{\textbf{eWLG}}^{\textbf{a}}$	$\textbf{Agr}_{\textbf{eWLG}}^{\textbf{a}}$	$\textbf{Neu}_{\textbf{eWLG}}$	$\textbf{Ext}_{\textbf{eWLG}}$
$\textbf{SWB}_{\textbf{Mean}}$	.33	.57***	.54**	.62***	-.38	.62***

Note:
Column 1: SWB_{Mean} = the mean of the four subjective well-being scores.
Column 2- 6: We used the personality structure generated via $\text{FA}_{\text{minres.v}}$ (6 factors) as basis of our personality correlations. Factors: Dom_{eWLG} = Dominance, Ext_{eWLG} = Extraversion, Con_{eWLG} = Conscientiousness, Neu_{eWLG} = Neuroticism, Opn_{eWLG} = Openness, Agr_{eWLG} = Agreeableness/ Sociability.
Factors: ^{a} = normally distributed.
Bold font indicates significant correlations *p< .05, ** p< .01 *** p < .001, Pearson's correlation reported.

As represented in **Table 27**, Opn_{eWLG}, Con_{eWLG}, Agr_{eWLG} and Ext_{eWLG} were positively correlated with $\textbf{SWB}_{\textbf{Mean.}}$

Correlations between Emotion (observer's subjective impression on gorillas' emotion) and Mood in eWLGs.

Table 28 includes listed correlation between emotion (Column 1, observer's subjective impression on gorillas' emotion), mood (sdb-r) and SWB_{Mean}, (both in Column 2) in eWLGs, which have been found to be significant to p<.05. The result of this correlation is represented in the Appendix (***TableAPP 11***). Listed behaviour in red are negative correlations, black are positive correlations between the listed variables. The listed behaviours allow for an easier overview of the correlations between the variables. Full list of the Ethogram can also be found in Appendix (***TableAPP 2***).

Table 28 *Significant correlations between Emotions (observer's subjective impression on gorillas'emotion), Mood (sdb-r) and* SWB_{Mean} *(longer-term persistence behaviour) eWLGs (N=24)*

Emotions	**Correlations shown with mood (sdb-r),** SWB_{Mean}
Anger (revenge)	Contactagg^{f}, Mdetach^{f}
Anxiety	-Contactr^{f}, Feeding, Holdong, Iantg, Icarry^{f}, -Mpsy^{g}, Negative-affect^{f}, Watch-attentively
Boredom	Follow^{g}, Grab, -M-failure-to-response, Shareatt^{f}, Start-focal, Watch-other
Contentedness	-Grab, -Iant, -Icarry^{g}, -Iseek^{f}, -Mdetach, More, Passby^{g}
Curiosity	Between, Close, Displace^{g}, Holdon^{g}, -Iant^{f}, Leave, -Mdetach^{g}, Mpsy^{f}, Nose-touch, Proxi-till-1.5, Proxi-till-5m,
Empathy	N/A
Excitement	Chestbeat, Feeding, Foodman, Gentleplay, Gentile^{f}, Icarry^{f}, Inactive, Join-play, Join^{g}, Locomotion, More, -Mpsy,
Fear	Passby^{f}, -Prosocial-positive^{g}
Frustration	-Beg^{f}, -Contact, -Contactrest, Feeding, -Follow^{f}, -Groom^{g}, -Ianticipation, -Icarrying, -Icarry^{f}, -M-Failure-to-
Gentle	N/A
Gratitude	N/A
Inspiration	N/A
Jealous	Start-focal, Snoutbrush
Joy	Beg^{f}, Contact^{f}, -Displace^{f}, Follow^{f}, Foodman, Gentileplay, Gentile^{f}, Groom^{g}, Holdon^{f}, -Iant^{g}, Inactive, Join-play,
Love	Contact, Follow^{f}, Groom^{f}, Groom^{g}, Holdon^{f}, Anticipation, Icarrying, Itravels, independent, M-Failure-to-
Pride	N/A
Sadness	Iseek^{g}, Mcon^{g}, Shareatt^{g},
Sensitive	Itray^{f}, M-failure-to-response, Mfail^{g}
Sympathy	N/A
Tenderness	-Feeding, -Inactive, -Leave, -Negative-affect^{f}
Restless	N/A
SWB_{Mean}	Emotions: Joy, Curiosity, Excitement; Mood: Proximity (close and between 5-10m), Chestbeat, Follow^{f} , Play,

Note:
Column: 1: List of coded emotions (Level 1) during observations and last row: SWB_{Mean}
Column 2: Listing of correlated behaviours (mood, longer (state-behavioural response), Level 2).
I=Infant; M=Mother. ^{f}=received behaviours, ^{g}=performed behaviours. negative correlation, red text.

Correlation between Emotion, SWB_{Mean} and personality factors in eWLGs

Same list of coded emotions (Column 1, **Table 29**, observer's subjective impression on gorillas' emotion) are correltaed with the Mean of the SWB and all six personality factors generated for eWLGs in Chapter 3.

Table 29 *Correlations between Emotion,* SWB_{Mean} *and personality factors in eWLGs (N= 24)*

Emotions	$\mathbf{SWB}_{\mathbf{Mean}}$	$\mathbf{Dom}_{\mathbf{eWLG}}$	$\mathbf{Opn}_{\mathbf{eWLG}}^{\mathbf{a}}$	$\mathbf{Con}_{\mathbf{eWLG}}^{\mathbf{a}}$	$\mathbf{Agr}_{\mathbf{eWLG}}^{\mathbf{a}}$	$\mathbf{Neu}_{\mathbf{eWLG}}$	$\mathbf{Ext}_{\mathbf{eWLG}}$
Anger	-.26	.23	-.29	-.32	-.35	.20	-.20
Anxiety	-.28	-.02	-.17	-.31	-.05	-.11	.08
Boredom	-.34	-.02	.11	-.35	-.07	-.05	.02
Contentedness	.39	.25	.24	.37	.27	-.08	.24
Curiosity	$\mathbf{.58{*}{*}}$	$\mathbf{.52}^{*}$	.19	.22	$\mathbf{.50}^{*}$	-.34	$\mathbf{.42}^{*}$
Excitement	$\mathbf{.42{*}}$	.09	$\mathbf{.59}^{**}$	-.06	.38	.10	.28
Fear	-.38	-.23	$\mathbf{-.41}^{*}$	-.30	-.35	.30	-.28
Frustration	.13	.21	.19	-.12	-.08	-.25	.22
Jealous	-.12	-.01	.10	-.17	.02	-.05	.04
Joy	$\mathbf{.50{*}}$	-.03	$\mathbf{.72}^{**}$	.19	.33	.11	.35
Love	.15	-.06	-.09	.22	.26	.07	.04
Sadness	-.31	-.29	-.27	-.01	-.24	-.06	$\mathbf{-.41}^{*}$
Scratch	-.11	.09	-.07	-.35	-.11	.04	-.40
Tenderness	.04	.08	-.08	.36	-.02	.27	-.04
Restless	.11	-.05	.10	.14	-.07	$\mathbf{-.53}^{**}$	.55

Note:
Column: 1: List of coded observer's subjective impression on gorillas' emotions during observations.
Column 2: SWB_{Mean} = the mean of the four subjective well-being scores.
Column 3- 6: We used the personality structure generated via $\text{FA}_{\text{minres.v}}$ (6 factors) as basis of our personality correlations. Factors: Dom_{eWLG} = Dominance, Ext_{eWLG} = Extraversion, Con_{eWLG} = Conscientiousness, Neu_{eWLG} = Neuroticism, Opn_{eWLG} = Openness, Agr_{eWLG} = Agreeableness/ Sociability.
Factors: ^{a} = normally distributed.
Bold font indicates significant correlations $*p< .05$, $** \; p< .01$ $*** \; p < .001$, Pearson's correlation reported.

Only the factor Conscientiousness did not show any correlation to the observer's subjective impression on gorillas' emotion as described in the Ethogram in ***TableAPP 2***.

Effects of sex and age differences on SWB$_{\text{Mean}}$.

SWB$_{\text{Mean}}$ factor was compared between gender and according to age (more information on number of females, males and age classes can be found in Chapter 3, **Table 3**. The results of the linear regression using z-score are included in **Table 30**, below.

Table 30 *Age, Sex and Age x Sex Differences on SWB$_{Mean}$ in eWLGs (N=162)*

Factor	Tested effect	b	SE$_b$	T	p
SWB$_{\text{Mean}}$	Age	-.02	.00	-4.65	< .001***
	Sex	.10	.14	.67	.02
	Age x Sex	-.00	.01	-.18	.85

Note.
b = unstandardized linear regression coefficient
SE$_b$ = SE of linear regression coefficient
t = t value
p = correlation coefficient, bold font indicates significant

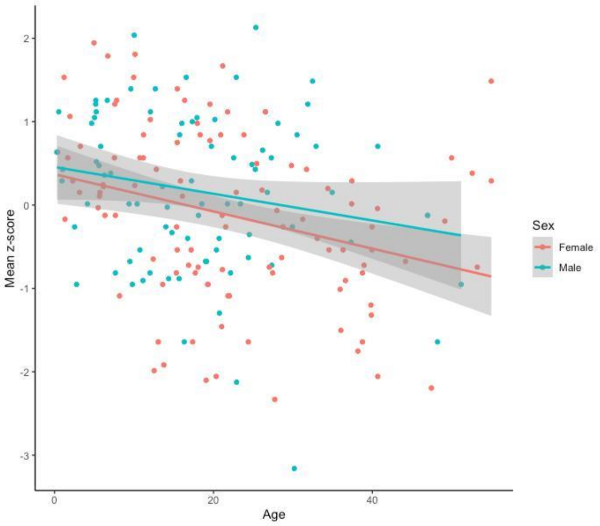

Figure 18 *Sex and age effect on SWB$_{Mean}$ in eWLGs*

Note.
Score distribution of female (red) and male (blue) on the SWB$_{\text{Mean}}$ factor presented by eWLG age.

A significant negative age effect on SWB$_{\text{Mean}}$ is shown in **Figure 18.** No differences between genders were found to be significant on the SWB$_{\text{Mean}}$. Addition, no effect of age x sex interactions was observable.

Zoo records: Analysis on the International Studbook in relation to SWB_{Mean}

To test whether social companions (social effect) have an effect on happiness, the influence of group composition (total number of gorillas in the group), the effect of relatedness (sibling, half-sibling, kins, parents, infant), living in a breeding group vs. bachelor group, transfers from in situ to ex situ and total number of transfers are tested in the Regression below.

Table 31 *Linear Fixed-Effect Models on eWLGs' SWB$_{Mean}$ (N=162)*

	b	**95%**	**Cl**	**p**	**b**	**95%**		**p**	**B**	**95%**	**Cl**	**p**	**b**	**95%**	**Cl**	**p**
Intercept	.49	.08	.90	.02	.90	-.00	1.80	.05	2.58	1.23	3.93	.00	2.55	.89	4.21	.00
[Sex=0=]	-.01	-.50	.48	.97	-.08	-.57	.40	.74	-.10	-.60	.40	.69	-.06	-.57	.45	.82
Age	-.02	-.03	.00	.08	-.01	-.03	.01	.40	-.01	-.03	.01	.24	-.01	-.04	.02	.25
[Sex=0] * Age	-.01	-.03	.01	.37	-.01	-.03		.41	-.01	-.03	.01	.49	-.01	-.03	.01	.46
[sibling_dummy=.00]					-.00	-.40		.99	-.08	-.46	.33	.74	-.05	-.45	.35	.80
[half_sibling_dummy=.00]					.20	-.20		.34	-.01	-.42	.41	.98	-.03	-.46	.39	.89
[kins_dummy=.00]					-.13	-.58		.56	-.27	-.71	.18	.24	-.27	-.72	.19	.25
[parents_dummy=.00]					**-.70**	**-1.12**		**.00**	**-.84**	**-1.29**	**- .39**	**.00**	**-.86**	**-1.31**	**-.40**	**.00**
[infants_dummy=.00]					-.14	-.46	.18	.41	-.37	-.72	-.02	.04	**-.39**	**-.74**	**-.02**	**.04**
related_ratio					.23	-.38	.84	.44	-.19	-.89	.52	.60	-.20	-.90	.52	.58
Total nr of eWLGs in the group									**-.13**	**-.21**	**-.05**	**.00**	**-.13**	**-.21**	**-.05**	**.00**
[breeding_dummy=.00]									-.23	-.82	.36	.45	-.20	-.79	.40	.52
[rearing_dummy=.00]													.00	.31	.33	.99
[transferdfromthewild=0]													.00	-.55	.55	.99
Total Transfer wild, loan to													.06	-.12	.24	.52

Note.

N = 162 gorilla, bold font indicates significant correlations at p < .05.

Column: Column 1, Information on group composition and transfers is gathered from the International gorilla Studbook (2017): sex; age; sex*age; number of siblings; number of half-siblings; number of kins; number of parents (none, only father, both, only mother); total number of infants living in the group; number of unrelated gorillas; group size = total number of gorillas living in the group; breeding group = mixed-sex group vs. bachelor group; status of rearing; number of transfers = total number of transfers, including also loan to, from the wild; transferred from the wild.

1st model: sex, age, and the sex x age interactions.

2nd model included the 1st and in addition relationship/social support.

3rd model included the 2nd and in addition effects such as group specifics (group size/ breeding).

4th model included the 3rd and in addition effects such as transfer or rearing. Zoological facility was included in all four models as a random effect.

The Linear Fixed-Effect Models on eWLGs' SWB_{Mean} as shown in **Table 31** demonstrates that eWLGs' SWB scores are higher when they live either together with their parents (in all 4 models) or offspring (4th model), and in smaller groups (3rd and 4th model).

In the wild, the average group size is 9.2 and undergoes permanent flexibility within a female choice system. In eWLGs setting, the Studbook decides on group size and combination of group members.

Homophily: Dyadic Similarity in personality and its relationship with proximity/friendship

Correlation between ranked personality similarity/homophily and social preference (proximity)

Table 32 shows the result on the correlation of time spent together (proximity, ranked) and ranked personality similarities of the 136 dyads in eWLGs.

Table 32 *Correlation between Ranked Personality Similarity and Ranked Social Preference in eWLGs (N=136)*

Spearman	**Dom_{eWLG}**	**$Opn_{eWLG}{}^{a}$**	**$Con_{eWLG}{}^{a}$**	**$Agr_{eWLG}{}^{a}$**	**Neu_{eWLG}**	**Ext_{eWLG}**	**SWB_{Mean}**
Time together	-.17	-.14	-.07	**-29****	.05	-.14	**-.22***

Note:
Personality structure is generated via $EFA_{minres,v}$ (6 factors) as basis of our personality correlations with behavioural data.
Factors: Dom_{eWLG} = Dominance, Opn_{eWLG} = Openness, Con_{eWLG} = Conscientiousness, Agr_{eWLG} = Agreeableness; Neu_{eWLG} = Neuroticism, Ext_{eWLG} = Extraversion.
SWB_{Mean} = the mean of the four subjective well-being scores.
N = 136 dyads.
Bold font indicates significant correlations *p< .05, ** p< .01 *** p < 0.001, non-parametric.

The factors Agr_{eWLG} and SWB_{Mean} showed positive correlations with ranked social preferences in eWLGs.

Summary of findings for ex situ WLGs multi-dimensional approach to positive welfare based on individual differences and SWB.

Below, I introduce a matrix on the core welfare measurer **Figure 19** and refer to the highlights in the Figure. **Figure 15** of Chapter 3 is used as the groundwork of **Figure 21**, with the personality structure (Level 4) and the correlated behaviours (Level 2), such as play, attachment behaviours, and close social contacts as shown earlier, which leading to optimism or pessimism on a longer state (mood).

Figure 15, Chapter 3 extended with additional findings from the multi-dimensional approach and includes measured **emotions** (level 1, hedonic short lived happiness, such as joy, love, fear or anger), as well as the overall **life satisfaction measure** (Level 4, eudemonic concept of happiness (SWB), measured via the **SWB** questionnaire, with high and low overall life satisfaction). The overall correlations between Levels 1, 2, 3 ,4 and the effects on happiness (such as group composition, friends) underpin this multi-dimensional model.

The arrow represents the direction of increased positive welfare.

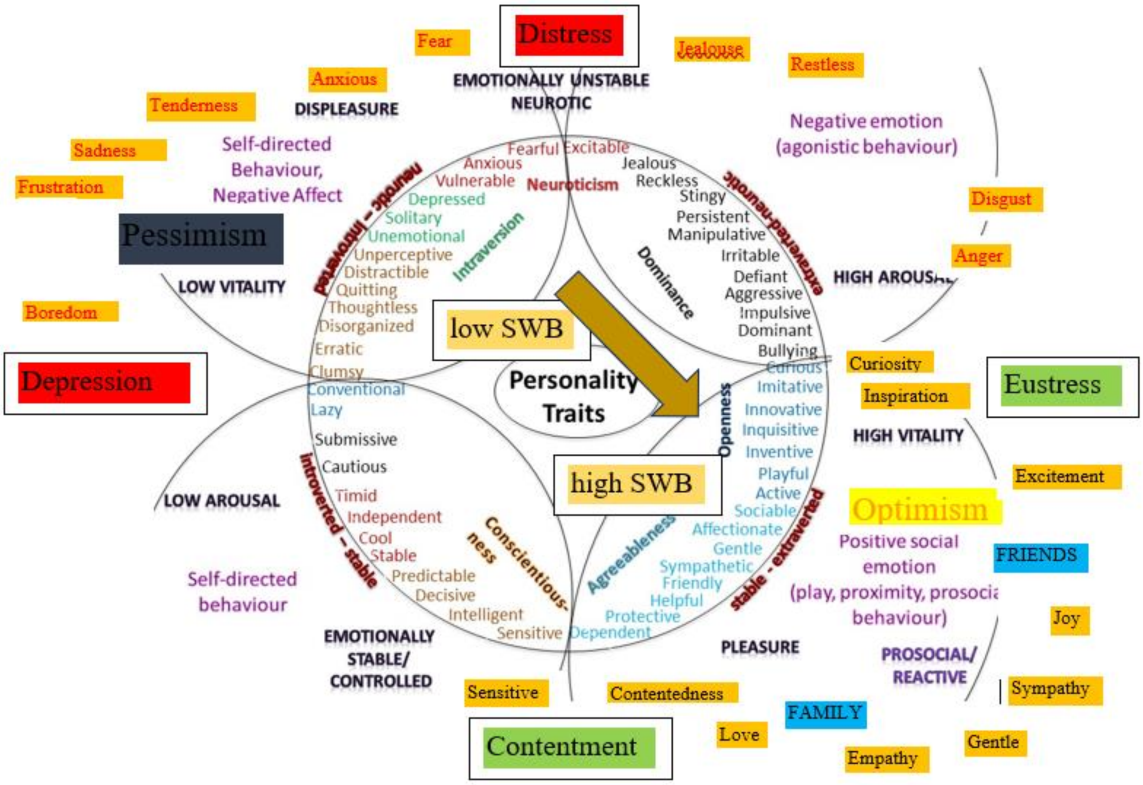

Figure 19 *Matrix of the core welfare space, ranging from emotions via mood to zoo records and personality/ SWB differences*

Note.

Within the matrix, all four welfare measures (Emotion (Level 1), Mood (Level 2), Zoo records (Level 3), Personality and SWB (Level 4) are interlinked (see **Figure 17** and **Figure 21**.

Inside the circle, the personality traits (52, as identified in Chapter 3 in eWLGs) are listed in accordance with their personality factors on the axes, ranging from a) HIGH to LOW AROUSAL, b) PLEASURE to DISPLEASURE, c) HIGH to LOW VITALITY d) STABILITY to INSTABILITY. The personality traits are colour coded as described in Chapter 3 in accordance with their personality factors. The arrow represents the direction of welfare improvement (low and high), between eustress and contentment, towards an optimistic state and short-term positive emotions lived, including social positive needs the gorilla needs the gorilla has to have a happier life (having friends and family (parents or infants in the group).

The further we go from the inside (from personality and SWB measure, which are consistent in time and context) to the outside of the matrix to short lived emotions (expressions, such as joy or love), as more short lived the welfare measures becomes and as more flexible the reaction will be (emotions=short lived) and changeable (in contrast: personality and SWB=consistent overt time and context).

Now starting from outside to inside to increased consistency and persistency, but there is still some flexibility within the system (e.g, on the level of the personality, see Chapter 3 and Chapter 4):

1) Core Emotions (**Level 1**) have the capacity to undergo rapid changes, normally, reverting (bouncing) back to the prevailing emotional state (**mood, Level 2**, optimism, or pessimism), that an individual more persistently experiences. Therefore, what needs to be mentioned is that the whole model undergoes temporal fluctuation, depending on where the gorilla in the matrix is. Meaning, his mood and what kind of personality and SWB (**Level 4**) he is underlying, plus the socio-ecological factors the gorilla is dealing with.
2) Mood - the Level (2) of welfare within the longer-term affective states – as an example: The mood gives information on whether an individual remains in a **certain emotional state for a longer period** and where it usually bounces back to after experiencing short lived emotions. Mood states may be seen as manifestations of the predominant region within a matrix in which gorillas remain most of their time. It is noteworthy to state that mood states have a significant impact on their perception (optimism or pessimism). This means that the mood is determining whether and how an individual react on certain stimuli, and whether the gorilla see a "red flag," such as danger and will react accordingly, or whether the gorilla for instance reacts positively, e.g., in terms of social response, when an unknown gorilla or human is spotted. Moods can alter both, the perceptions and subsequent behaviours. I propose that there is the capability to assist gorillas in altering their emotional states (mood) by modifying their behaviour. It is worth noting that the shifting takes time, it is part of a learning process.
   The mood state can either be measured via cognitive/ judgment bias tasks or observing behaviours over a longer period to see whether the expressed behaviour remains within his core area for longer. Optimal would be if the gorilla's mood remains in a more optimistic state (see arrow). The assessment of wellbeing may be conducted in relation to extended exposure to various emotional states or being confined inside a certain region of the core effect space in such instances.
3) Social positive relationships (**Figure 21**, Level 1 and 2), and zoo records of social events (of longer-term: friends or family (measured via Level 3), are positively associated with happiness/ wellbeing on both ends (hedonic, via the expressions of emotions (Level 1), or eudaimonic, via life-satisfaction outcomes (Level 4, SWB). Sociability was identified to be key for happiness and personality.
4) As mentioned in Chapter 1, 4,5 and here, personality and SWB can be measured on the ultimate and proximate level and for an individual's welfare, optimal welfare (Veasey, 2017). Therefore, it is important to improve SWB, and increase welfare based on individual differences.

The overall goal of the OPA is to improve the survival of the species and therefore, the level of the proximate and the ultimate level personality plays a key role.

The little images within the mosaic **Picture 25** in the title represents the positive state-depending behavioural response – from mother-child interactions, friendship, close-contact behaviours and play as well other known pleasurable experiences as the fundament of the laughing facial expression of the gorilla male on the foreground. An increase in those short-term (hedonic) expression is linked to increased mood states (optimism) and leading to long-term happiness (eudemonic level of happiness). The positive welfare concept on the ex situ population is key to underpin the overall goal in the OPA and can also be used for in situ gorillas, as they also facing welfare issues.

- ⇨ Sociability is key to happiness and personality and is linked to in situ welfare and conservation.

5.4.2 In Situ WLGs

Missing data. From the 189 iWLGs, 166 gorillas remained in the further analyses. 29 gorillas were single rated and were excluded from the analyses, the remaining three had to be exluded in respect of the data in the questionnaire.

Inter-rater reliabilities for SWB traits. None of the traits were rejected based on the ICCs 0 criterion (references in Chapter 3). The trait reliability ICC (3,1) of the SWB traits reached from .20 ($\mathrm{Soc}_{\mathrm{Int}}$) to .38 (Goals), respectively and therefore, all four traits have been reliable. The ICC (3,k) represents values ranging from .38 ($\mathrm{Soc}_{\mathrm{Int}}$) to .60 (Goals), respectively of a total of 603 ratings from 84 raters.

Extraction of the SWB structure. A PCA extracted a single component (adjusted eigenvalue 2.35). Same as for eWLGs, see above.

In the following section, the correlations to SWB are presented:

Correlation between SWB and Personality

Table 33 shows the correlation between $\mathrm{SWB}_{\mathrm{Mean}}$ and the personality factors of iWLGs.

Table 33 *Correlation between Personality and SWB (N = 162)*

Happiness Factor	**$\mathrm{Neu}_{\mathrm{iWLG}}$**	**$\mathrm{Soc}_{\mathrm{iWLG}}{}^{a}$**	**$\mathrm{Dom}_{\mathrm{iWLG}}{}^{a}$**	**$\mathrm{T\text{-}SC}_{\mathrm{iWLG}}{}^{a}$**
$\mathrm{SWB}_{\mathrm{Mean}}$	-.46**	.18**	.18	-.18

Note:
Bold font indicates significant correlations *p< .05, ** p< .01 *** p < .001
Column:
Column 1: $\mathrm{SWB}_{\mathrm{Mean}}$ = the mean of the four subjective well-being scores.
Column 2- 5: We used the personality structure generated via $\mathrm{FA}_{\mathrm{minres.v}}$ (4 factors) as the basis of our personality correlations. Factors: $\mathrm{Neu}_{\mathrm{WLG}}$ = Neuroticism, $\mathrm{Soc}_{\mathrm{iWLG}}$ = Sociability, $\mathrm{Dom}_{\mathrm{iWLG}}$=Dominance, $\mathrm{T\text{-}SC}_{\mathrm{iWLG}}$ = ToleriWLG/ Self-Control.
Factors: ^{a} = normally distributed.
Bold font indicates significant correlations *p< .05, ** p< .01 *** p < .001, Pearson's correlation reported.

Two personality factors ($\mathrm{Neu}_{\mathrm{iWLG}}$ and $\mathrm{Soc}_{\mathrm{iWLG}}$) showed significant correlation to the happiness factor ($\mathrm{SWB}_{\mathrm{Mean}}$).

Correlation between SWB and behaviours

In **Table 34**, in order to validate the Happiness factor ($\mathrm{SWB}_{\mathrm{Mean}}$) I used observational data of N=124 iWLGs. Prescription of behaviours and categories are listed in Chapter 4.

Table 34 *Correlation coefficients between the Happiness factor (SWB_{Mean}) of iWLGs and behavioural measures (N= 124) using Spearmans's rank correlation*

Behaviour	**$\mathrm{SWB}_{\mathrm{Mean}}$**
Agonism[b]	**.29****
Activity[b]	**.28****
Approach[b]	**.20***
Vigilance[b]	**.23***
Submissive behaviour[b]	**.18***
Sexual behaviour[b]	.16
Playing[a]	**.27****
Affiliative behaviour[a]	**.31****
Mother-infant Affiliative behaviour[a]	-.02

Note.
Bold font indicates significant correlations *p< .05, ** p< .01 *** p < 0.001
[a] Focal individual coded as either actor or recipient. [b] Focal individual coded as actor (behavioural performed).
Column 1: Behaviour Categories: All behaviours were recorded as ad libitum sampling and the frequency of the occurrence of the behaviour was divided by the total number of days the individual was observed between 2013 and 2016. MI=Mother-Infant.
Column 3: $\mathrm{SWB}_{\mathrm{Mean}}$= Mean of the four SWB factors.

The selected behaviours validated the $\mathrm{SWB}_{\mathrm{Mean}}$ and showed significant correlations with all, but not two, behaviours. Surprisingly, no correlation was found to Mother-infant affiliative or sexual behaviour.

Effects of sex and age differences on $\mathrm{SWB}_{\mathrm{Mean}}$ in iWLGs

The effect of gender and age classes (according to age classes in Chapter 3, **Table 8**) was tested with the linear regression using t-score (result see **Table 35** below).

Table 35 *Age, Sex and Age x Sex Differences on SWB_{Mean} in iWLGs (N = 162)*

Factor	**Tested effect**	**b**	**SE_{b}**	**T**	**p**
$\mathrm{SWB}_{\mathrm{Mean}}$	Age	-.02	.00	-4.65	< .001***
	Sex	.10	.14	.67	.02
	Age x Sex	-.00	.01	-.18	.85

Note.
b = unstandardized linear regression coefficient
SE_{b} = SE of linear regression coefficient
t = t value

p = correlation coefficient, bold font indicates significant

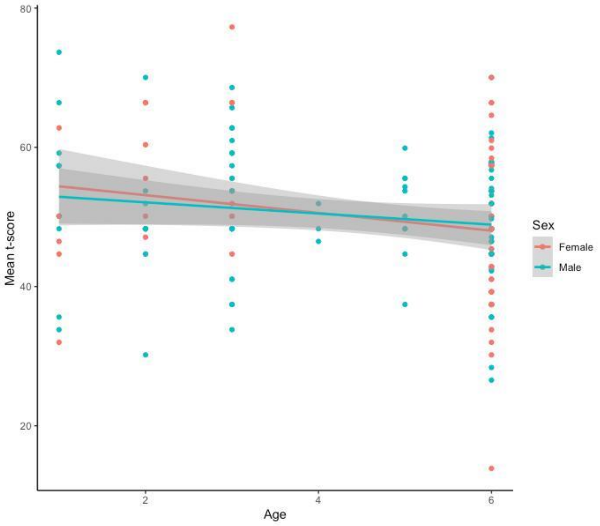

Figure 20 *Sex and age effect on SWB_{Mean} in iWLGs*

Note.
Score distribution of female (red) and male (blue) on the SWB_{Mean} factor presented by iWLG age categories (according to **Table 12**, Chapter 4, see also description in the text on **Table 11**).

Significant effects on age (**Table 20**) is found for $SWB_{Mean.}$ In both genders, SWB_{Mean} shows a slight downward trend, indicating that SWB_{Mean} decreases marginally with age, whereas males remain a bit higher as females overall in age, but starting a bit lower as infants.

The Sociality Trait Constructs for Great Apes' Personality Structures.

Using Fuzzy Set Analysis, the membership of the traits between the personality factors of different great ape species (ex situ bonobos: (Weiss et al., 2015), humans: (Weiss, 2022), ex situ orangutan: (Weiss, Adams, & King, 2011), Virunga mountain gorilla: (Eckardt et al., 2015), ex situ chimpanzees: (Weiss et al., 2009), eWLGs and our in situ data) is compared. The extracted sociality construct gives a fuzzy set of social traits generated across *Hominidae*'s. The generated constructs built appropriate upper-order social personality dimensions as found for Macaques species (Adams et al., 2015).

TableAPP 12 represents the cut-off points generated via permutation test (Adams et al., 2015).

Table 36 shows the results of the upper-order of the generated social constructs (DOM$_{soc}$, EXT$_{soc}$, NEU$_{soc}$, OPN$_{soc}$, AGR$_{soc}$, and CON$_{soc}$). A trait was loaded into the dimension with the highest overall loading, and the cut-off point determined whether the trait remained in the dimension or needed to be deleted. If a trait was represented in different dimensions with the same value, they remained in the stronger dimension (from DOM$_{soc}$ to CON$_{soc}$) or otherwise in the dimension with the highest overall value.

Table 36 *Sociality personality construct of Great Apes analysed via Fuzzy Set Analysis*

DOM$_{soc}$	**Dom**	**Defn**	**Aggr**	**Errc**	**Unper***	**Pers**	**Sub**	**Indp**	**Pred**
	.88	.31	.25	-.25	-.25	.24	-.23	-.20	-.17
	Sens	Stngy	Gntl	Reckl	Irri				
	.15	-.13	.11	-.09	-.08				
EXT$_{soc}$	Soc	Affc	Frdy	Invt	Actv	Depd	Play	Indp	
	.34	.32	.22	.22	.21	.20	.20	-.17	
NEU$_{soc}$	Indp	Depd	Stbl	Dsor	Defn	Depr	Irri		
	-.26	-.22	.17	.12	-.11	-.08	-.08		
OPN$_{soc}$	Imit	Exct	Impl	Invt					
	.19	.27	.12	.10					
AGR$_{soc}$	Frdy	Help	Symp						
	.22	.15	.14						
CON$_{soc}$	Dsor	Tim							
	-.17	.12							

Note.
Dimensions are listed as follows: DOM$_{soc}$ = Dominance, EXT$_{soc}$ = Extraversion, OPN$_{soc}$ = Openness, AGR$_{soc}$ = Agreeableness, NEU$_{soc}$ = Neuroticism. Con = Cons.
Traits are listed to compare the membership between the personality dimensions (fuzzy sets). E.g. in AGR, the traits are shortcuts of the original trait, thus here the traits standing for: Helpful, Friendly, Gentle.
Traits in the same colour represent a trait, which is listed in different personality dimensions.
Numbers in boldface and Italic = highest salient loadings of the traits, which is listed in more than one dimension. Only the highest will be respected. As more unique a trait itself is, as higher is the degree of membership of that trait.
Highlighted in green or red= trait is loaded in more than one dimension; it will be decided on the trait in which dimension it fits best.
Green = will be loaded into this dimension, Red = it will be deleted from this dimension (due to lower loading compared to the other loading into the other dimension.
'-' = negative loadings.

'*' = traits that have not been included in the personality ratings in all species will not be further included in the shared constructs.
For more information on the full list of traits in different species, see ***TableAPP 10***
List of dimensions used to run fuzzy-set analyses. The number in the bracket resembles the personality dimension used to run the analyses. The number is based on the order of the appropriate dimension in the personality structure of the species.
Dominance: eWLG(1); iWLG 3); ex situ chimpanzee(1); human(1); VMG(1); ex situ orangutan(2) & ex situ bonobo(2)
Agreeableness: eWLG(6); iWLG (2); ex situ chimpanzee(4); human(2); VMG(4); ex situ orangutan(4) & ex situ bonobo(5)
Extraversion: eWLG(2); iWLG (2); ex situ chimpanzee(2); human(2); VMG(3); ex situ orangutan(1) & ex situ bonobo(6)
Neuroticism: eWLG(4); iWLG (1); ex situ chimpanzee(5); human(1); VMG(1); ex situ orangutan(3) & ex situ bonobo(1)
Openness: eWLG(5); iWLG (2); ex situ chimpanzee(6); human(3); VMG(2); ex situ orangutan(1) & ex situ bonobo(3)

The Sociality Trait Constructs for Great Apes' Personality Structures.

When a trait was represented in different dimensions, it remained in the stronger dimension when the value of the trait was the same or the trait loaded into the dimension with the highest absolute loading.

The following traits were excluded from analyses as they were not represented in all the attended personality studies: *Autistic*, *Conventional*, *Cool*, *Curious*, *Distractible*, *Individual*, *Innovative*, *Thoughtless*, *Unemotional*, *Unperceptive*, and *Vulnerable*.

1. **Dominance** (**DOM$_{\text{soc}}$**): The first social dimension was Dom$_{\text{Soc}}$ and it contained shared traits such as *Dominance, Defiant*, *Aggressive*, (not) *Erratic*, (not) *Unperceptive**, Persistent, (not) *Submissive*, (not) *Independen*t, *Predictable*, *Sensitive*, (not) *Stingy, Gentle, Reckless, and Irritable*. Both, DOM$_{\text{soc}}$ and NEU$_{\text{soc}}$ intersections extracted the same trait *Irritable* in their shared social trait construct. *Irritable* remained in the Dominance dimension as the trait is represented in Dominance far more often as shown in **Table 23**, Chapter 4 (*Overview of traits underlying personality structure in ape species*).

2. **Extraversion** (**EXT$_{\text{soc}}$**): Traits, such as *Sociable*, *Affectionate*, *Inventive, Active, Dependent*, *Playful,* and *Independent* loaded into the shared EXT$_{\text{soc}}$ dimension. *Friendly* (in AGR$_{\text{soc}}$), *Dependent* (in NEU$_{\text{soc}}$), and *Independent* (NEU$_{\text{soc}}$) however, loaded into the dimensions, where the trait was showing a higher loading.

3. **Neuroticism** (**NEU$_{\text{soc}}$**): The traits *Independent* (DOM$_{\text{soc}}$) and *Dependent* (EXT$_{\text{soc}}$) loaded higher in the NEU$_{\text{soc}}$ intersections (green highlighted). Additional traits are *Stable* and *Depressed*. The traits *Disorganised* and (not) *Irritable* ended up in the DOM$_{\text{soc}}$ dimension for the same reason as mentioned above in the description of the dimension and were represented in the NEU$_{\text{soc}}$ dimension.

4. **Openness (OPN$_{soc}$)**: The dimension OPN$_{soc}$ was resembled using the following traits: *Imitative*, *Excitable*, *Impulsive. Inventive* loaded higher in EXT$_{soc,}$ and thus loaded into the dimensions, where the trait was showing a higher loading.

5. **Agreeableness (AGR$_{soc}$)**: The silent loadings of the fuzzy intersection Agreeableness were *Friendly*, *Helpful*, and *Sympathetic*. *Friendly* was also added into EXT$_{soc}$ however, it remained in AGR$_{soc}$ as it is a trait which is more shared between the compared species in the Agreeableness dimension.

6. **Concientiousness (CON$_{soc}$)**: In the last component, two traits were shared across the included species: (not) *Disorganised* and *Timid.*

5.5 Discussion

Bridging the gap between optimal welfare of eWLGs and iWLGs

The expansion of model on state-dependent feedback loops (**Figure 17 and Figure 21**) offers a robust framework for incorporating both ultimate (evolutionary context, level 4) and proximate (immediate, Level 1,2,3) levels of personality, SWB, and sociability, which are key components of overall optimal wellbeing and happiness within my thesis. **Figure 17** shows the integrated multiple measures analysed in this and previous chapters (Chapter 3 and Chapter 4) and include it into the overall model on state-dependent feedback loops. This approach can help bridge the gap between understanding the adaptive significance of personality and his related SWB (Level 4) and the mechanisms driving their expression. State-dependent feedback loops refer to the processes where an individual’s state (Level 1) influences their behaviour, which in turn affects their state (state dependent behavioural response, Level 2). This creates a dynamic and continuous interaction between an animal’s internal conditions and its external environment. For a summary of all measurers included see notes below **Figure 21**.

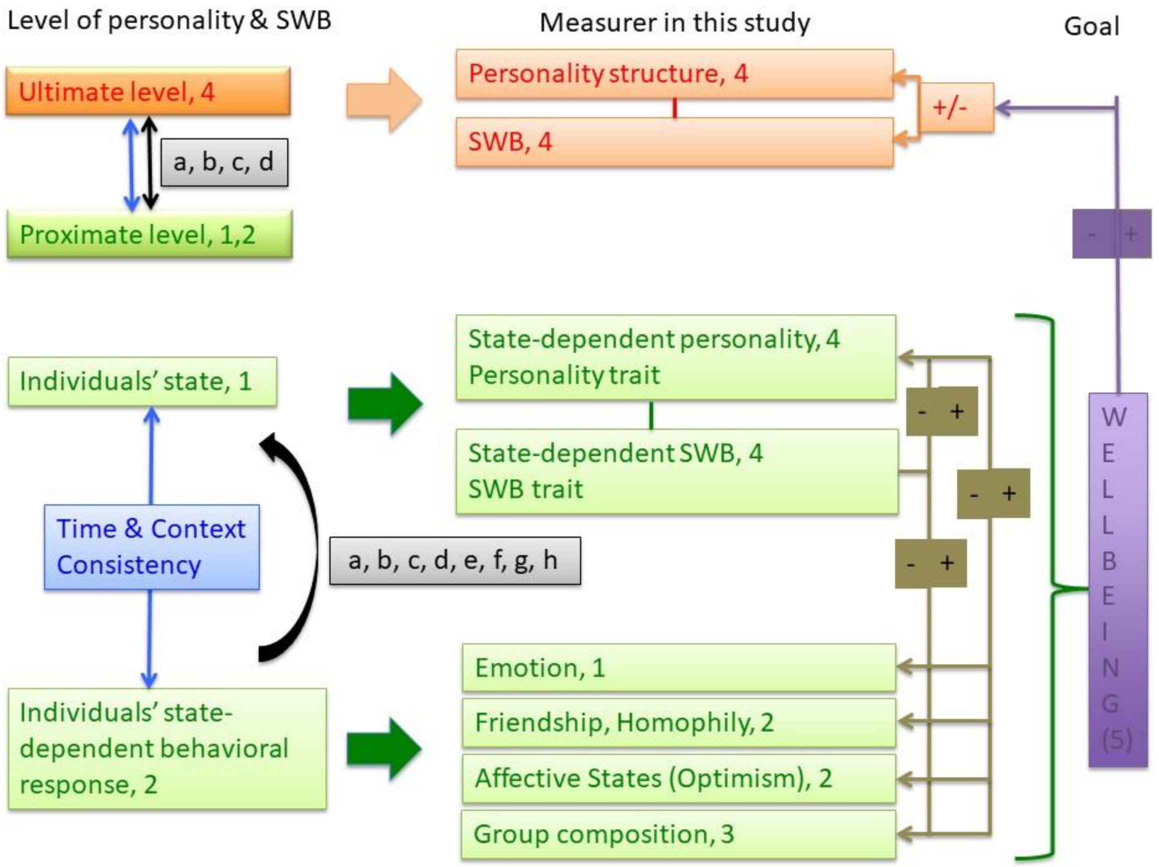

Figure 21 *Expanded model from* ***Figure 17****: multi-dimensional measurements according to this study are included*

Note.
Middle: Measurements in this study
Green:
On the proximate level, gorillas' individual state (1) is represented via their state-dependent personality (= individual personality traits (4a), state-dependent SWB (= individual subjective wellbeing traits, 4c) and their state-dependent behavioural responses (2).
On the level of an individuals' responses, I measured indicators showing positive welfare value. Here, positive emotional animal-to-animal interactions; such as play (2nd Level), friendship (proximity and homophily, 2rd Level) , social structure (via group composition, 3rd Level) were correlated. Positive emotional states (1st Level) and mood (2nd Level, optimism) are used to validate the personality structure and SWB.

Orange:
On the ultimate level (4) In the case of gorillas, I compared the personality structure of ex situ and in situ WLGs, Virunga mountain gorillas, and with those of other ex situ great ape species and humans on the higher-order dimension and on lower-trait constructs to show phylogenetic relationships (Chapter 3 and 4). I also extracted a shared social personality construct across great apes species and humans via fuzzy set analyses and identified shared social dimensions in respect to the genus *Gorilla* (Chapter 4).
Khaki arrows represents the consequences and correlations between different features and underlying mechanisms. Whereas + sign indicates positive value and – shows the negative value of the feature, expressed.

Right side: Overall goal of this chapter and thesis is to find indicators for an increased status of wellbeing and possibilities to enhance it.

Purple arrow: This can have an impact on the survival of the population or species (on the ultimate Level, 4 as well as on SWB).
Upward spiral: sociability, the key to increased wellbeing!
Sociability was found to be the suitable connection between all research interests and the overall key to improve wellbeing. Sociability is the driving force for positive emotion, optimism, increased happiness, and vice versa, and is identified as key to personality (see Chapter 4 across the genus *Gorilla*; and in this chapter across great ape species).

The impact that environments have on the expression of emotions, perception, and behaviours of non-human animals – especially primates – and their wellbeing has become an increasingly important area of study (K. Baker, 2012; Barnett & Hemsworth, 2009; Beisner & Isbell, 2008, 2009; Brent et al., 2011; Buchanan-Smith, 2011; Jennings et al., 2009; Mallapur & Chellam, 2002; Rasmussen et al., 2020; S. R. Ross et al., 2011; Swaisgood, 2007). Understanding the impact of confinement is important for zoological institutions that incorporate the building blocks of conservation, education, research, animal welfare, while also allowing for visitors' recreation and engagements in their declarations of purpose (Buchanan-Smith et al., 2001; Greenwell et al., 2023; Rose & Riley, 2022) and are actively working towards the One Plan Approach (OPA). Hence, the promotion of optimal animal welfare is crucial not only for the wellbeing of individual animals or populations, but also for the attainment of elevated standards in effective conservation, research, education, and recreational initiatives (Bovenkerk & Keulartz, 2018; Keulartz, 2023).

Veasey (2017) proposes an optimal animal welfare strategy that covers both quantifiable indicators and the subjective wellbeing and meaningful experiences of animals in ex situ conditions. This viewpoint emphasises the need to establish settings that consider the psychological and emotional requirements of animals, so promoting their general wellbeing and adhering to ethical principles and conservation goals.

In ex situ context, enhancing our understanding of emotions may lead to improvements in our care and interactions with animals. Understanding emotions has significant promise as a valuable resource in mitigating and resolving problematic behaviours and increasing positive welfare. It is also important to be aware of the potential of the human-wildlife interactions (including keepers, and zoo visitors), especially in solitary species, as this social component can impact on their wellbeing (see Mellor et al., 2020). This concept also applies to in situ populations, such as the case of poaching, tourism and landscape usage. Social interactions and other positive behaviours, (e.g., foraging and food-context behaviour, or exploration-driven behaviours within the environment) allow humans to test for associations within the hedonic and eudaimonic concepts of wellbeing in gorillas (eWLGs and iWLGs, Level 5, **Figure 21**) as shown within my thesis.

To examine associations between the hedonic and eudaimonic concepts, I interlinked a range of measures (see **Table 17**, **Table 19, and Table 21**) of an individual's happiness (both short- and long-lived) in social living WLGs, and tested animal wellbeing as part of a multi-dimensional concept. This is the first study to explore this inter-relationship between personality, "sociable happiness" and the potential of positive emotions (action-oriented rewarding experiences), and mood states (state-dependent behavioural responses) in non-human primates. The range of measures and the outcomes are discussed below.

Within the **eudaimonic subjective wellbeing concept (Level 4, SWB)**, I validated a standardised questionnaire to measure SWB in ex situ and in situ WLGs. Direct observations of pleasurable experiences (Level 1, emotions) as well as engagement in activities that have been shown to be meaningful (Veasey, 2020) – such as e.g. play (Level 2, s-dbr (mood), bonding, close social interactions (Level 2; Level 3, Zoo records, e.g. on group composition) which are assumed to foster positive emotions – were linked to SWB, and personality (Level 4). The hedonic happiness concept is associated with the pursuit of pleasure and the minimisation of pain and suffering. A wide range of eWLG related behaviours were correlated with emotions (both negative and positive) ranging in the matrix (see **Figure 19**) from eustress to distress, contentment to depression within diverse levels of activity, vitality, and arousal.

The goal was to investigate hedonic wellbeing associated with emotions, such as joy, excitement, or love, which play a vital role in the improvement of happiness in the short-lived concept. With mood fluctuations (ranging from pessimism to optimism) and individual personality differences playing an interlinked role. Emotion and mood have been shown to impact and influence behaviours, coping mechanisms, and physiological responses. Emotions such as fear and anxiety have emerged as evolutionary adaptations, enabling the organism to effectively respond to challenges, such as experiencing a sense of danger, a smell of a mating partner, or during exploratory behaviour to seek out and acquire resources. The process of acquiring resources, nurturing offspring, and experiencing emotions entails several physiological alterations, such as fluctuations in heart rate, cortisol levels, adrenaline release, and other related factors. Gaining comprehension of emotions may facilitate the prevention and mitigation of negative influences and avoidance behaviours. My study on eWLGs (Chapter 3 and Chapter 5) and iWLGs (Chapter 4 and Chapter 5) therefore highlight the significant influence that emotions have on social factors. This discussion focuses on the dynamics of animal interactions both within their own species and with the human context, as well as within confinement or during human-wildlife interaction in their natural environment.

Below, I explain social drivers for happiness within my study:

Play is an indicator of rewarding pro-social behaviours. I found a significant positive relationship between SWB and play (Average Play, however also in all forms of play) in eWLGs and iWLGs. Animal play is linked to the experience of positive emotions (e.g. pleasure, Burgdorf & Panksepp, 2006; D. Fraser & Duncan, 1998; Špinka et al., 2001) and there are some indications that the physical play activity releases "feel-good" hormones (endorphins) in the brain, giving a feeling of wellbeing. My research supports earlier statements that play shows itself to be self-rewarding, a reinforcing reward, and an experience of pleasure (Berkson et al., 1963; Berridge & Kringelbach, 2008; Berridge & Robinson, 2003; Burghardt, 2005; D. Fraser & Duncan, 1998; Held & Špinka, 2011; Martin & Caro, 1985; Špinka et al., 2001; Vanderschuren, 2010), as gorilla play was interlinked between the expression of positive emotion, mood, personality and SWB. Play is also social and can spread to others, causing a contagious build-up of play within the group (Baerends, 1989; Bekoff, 2001; Bekoff & Byers, 1981; Fagen, 1981; Ferrari et al., 2009; Gomendio, 1988; Held & Špinka, 2011; Leca et al., 2007; Pellis & McKenna, 1992; M. D. Ross et al., 2008; Varlinskaya et al., 1999). This suggests that offering appropriate opportunities to play through social and environmental enrichment stimulates play behaviour and increases SWB. I therefore measured the possibility to join or start play (also with drumming and chest beating to offer play opportunities (Palagi, 2008) within the social context). Play is also said to result from good welfare and lead to it (Held & Špinka, 2011) giving immediate, delayed, and long-term benefits. My data confirm this as play (Level 2) was linked to emotions like joy, excitement, and curiosity within the hedonic concept

(Level 1), and SWB_{Mean} on the eudaimonic (Level 4). Play is therefore a potentially useful tool to improve current and future welfare of individuals and the group (Balcombe, 2009; Boissy et al., 2007; Held & Špinka, 2011; Oliveira et al., 2010) as increased play leads to increased welfare, which again leads to an increased status of happiness (see SWB, via positive feedback loop, see **Figure 17** and **Figure 21, Level 5**).

In the context of close relationships, gorillas with higher levels of social contact through proximity behave more socially and play more with social partners (i.e., have more connections with others, such as in proximity or during play). However, as "Happiness is a personali(ty) thing" (Weiss et al., 2008, p.1. title), it is possible that play might not work for every animal as the same driver towards a pleasurable outcome. This was demonstrated in Chapter 4 and Chapter 5 where more play was found in open and more social gorillas. Open individuals also generally seek more high arousal pleasant emotions (excitement), whereas introverts might prefer calmness (in humans, Rusting & Larsen, 1995). This instrumental approach to emotional regulation explains why different gorillas can be motivated to express different emotions (sometimes bad ones, in different contexts (Tamir & Gross, 2011) as it depends also on earlier experiences of emotions, values, and knowledge about pleasure or pain.

Social connection to happiness. Happier gorillas (higher scores on overall $SWB_{Mean,}$ Level 4) were shown to have higher levels of socio-positive interactions (Level 2), such as social proximity (social partner within proximity excluding own infants/mother), contact resting, and other social engagement behaviours like holding, touching, or sharing other positive emotions. In humans, social connections foster positive emotion. Introverts might "enjoy" calmness more (Fredrickson, 2003) and help to develop trust and harmonious relationships within groups (Walter & Bruch, 2008). More meaningful relationships have been found in happier gorillas, and it is said that social connection in general is an essential influencer of happiness (Kringelbach & Berridge, 2010). My findings are in line with human research as joy, curiosity, and excitement were related with SBW ratings and prosocial interactions. I underpin this by showing that happier gorillas lived in groups with their offspring or their parents, but large groups with more unrelated gorillas were too big and lowered their overall SWB. Sociability seems to therefore be the driving force for happiness and vice versa (Diener & Seligman, 2002).

Gaining this understanding of emotions enables us to create an environment conducive to the wellbeing and contentment of animals while simultaneously mitigating the likelihood of them developing behaviours that may cause negative welfare. Enhancing interpersonal relationships can have a major influence on their lives. The objective is to deter and eradicate undesirable animal behaviour but to stimulate what makes their life enjoyable no longer.

Correlation between Personality factors and SWB.

A relationship was found between SWB, and all six personality factors described in eWLGs. Dominance, Conscientiousness, Agreeableness/Sociability, Openness, and Extraversion were positively associated with SWB and Neuroticism was negatively associated). In iWLGs, I was able to demonstrate that all four personality factors are associated with SWB (Neuroticism, negatively; Sociability, Openness and Dominance, positively).

Earlier studies on chimpanzees and eWLGs found a positive relationship between two personality factors (Dominance and Extraversion) and SWB (King & Landau, 2003; Schaefer & Steklis, 2014). Further, Conscientiousness was positively related to SWB in chimpanzees (Weiss et al., 2009). In orangutans, Extraversion and Agreeableness have been positively related, whereas Neuroticism showed a negative association to SWB (Weiss et al., 2006). Within capuchin monkeys, only one factor labelled as Sociability was related to SWB, whereas none of these dimensions were related in rhesus macaques (Confidence, Friendliness or Anxiety) (Weiss, Adams, Widdig, et al., 2011). The lack of association between Conscientiousness and SWB in rhesus macaques may be explained by the non-social nature of items loading on this factor. Conscientiousness was also the only factor where no correlations were identified to either positive or negative emotions (see **Table 32**). However, it was associated with life-satisfaction. Overall, SWB in primates seems to be most consistently associated with personality factors that are associated with social motivation.

In humans, numerous studies found the relationship between the FFM (see also Zuckerman's Alternative Five-Factor Model of personality) and SWB (DeNeve & Cooper, 1998; Diener, 2000b; González Gutiérrez et al., 2005; Jovanovic, 2011; McCrae & Costa, 1991; P. Steel et al., 2008; Weiss et al., 2008). Correlations between SWB and personality traits are found 39-63% in multiple correlation of traits with SWB (P. Steel et al., 2008), primarily the dimensions of Neuroticism (with negative affect and life satisfaction (in FFM)), Extraversion (with positive affect), Agreeableness (with positive affect and life satisfaction) and Conscientiousness (with life satisfaction) (Costa & McCrae, 1980; González Gutiérrez et al., 2005; McCrae & Costa, 1991; Weiss et al., 2008). Furthermore, Openness was correlated with being open to experience negative and positive states.

A strong relationship was found between SWB and Extraversion as well as with a dimension labelled Emotionality in humans (Costa & McCrae, 1980; Diener, 2000b; Diener et al., 1998). Emotional stability was established to be as important as the dimension of Extraversion to achieve happiness (Hills & Argyle, 1998). Moreover, Weiss et al. (2016) show that Neuroticism and Extraversion predict SWB in humans living in the U.K. The polygenetic effect (genetic component of SWB) found in this study confirms earlier findings in twins (Hahn et al., 2013; Weiss et al., 2008). In great apes, genetic disposition of SWB was also found (Adams et al., 2012; Weiss et al., 2002). This limits the prospect for enhancing SWB in humans to round 50% (like personality). However, according to Weiss et al. (2016), more attention needs to be drawn to Extraversion and the remaining human personality dimensions, in respect to the polygenetic effect and the impact on mental wellbeing, as previous studies focussed on Neuroticism. Lyubomirsky and colleagues (2005) noticed that sociality leads to a relationship between Extraversion and SWB. The genetic component of SWB also limits the increase in SWB in gorillas and other species.

Sociability

My investigations found support for the relationship between personality and sociability in great apes. Subspecies of gorillas share Sociability constructs within the common personality factors. Personality structure in iWLGs and the interpretation within the socio-ecological approach showed that iWLG tend to have a strong association with tolerance in their personality structure. The concept of intergroup tolerance pertains to their capacity to engage in harmonious interactions with different gorilla groups within their ecosystem. This observed behaviour has significant ramifications regarding the sharing of resources, establishment of territorial borders, and general dynamics within the group.

All great apes share social personality.

The concept that all great apes share a social personality construct might be explained by the phenomenon of self-domestication and enhanced self-control also seen in humans. The growth of friendliness is fundamentally congruent with overarching themes of collaboration, less emotional reactivity, heightened self-regulation, and the cultivation of sophisticated social and cognitive capacities. Here, I argue that great apes can be aligned along the despotic/less tolerant axis towards the egalitarian/tolerant/less/prosocial axis with humans being the most egalitarian and prosocial species. This underscores our distinct ability to engage in collaboration, exhibit justice, and foster the formation of intricate social structures, so highlighting the importance of our inherent sociability and the influence of cultural development in creating these characteristics.

As an example, Hare and colleagues (2012) revealed that bonobos – who are known for their egalitarian social structures – are also characterised by female domination, and set the devilment of humans into the concept of friendliness. Whilst chimpanzees live in a male dominated hierarchical systems that seems less tolerant and more aggressive. These variants – including findings from Chapter 3, Chapter 4, and Chapter 5 discussing the personality structure of iWLGs and other non-human primates – show that the heterogeneous social personality structures within the great ape lineage can help to understand the roots of cooperation, social hierarchies, conflict resolution, and social learning. This also includes reciprocity, reconciliation, and altruism, all of which are vital to the advancement of egalitarianism. Thus, studies on great apes reveal that our closest relatives exhibit various levels of social organization, from hierarchical to more egalitarian structures, resembling aspects of human societies. Studying primate personality offers valuable insights into the field of human evolution, specifically our inclination for egalitarianism, cooperation, social intelligence, from the personality angle.

Individuals who are similar may also be more predictable in their behaviours and thus preferred as social partners (Massen & Koski, 2014; Morton et al., 2015; Weinstein & Capitanio, 2008). This is known as homophily or friendship. In humans, homophily is evident for Extraversion, Agreeableness and Openness (Digman, 1990; Selfhout et al., 2010) but not in Conscientiousness and Neuroticism (Kurtz & Sherker, 2003). In this study, it was found that eWLGs tended to exhibit homophily in their partner preferences, measured in terms of similarity in personality between dyads and time spent in proximity. I found Agreeableness and SWB predicted friendship. Similar findings have been reported for other non-human primate species, including chimpanzees (similarities in Sociability/ Extraversion, Massen & Koski, 2014), capuchin monkeys (similarities in Sociability, Openness and Neuroticism, Morton et al., 2015), infant rhesus macaques (for Adaptable and Equable, Weinstein & Capitanio, 2008) and in successfully pair-housing of female macaques (Capitanio & Cole, 2015). Homophily is important for establishing and maintaining relationships and has advantages for fitness outcomes (e.g. offspring survival, reproduction, access to mates, Capitanio, 2011; Massen & Koski, 2014). Similarities of group-behaviours regarding synchrony, contingency and reciprocity have been found to be beneficial in species high in cooperation tendencies (Koski & Burkart, 2015). As mentioned for different macaque species, those who were closer related in their social organisation also showed a more similar "social style" (from aggression to social competence) and therefore shared more social personality trait constructs (Adams et al., 2015).

5.6 Limitations and Future Directions

To the limitations and future directions already mentioned in Chapter 3.6 and Chapter 4.6, I will include some here, which resulting out of this chapter in addition.

5.6.1 Limitations

Studying happiness or subjective wellbeing (SWB) in eWLGs presents different challenges and limitations compared to in situ populations. Some of the constraints are:

Social dynamics. In ex situ, social groups are set/ controlled by studbook keepers, there is e.g. no female choice in selecting the preferred breeding/ protective male or multiple transferences between groups possible. This does not reflect the natural social structures and dynamics of in situ populations. See eWLG life cycles Chapter 4 for more information on social differences. The lack of natural intergroup interactions and the presence of human interactions can alter social behaviours and affect SWB. Whereas in situ, gorillas interact within natural social groups, this provides better insights into genuine social relationships, dynamics, alliances, and conflicts.

Behavioural repertoire and psychological wellbeing. A limitation of this study is that only on very limited occasions eWLGs showed negative emotions or other negative behaviours. This low average of negative emotions could be of an artefact that they do not express a high amount of negative behaviour or due to the sampling methods, therefore, negative emotion needs further to be investigated as stress-induced behaviours can be developed due to artificial housing techniques (e.g. such as hand rearing) or stereotypies that can impact on eWLGs' SWB. IWLGs experience natural stressors such as predation, competition for resources, and environmental and climate changes, which can provide a more comprehensive understanding of their life challenges, but can on the other hand also impact on their SWB.

Measurement challenges. Within the framework to **measure emotions**, I identified behaviours that are indicative of specific emotional states (such as play or other close social interactions). With defined emotions, I investigated short-term expressions, such as joy, and subjectively accounted for emotional changes. Using additional non-invasive methods, such as heart rate, body posture, eye gaze, cortisol levels, vocalisations, facial expressions (via the Facial Action Coding System (FACS)), or body temperature could have helped to identify those emotional expressions more valuable and reliable and reduce the risk of attribution human-like emotions into gorillas. These multiple measurers could be used in the future to investigate emotions in gorillas. And as emotions can fluctuate rapidly, a longer-term study to capture variations over time and ensure consistent data collection periods, also in different environments and context is advisable.

5.6.2 Future directions

Non-invasive advanced multi-faceted approach to positive welfare

- Monitoring the quality and quantity of social behaviours as recommended by Silk et al. (2013) for in and ex situ WLGs can help assessing positive welfare indicators and compare outcome (e.g. play as a strong indicator of positive emotional states (Held and Spinka, 2011)).
- Conducting **long-term studies** to track changes in personality, SBW and positive welfare to assess how they evolve over time to capture the dynamic nature of animal personalities and account for developmental and environmental changes.
- When dealing with ex situ WLGs, a **tailored welfare questionnaire** to the specific behavioural and cognitive species-specific questions can help to assess ex situ welfare issues and improve SWB and positive welfare, accounting for the influence of captive environments and human interactions.
- Integrating **additional multi-dimensional welfare measures**, e.g. physiological (e.g. hormonal levels) or genetic measures and overall health indicators can provide insight into the internal state and complement the behavioural assessment and provide am more comprehensive view of eWLGs' personality and SWB.
- Allowing eWLGs to make **choices** and have **control,** and to recognise individual differences can provide insight into their preferences and improve their wellbeing by providing control over their environment.
- Evaluating flexibility and adaptability of behaviours in different contexts can help to understand how personality traits manifest across environments. Examining stress

responses and coping mechanisms as part of personality assessments captures the impact of captivity on eWLGs wellbeing.

- **State-dependent feedback loops** showed that personality and SWB can change over time due to age, health, or environmental changes. Therefore, Longitudinal studies are necessary to capture the dynamic nature of personality traits. This could be done by comparing generation 1, 2, etc. on the personality structure level to assess the dynamic of the personality structure. Another way would also be to compare the personality of in situ captured vs. ex situ born WLGs to compare those ex situ populations and to the generated personality structure. The information on different cultural backgrounds as shown within gorilla subspecies and populations might be crucial for understanding how personality structures might developed and manifested within different populations. Therefore, a comparison on the basis of cultural traits on personality seems vital to identify cultural variations in the expression and interpretation of personality trait.
- Developing mathematical or computational models to simulate the feedback loops between states and behaviours can help predict how changes in one aspect of the environment or physiology might influence overall personality traits and social behaviours.
- Utilizing non-invasive advanced technologies, such as remote monitoring and bio-logging, to gather data without disturbing the animals but the integration of e.g., machine learning, or natural language processing to analyse large-scale data and its impact on personality and SWB in both populations of WLGs.
- Personality assessment should also be applied to **improve social groupings.** Understanding personality traits can help in pairing animals that are more likely to be compatible, thus increasing reproductive success or within the formation of bachelor groups. For instance, pairing WLGs with complementary personalities can reduce stress and aggression, fostering a more conducive environment for mating and enhancing social cohesion and forms friendships and collaborations. Also, certain personality traits can influence parenting behaviours. By selecting gorillas with desirable traits (e.g., high nurturing tendencies), breeding programs can ensure better offspring care, leading to higher survival rates. Within bachelor or breeding groups, WLGs with higher sociability scores or complementary personalities can be grouped together to foster

positive social interactions, which will feed back via state-dependent loops to a more stable, adaptable, and happy population and secure survival in diverse environments.

- n conducting multiple correlational analyses within this study, the issue of non-independence of data points was addressed to mitigate inflated Type I error rates. Initial attempts to apply p-value correction methods such as Bonferroni, Holm's correction, and the False Discovery Rate (FDR) control were overly conservative and resulted in a lack of significant findings. To manage Type I errors without compromising the study's power, behaviours were regrouped into broader categories. Despite these adjustments, p-value corrections continued to complicate the interpretation of results. Consequently, Spearman correlations were ultimately used for non-normally distributed behaviours, and Pearson correlations for normally distributed data. This approach allowed for a more practical analysis of the data while acknowledging the limitations in statistical rigor due to the exploratory nature of the research and data constraints. These findings set the groundwork for future studies to address these statistical concerns more rigorously.
- As earlier findings highlight stress is related to personality differences which directly interfered with pregnancies or offspring survival as well as group instability. Therefore, **health, medical issues, risk of earlier offspring death and mortality** could be analysed in relation to personality. Personality assessments can help in identifying individuals that might need special interventions or monitoring, ensuring timely and effective management actions. Healthier and happier animals are more likely to contribute positively to conservation goals.

Environmental enrichment

- Improving the complexity and variability of ex situ environments (social and ecology) to more closely mimicking natural conditions will allow for a broader range of natural behaviours. It indicates cognitive stimulation and physical activity, both of which are critical for wellbeing.
- Facilitate more natural social interactions as shown in the life cycle of iWLGs within ex situ groups will allows the expression of species-typical behaviours and interactions. The quality of social interactions is crucial for social species, reflecting good mental health and social wellbeing and as show it is key to happiness and welfare.

- Identifying specific traits can help in designing targeted training programs that align with an animal's behavioural tendencies, making training more effective. For instance, understanding a gorilla's fearfulness can guide the use of gradual desensitisation techniques in rehabilitation, translocations or outplacements.

Integration of human impact within the personality and SWB questionnaires. Considering the impact of human interactions on both WLG populations, this variable should be integrated into personality and SWB assessment forms. Where possible, human interference in eWLGs conditions should be minimalized to allow for more natural behaviour expression. The impact of humans in iWLGs and eWLGs should be measured.

Ethical Considerations. Ensure that all future research is conducted with a strong emphasis on positive welfare, minimizing stress and discomfort. Ethical considerations and welfare impacts needs to be reported transparently to all stakeholder to facilitate better understanding and replication in other species. Ensuring that research and interventions prioritize the welfare and ethical treatment of WLGs is paramount. Ongoing evaluation of welfare outcomes is necessary to ensure that personality-based interventions are beneficial and interventions and management practices based on personality research should aim to enhance the wellbeing of the animals while achieving conservation goals.

Conclusion

While the ex situ environment provides controlled conditions that can facilitate certain types of research, it also imposes limitations on the study of happiness and SWB in primates. In contrast, studying wild populations offers a more natural context but comes with its own set of challenges. Understanding these limitations and differences is crucial for interpreting findings and applying them to improve the management of both ex and in situ WLG populations and promote welfare.

By addressing these limitations and following these recommendations, future research can improve the understanding of animal personality across different environments, ultimately contributing to better conservation strategies and animal welfare practices.

Chapter 6

Bridging the Gap in Ex Situ and In Situ Population Management and Conservation of Western Lowland Gorillas

Picture 26 *One Welfare Plan*

“It’s not enough to love animals; we must actively protect and preserve them. It’s our duty and responsibility as custodians of this planet.” Daphne Sheldrick

6.1 Introduction

The concluding chapter serves as a synthesis and discussion of my overarching findings, elucidating how they effectively address the various theories outlined in earlier chapters. This chapter will serve as a **bridge connecting the ex situ and in situ perspectives**, and presenting recommendations for both contexts. It emphasizes the critical importance of personality and Subjective Wellbeing (SWB) as meaningful measures for evaluating the wellbeing of wildlife within the larger context of animal ethics, recognizing the One Plan Approach (OPA) as a valuable framework given that animals exist along a continuum spanning from in situ to ex situ conditions (Bovenkerk & Keulartz, 2018; Veasey, 2017).

Zoological institutions have the potential and obligation to actively contribute to the in situ conservation of animals, in this case gorillas in their natural habitats (see Chapter 1). The OPA emphasises the immediate necessity for novel and enhanced strategies in their conservation efforts. Given the acceleration of species extinction rates by human-caused forces, which are estimated to be 100 to 1000 times higher than the natural rate, the preservation of biodiversity becomes imperative to ensure the long-term viability of the natural environment and species survival (Bolam et al., 2023). A comprehensive and integrated strategy for wildlife conservation across various sectors is therefore necessary to secure the survival of all gorilla subspecies (Bovenkerk & Keulartz, 2018; Byers et al., 2013; Keulartz, 2023; Traylor-Holzer et al., 2019).

Zoos and aquariums play a crucial role within this approach, engaging in a wide range of activities such as ex situ breeding, head-start programs, wildlife health assessments, rescue and rehabilitation, supplementation initiatives and reintroduction/translocations (Byers et al., 2013, 2022; Traylor-Holzer et al., 2019). So far, there is a Regional Action Plan for the Conservation of iWLGs and in situ Central Chimpanzees (2015, IUCN), ending 2025. Eastern and Western gorillas are critically endangered (IUCN, 2018b, 2018a), yet an OPA still appears to be missing for the genus *Gorilla*. Below, I discuss recommendations based on my findings for approaching the plan's design, with a specific focus on its application within gorilla populations.

6.2 Thesis summary

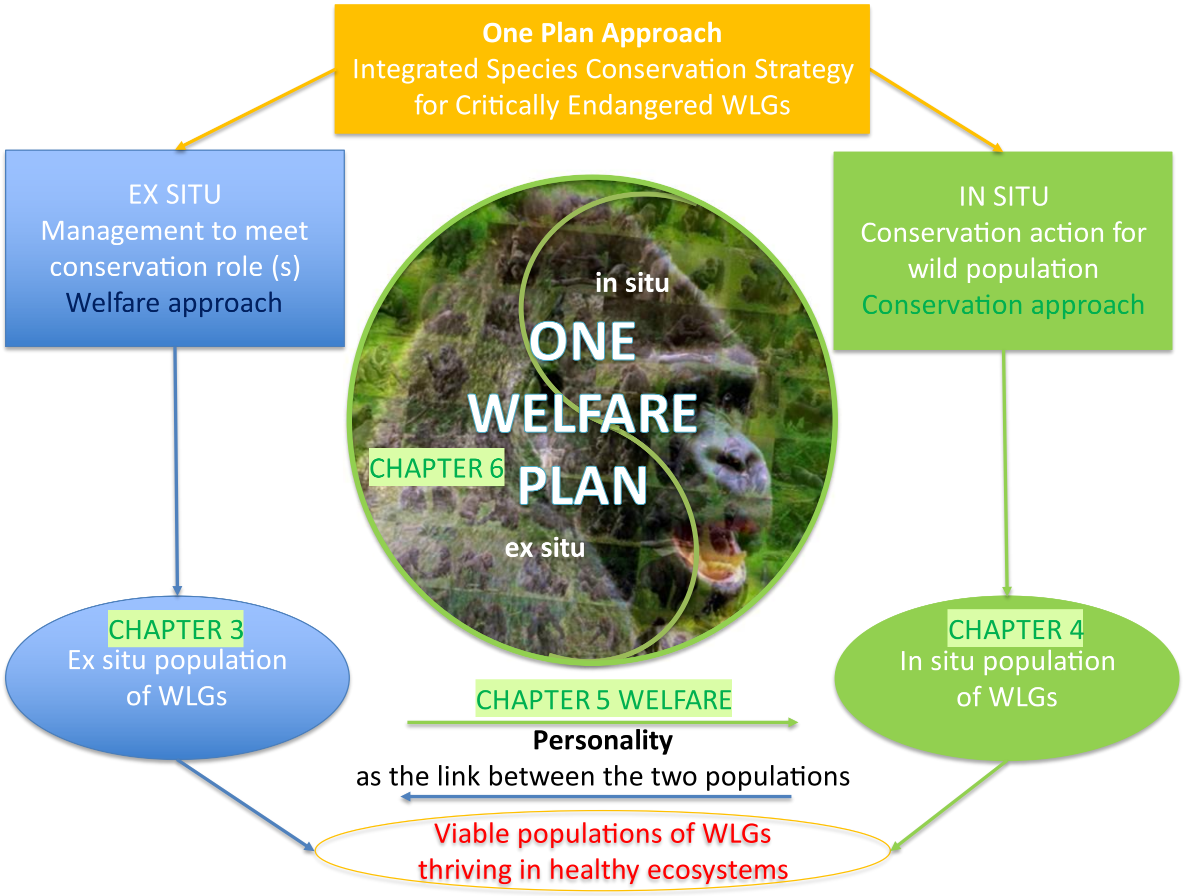

Figure 23 *Personality and SWB as an extended conservation tool kit and the link between in situ and ex situ Conservation and Welfare within the One Welfare Plan*

I have shown that personality and SWB have been shown to be a useful additional tool kit (see **Figure 23**) for the One Plan Approach to compare in and- and ex situ populations regarding increase conservation and welfare strategies. This research showed the impact of diverse environments on personality and SWB development in different gorilla populations and its relation to animal wellbeing. Ex situ-induced alterations in personality were observed, emphasizing the need to consider personality in predicting animals' responses to their surroundings and social interactions. This knowledge can inform conservation efforts and enhance the welfare of both ex situ and in situ populations. The "Positive Psychology for Animals" paradigm (integrating principles from human positive psychology, see Chapter 5) holds promise for enhancing animal welfare, in this case within Western lowland gorillas

(WLGs), especially in ex situ populations. Personality is linked to SWB and social engagement in gorillas with implications for their conservation and welfare. I provide robust evidence that sociability is the key to overall short-term (hedonic) and long-term (eudaimonic) wellbeing and happiness.

In the following section, I introduce a novel welfare model that represents an expansion of the One Plan Approach (OPA) by incorporating a new conservation tool kit and combine elements of the One Welfare Approach (OWA). This model aims to create a unified framework that addresses welfare comprehensively, linking the health and wellbeing of both in situ and ex situ Western Lowland Gorillas (WLGs). This integrated approach is designed to secure species survival within the broader context of conservation, welfare and management strategies, termed the **"One Welfare Plan" (OWP).** For a comparison of the models, see **Table 37**, below.

Table 37 *Comparison of One Plan Approach, One Welfare Approach, and One Welfare Plan*

	One Plan Approach (OPA)	**One Welfare Approach (OWA)**	**One Welfare Plan (OWP)**
Primary Focus	Species conservation	Interconnectedness of animal welfare, human wellbeing, and environmental health	Comprehensive welfare and conservation integration: Interconnectedness the OPA (species conservation, ex situ and in situ, Reserve the Red, One Health, One Health, OWA), divers models on animal welfare, humans being central to take responsibility for secure species survival and environmental health
Goals and Objectives	Species survival, genetic diversity, habitat preservation	Enhance welfare in animals, human health, and the environmental conservation	Integrate in situ and ex situ conservation efforts with a focus on improving overall welfare, including genetic diversity, habitat preservation, humans are central to conservation
Scope	Conservation biology, captive breeding, reintroduction	Animal welfare science, public health, human socio-economic wellbeing, environmental sustainability	Conservation, captive breeding, reintroduction, management, all in the scope to improve welfare (ex and in situ)
Implementation	Species-specific action plans, collaboration among conservationists, research, zoos and governmental agencies	Interdisciplinary collaborations, policy and practice changes	Species-specific action plans, collaboration among all stakeholders, policy and practice recommendations, enhancing OPA tool kit by integration personality and welfare
Integration	In situ and ex situ conservation strategies	Welfare aspects across species, ecosystems, and human communities	In situ and ex situ conservation strategies with the scope of welfare improvement
Interdisciplinary Collaboration	High (conservationists, researchers, zoos, governments)	High (veterinarians, social scientists, environmentalists, policymakers)	High (Emphasizes the need for collaboration across disciplines, sectors and stakeholders. Aligns with existing policies, advocating for integrated welfare and conservation goals)
Holistic View	Yes, considers multiple factors affecting species	Yes, considers multiple welfare aspects across three domains	Yes, considers the interconnectedness of welfare and conservation aspects across five domains/ needs
Sustainability	Focus on sustainable species populations	Focus on sustainable welfare improvements	Focus on sustainable welfare improvements to secure species survival (ex and in situ)
Shared Benefits	Recognizes benefits of species conservation for ecosystems and humans	Recognizes improvements in one welfare area can benefit others	Recognizes benefits of species conservation via the help of all stakeholders by welfare improvements for species, ecosystems and humans

Systemic Change	Advocates for comprehensive conservation strategies	Advocates for comprehensive welfare strategies	Advocates for comprehensive conservation, welfare, and management strategies
Community Engagement	Engages local communities and stakeholders	Involves stakeholders in conservation planning	Engages communities and stakeholders in welfare and conservation planning

Furthermore, the adapted OWP, developed from the findings of this thesis, expands on existing welfare models and transcends traditional boundaries, encompassing both in situ and ex situ perspectives as mandated by the OPA and elements of the OWA (as described above). It integrates the conventional "Five Domains" welfare model (Mellor, 2016; Mellor et al., 2020), Maslow's Hierarchy of Needs (Maslow, 1943), as addressed in the World Association of Zoos and Aquariums' Animal Welfare Strategies (WAZA, 2015), the 24/7 across the lifespan approach (Brando & Buchanan-Smith, 2018), Veasey's (2017) captive-wild continuum, and the "bifocal view" (Keularzt, 2023, p 2). These elements are combined within the OWP (see Figure 24), creating a comprehensive and unified framework for animal welfare, conservation and management. This holistic framework also considers the in situ framework as a blueprint for guiding ex situ management practices (in respect to habitat management, see Brando & Buchanan-Smith (2018)). It also addresses the necessary exchange and collaboration between all shareholders as well as the exchange of animals to improve genetic diversity if necessarily (Byers et al., 2013; Sauve et al., 2022) as recommended within the OPA.

To achieve better global conservation outcomes, it is essential to adopt a multifaceted approach (outlined within the thesis) that integrates positive psychology with traditional conservation strategies as provided in Chapter 5. This involves holistic and optimistic conservation planning, incorporating wellbeing metrics (as shown in Chapter 4, **Table 19**) to ensure that all "The Needs/ domains" for ex and in situ populations are met to significantly enhance both human and animal welfare. By fostering positive welfare states, this approach not only addresses the immediate needs of wildlife but also promotes their long-term wellbeing and survival and ecological contributions. Adaptive management, which continuously monitors and adjusts conservation, welfare and management strategies based on feedback loops and outcomes (see Chapter 4, **Table 21**), ensures they remain effective and responsive to changing conditions. Cross-disciplinary collaboration, engaging experts from diverse fields, including psychology, conservation, ecology, and economy (just to mention a few), can develop comprehensive conservation solutions. Public awareness and education are crucial, raising awareness about the importance of positive welfare in wildlife conservation and encouraging public participation in conservation efforts.

Recommendations for the fulfilment of the goals of this comprehensive welfare and conservation strategy are provided.

In **Figure 24**, I illustrate how the mentioned models and approaches converge within the unified **One Welfare Plan** (**Figure 26**).

Figure 24 *One Welfare Plan: Integration of Maslow's Hierarchy of Needs, and Five Domain Model within an optimistic conservation and welfare approach*

Note:
Left: **WAZA, Animal Welfare Strategies** (2015) based on Marslow's Hierarchy of Needs: 6 steps pyramid going from Physical (brown), Veterinary Care (red), Safety (orange), Social Needs (yellow), Mental Stimulation (green), to similar to the social domain/ behavioural interactions and group dynamics (4th domain) in the "Five Domains Model" (Mellor et al., 2020).
One key adaptation to the original Hierarchy of Needs (Maslow, 1943) is to elevate/lift the "Social Needs" as the 2nd domain instead of the original at 4th domain,
Center:
From left to right: **One Welfare Plan**, based on the following welfare models:
Left: the adapted WAZA Animal welfare strategy based on a five steps pyramid: **Maslow's Hierarchy of Needs** (going from Physical (orange), Social (yellow), Emotional (green), Cognitive (blue), to Beyond individual needs (purple). This represents the fundamental Needs of all living beings, including animals. Needs and order of needs has changed!
Mittle: based on OPA (**Figure 1**, Chapter 1) (Traylor-Holzer et al., 2019): based on continuum reaching from in situ to ex situ (concept: Veasey, 2017). The balanced approach (Keulartz, 2017, 2023) and the 24/7 Across the lifespan (Brando and Buchanan-Smith, 2018) to reach optimal in situ and ex situ welfare and conservation.
Right: **Five Domain Model**: illustrate the Five Domain Model by Mellor (2020), which includes the five domains, 1-5: Nutrition (orange), Physical environmental conditions (yellow), Health (green), Behavioural interactions (blue), and Mental State (incl. human-animal interactions, purple).
These domains represent key aspects of animal wellbeing and quality of life.

One Welfare Plan

Prior to the establishment of an optimal **One Welfare Plan (Figure 26)**, factors that impact the level of survival, wellbeing and happiness, the needs of animals, in this case of WLGs have to be considered.

First, I adapted “The Needs” addressed in the WAZA Welfare Strategy (WAZA, 2015, left side, **Figure 24**): the original physical needs (brown), veterinary care (red), safety (orange), social (yellow); mental stimulation (green), and choice (blue) and extended or changed those, to increase longer lasting happiness/ subjective wellbeing thoughts by going beyond the WAZA (WAZA, 2015**.** And these “Five” adapted “Needs” (left side in the adapted OWP model, **Figure 24),** have been matched with the Five Domain Model (Mellor et al., 2016, 2020), right side on the adapted OWP model, see **Figure 24**).

I listed below “the Needs” on different levels, first on the level of the eWLGs, then the operating level in the OPW (collaborative level, as in OPA), the iWLGs make implications for the OWP.

The **“Needs”,** respective **“domains”** are colour coded as in **Figure 24.**

1, “Biological Needs”: This first need contains the following components: Nutrition, Physical Environment, Enriched Environment, Natural Habitat, Climate “a place like home”, Safety of the Environment, iWLG as a template for eWLGs (e.g., Brando & Buchanan-Smith, 2018; Veasey, 2017). It also contains Physical Health aspects, as in the first three domains in the “Five Domains Model” (Mellor et al., 2020, such as Nutrition, Health, and Physical Environment). Furthermore, Physiological (brown), Veterinarian Care (red), and Safety (orange), as the foundational steps in Maslow's hierarchy, which encompassing basic survival needs such as food, water, shelter, and safety are represented in the “Biological Need”.

On the level of the:

eWLGs. The assurance that these components are met is fundamental. Zoos and conservation institutions should continue to prioritize healthy nutrition, healthcare, and work on habitat design and enrichment to meet these needs. They need to strive to create an ex situ environment that mimic natural challenges and encourage natural behaviours, promoting the wellbeing, health and safety of individual animals (Brando et al., 2023; Brando & Buchanan-Smith, 2018).

OWP. Within the OWP, providing the “Biological Needs” for species by ensuring the protection and preservation of their habitats and natural resources is the basis to start with by each of the stakeholders. Collaborative conservation efforts towards the prevention of habitat degradation and loss, securing essential resources for all species, and healthy ecosystem to increase biodiversity. By fostering partnerships among various stakeholders, the OWP creates a sense of safety for ecosystems and species. Cooperation in managing threats like poaching, habitat destruction, and pollution contributes to safer environments that the animals can thrive.

IWLG. In situ habitat preservation, reduction of health and safety risks, reduce pollution and climate change effects, and protecting are essential to secure natural resources they need for survival.

2, “Social Needs”: These consist of the subsequent core social components: Connectedness, Belonging, Social Interaction and Environment (also refers to humans in ex situ conditions as being keepers, visitors, or other human component: see Mellor et al., (2020), Early Life Experiences (i.e. rearing), Social Group (e.g. friends and family within their environment, other non-human animals, and humans), Social Life Cycle (in accordance to in situ conditions), Husbandry Constraints (i.e. external restrictive confinement or restraint, force free management, space, and presence/absence of social interactions), similar to the social domain/ behavioural interactions and group dynamics (4th domain) in the “Five Domains Model” (Mellor et al., 2020).

One key adaptation to the original Hierarchy of Needs (Maslow, 1943) is to elevate/lift the “Social Needs” as the 2nd domain instead of the original at 4th domain, due to the utmost importance of the sociability, as my thesis showed, that sociability is key to personality and happiness and thus plays an overarching role in conservation and welfare. This includes highlighting how social structure; life history and companions are important factors in shaping the personality structure and SWB in WLGs.

On the level of the:

eWLGs. The social structure of a species is a determining attribute. Therefore, it is crucial to ensure that animals are kept in appropriate social group compositions to flourish and foster their social wellbeing. According to C. Smith (1998), the presence of compatible conspecifics has been seen to mitigate stress and provide chances for engaging in welfare-enhancing activities, including grooming, play, and mating. When discussing social considerations, it is important to examine the many factors that impact both individuals and groups within a given species, in ex situ and in situ populations. The research presented here highlights the significance of **sociability** in gorilla personality and its positive correlation with SWB and conservation efforts. It is the **driver for long-term happiness and SWB**. Encouraging positive social engagements within ex situ and-in situ gorilla populations should be of highest priority. Therefore, the shift to a higher order / need seems essential. Additionally, it needs to be noted, that social needs also can change throughout the lifetime (Brando & Buchanan-Smith, 2018); in primates: (Brando et al., 2023) and therefore need to be taking into consideration.

OWP. The social component within the OWP raised to enhanced social engagement on all levels. Social interactions are not only a crucial aspect of gorilla wellbeing, but also the success of the OWP heavily relies on active involvement and collaboration with local communities, governmental bodies, non-governmental organisations, and various other stakeholders. Collaborative decision-making facilitates the establishment of robust and enduring support for conservation endeavours. Additionally, collaborative conservation efforts recognize the interconnectedness of species within ecosystems and understands that humans are central to ensure species survival. Protecting biodiversity and habitats ensures that species can continue to thrive in their natural communities, promoting a sense of belonging and a combined effort is essential to safe and protect animals in their natural habitats. Thus, the OWP's goal fostering a sense of community and belonging among individuals and sees the human as central in the endeavour to Reserve the Red to ensure our own survival.

iWLGs. Within this thesis, I was able to demonstrate that the social component is one of the major drivers for welfare and happiness in ex situ and in situ animals. The comparison of the socio-ecology between the in situ and ex situ and between the two in situ gorilla populations plays a crucial role in respect to their personality structure and therefore also to their survival.

The significance of social interactions, life cycle, group structures, and dynamic relationships cannot be overstated in the context of the overall welfare.

3, Emotional Needs: consist of the following social components: Mental/ Psychological Health/ Emotional Wellbeing / Subjective Emotional or Affective Experiences / Subjective Wellbeing (SWB); including Survival critical Negative Affects.; like the 5th Domain (mental state or affective experiences in Mellor et al. 2020) in the "Five Domains Model" and the 6th Need on Mental Stimulation (green) of Maslow's Hierarchy in WAZA's Animal Welfare Strategy (2015). Hedonic = short lived concept of Happiness; Eudaimonic = longer-term concept of Happiness.

On the level of the:

eWLGs. In both ex situ and in situ populations, emotional wellbeing is a critical component of overall welfare. Emotional needs encompass the need for psychological security, emotional stability (see Chapter 5 for relationship to personality and SWB), and the experience of positive emotional states (Chapter 5). These needs extend beyond basic survival and play a substantial role in the welfare of WLGs. Ensuring emotional wellbeing is essential, as stress and negative emotional experiences can significantly impact the health and happiness of individuals.

My findings related to hedonic happiness show that positive emotions, SWB and personality are interconnected in various ways, with personality traits influencing the experience and expression of positive emotions. Positive emotions are feelings such as joy, happiness, gratitude, contentment, and love that contribute to overall wellbeing and psychological flourishing. Different personality traits can shape how individuals experience, express, and respond to positive emotions.

In terms of eudaimonic happiness and SWB, recognizing the potential impact of personality on gorilla welfare underscores the importance of long-term wellbeing. Consistently monitoring the welfare of individuals – both in ex situ and in situ – and adapting management strategies based on their unique personalities can enhance quality of life for gorillas.

Therefore, in ex situ settings, establishing conditions that reduce stressors and improve psychological wellbeing is necessary to meet the emotional requirements of WLGs. This encompasses the reduction of events that provoke stressors, such as translocations or integrations of new group members and human-animal interactions (both keepers and visitors), which might negatively impact the wellbeing of eWLGs.

OWP. The preservation of settings that facilitate natural behaviours and social interactions is crucial for promoting emotional wellbeing among in situ populations, such as WLGs. It is imperative for conservation efforts to prioritise the mitigation of psychological stresses arising from habitat loss and human activities. This approach is crucial in enabling gorillas to attain emotional stability and a sense of security within their native habitats. When the OPA remains unfulfilled, people can exacerbate stress and anxiety in the face of the ongoing sixth mass extinction. Failure to achieve its goals can lead to a heightened sense of powerlessness and despair, impacting mental and emotional wellbeing. Therefore, already for our own wellbeing, it i.e. is of mental and physical wellbeing, it is essential to work towards the fulfilment of the OPA, or even adopt new welfare models that address these concerns, such as the proposed here within my OWP!

iWLGs. See above in OWP. It is imperative for conservation efforts to prioritise the mitigation of psychological stresses arising from habitat loss and human activities. This approach is crucial in enabling gorillas to attain emotional stability and a sense of security within their native habitats.

4. Cognitive Needs: Seven elements contribute towards the cognitive needs of the OWP: Choice, Freedom, Predictability, Self-Efficacy, Control, Feelings of Commitment and Participation in Life. It incorporates the last need in the WAZA (2015) Animal Welfare Strategy, resembling Choice. In the five domain model (Mellor, 2016; Mellor et al., 2020) the aspects of choice, control are interwoven into the behaviour and mental state domains.

Ensuring that animals have opportunities for choice, control, and engagement in complex, cognitively stimulating activities (social and within their environment) is crucial for their welfare, as these factors significantly impact their mental health and overall quality of life. Therefore, the cognitive needs also pertain to the intellectual stimulation, investigation, and problem-solving demands of group-living, including the mental capacity needed to find and remember locations of resources. These demands extend beyond basic survival and are essential to their overall welfare. Cognitive demands encompass the activation of cognitive capabilities, participation in intricate and innovative tasks, and the provision of opportunities for learning and problem-solving.

On the level of the:

eWLGs. The provision of enrichment in captive settings should be introduced in the form of cognitive stimulation using either the provision of play opportunities or environments that can be distinguished by their complexity and novelty. Allowing animals to exercise choice and control over their environment and offering opportunities to make decisions based on their personalities, such as choosing different types of food or engaging in various activities will increase their wellbeing. Situations like these promote positive emotions, minimise stress and maximise wellbeing (Buchanan-Smith et al., 2001). Thus, within ex situ environments, the cognitive requirements of individuals can be met by offering avenues for intellectual stimulation, such as the provision of environmental complexity, puzzle feeders, positive reinforcement trainings, autonomy in daily activities, problem-solving challenges, sensory stimulations, and opportunity for educational experiences. It is advisable to promote the exploration of the environment and the participation in cognitively stimulating activities for gorillas.

OWP. The cognitive component plays a crucial role in multiple facets of conservation, encompassing problem-solving, public engagement, data analysis, and interdisciplinary collaboration. By harnessing cognitive capabilities and comprehending the cognitive determinants that impact human and animal conduct, the OWP can enhance its efficacy in safeguarding and preserving endangered species and their ecosystems.

iWLGs. Gorillas in the wild exhibit remarkable cognitive abilities that are essential for their survival and wellbeing. These abilities are stimulated through various natural behaviours and interactions within their environment. Wild gorillas possess extensive knowledge of their landscapes, which they utilize for foraging, navigating territories, and avoiding predators. This landscape knowledge involves complex problem-solving skills, such as locating food sources that vary seasonally and adapting to changes in their habitat. Group living further enhances cognitive stimulation through intricate social dynamics, including cooperation, communication, and conflict resolution. Gorillas exercise choice and control in their daily activities, from selecting resting sites to making decisions about movement and group interactions. The predictability of environmental and social events also plays a crucial role, as gorillas develop routines and expectations that facilitate their adaptation to the ecological and social complexities of their habitats. Ensuring the stimulation of these cognitive abilities is vital for their survival, particularly in the face of habitat destruction and fragmentation. Conservation efforts must focus on preserving natural habitats that provide the necessary environmental and social challenges to maintain and enhance gorillas' cognitive functions, thereby securing their long-term survival. Therefore, the primary objective of conservation initiatives should be the preservation of habitats that facilitate cognitive engagement among gorillas, so enhancing their overall welfare. By fostering environments that stimulate their cognitive abilities, we can enhance the resilience and adaptability of gorilla populations, contributing to their long-term conservation.

The first 4 needs/ domains are based on the **individual level**/ level of the emotional, subjective wellbeing and safety. The 5th level is going beyond the individual need, meaning towards a level of society, what was used to be referred as the **beyond individual need**.

5, Beyond individual needs – the last need contains following components and operates on the level of the Society, including Cooperation, Conformity, Facilitation, Group Harmonization, Survival of the Species, Ex situ – in situ Conservation and Welfare, OPA, OWA, One Health, Reserve the Red, Mrality, Animal Liberation, Animal rights, Trust, Responsibility, Respect, Conservation, Compassion, Altruism, Empathy, Objective Wellbeing

The Need of "beyond-itself" entails the inclusion of higher-order aspirations, a sense of purpose, and the acknowledgment of the interdependence of species within ecosystems. These needs extend beyond the individual's survival and are associated with the greater good and a sense of meaning in life. Here is, where humans also come into play as being central for the survival of the species, solve global problems, such as the climate crises.

The "One Welfare" Plan (OWP). I emphasize the importance of collaborative conservation efforts that encompass not only the wellbeing of individual species but also the health and balance of entire ecosystems. This approach recognizes that conservation is a shared responsibility that requires cooperation, understanding, and a commitment to the broader goal of sustaining the natural world.

This **adapted Needs/ domain** model aligns with the OWP's commitment not only to conserve species but also to improve the quality of life for all individual animals. This extends to those in managed ex situ populations as well as those in situ, with a focus on enhancing in situ welfare. Animals, including gorillas, often exist within a "continuum between in situ and ex situ" living conditions, which represents a spectrum of varying degrees of naturalness and captivity experienced by these animals (Veasey, 2017). This means that ex situ animals can exist in conditions that can range from closely mimicking their in situ habitat to being entirely removed from it (Veasey, 2017). Furthermore, we must acknowledge that the distinction between in situ and ex situ is not always binary; rather, it encompasses a range of scenarios and degrees of freedom (Veasey, 2017). The continuum between in situ and ex situ highlights that animal welfare should be evaluated within the context of where an animal falls on this spectrum. The more an animal's environment and experiences resemble those in situ, the more likely they are to experience positive welfare. Prioritizing the meaningful over the measurable involves considering the animal's subjective experiences, emotions, and overall wellbeing. This perspective encourages a broader understanding of animal welfare that goes beyond physical health and barriers and includes psychological and emotional aspects which need to be recognised in the OWP. This understanding of how individual differences influence species' responses to conservation efforts can lead to more effective and personalized strategies that consider the unique characteristics of each animal and promote their long-term wellbeing, regardless of living in situ or ex situ.

The OWP aligns with the highest levels of Maslow's Hierarchy of Needs (1943) by transcending individual interests and focusing on the broader wellbeing of the planet. It encourages individuals and groups to work towards a sustainable future for all life. The OWP recognises the value of biodiversity and ecosystems and leads to greater esteem for the natural world, builds momentum for conservation by involving local communities, governments, organizations, and individuals. Recognition of the value of biodiversity and ecosystems leads to greater esteem for the natural world.

Conservation efforts often involve consider global ecological dynamics. This broader perspective fosters a sense of interconnectedness and a commitment to transcending geographic and cultural boundaries for the sake of nature. By integrating conservation into the Self-Actualization and Self-Transcendence Domain/ **Beyond individual needs**, we recognize that caring for the environment and prioritizing sustainability are not just individual actions but profound expressions of human potential and responsibility. It is about finding purpose, contributing to the common good, and addressing immediate concerns to ensure a healthy planet for current and future generations. Therefore, the humans stand central in his role to ensure his own survival by ensuring global species conservation, animal management and welfare.

Therefore, in respect to the ex- and in situ population: The fulfilment of demands that extend beyond the immediate self is achieved by preserving undisturbed ecosystems in their natural habitats. The primary objective of conservation initiatives should be directed towards the preservation of harmonious habitats that sustain the wellbeing of WLGs, while simultaneously acknowledging the significance of the multi-species in wider ecological frameworks.

Below in **Figure 25**, I transitioned the pictured OPA (**Figure 1**, Chapter 1) into the new OWP to show the difference between the former model on the OPA to the novel model on the OWP with the integrated welfare models as introduced in **Figure 24** and text, below.

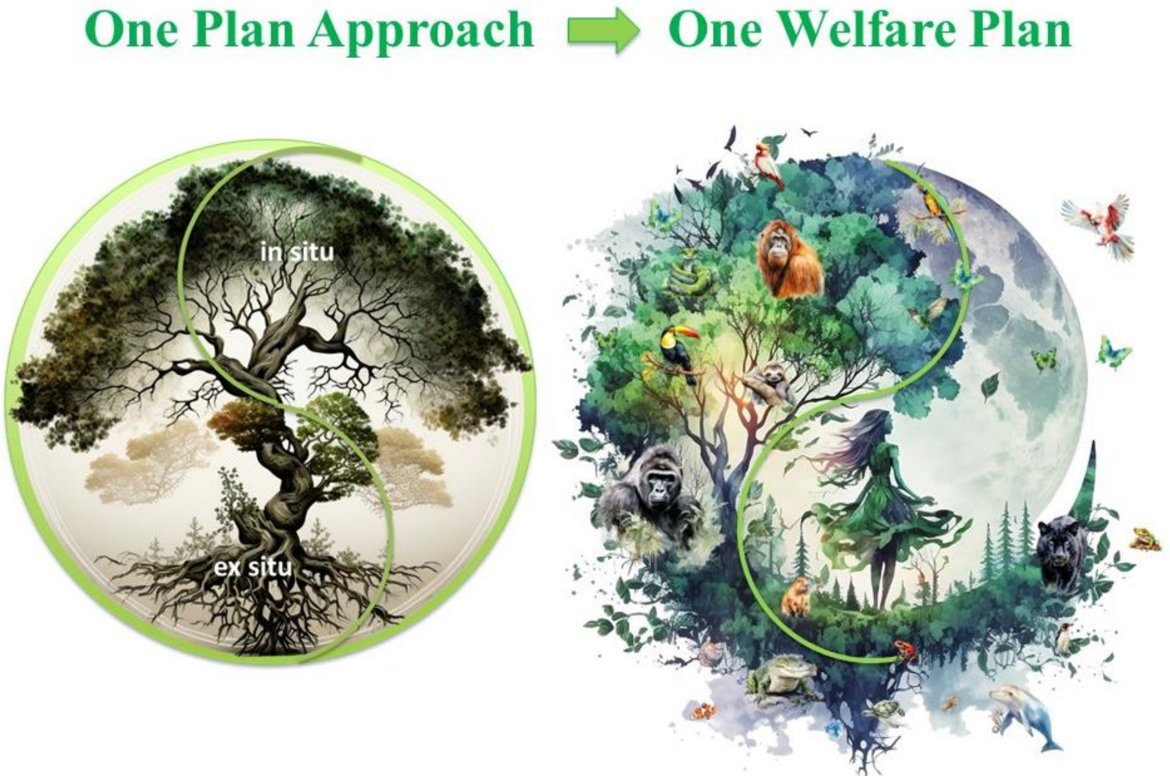

Figure 25 *Transition from One Plan Approach to the One Welfare Plan: image representation*

The **Figure 26** below illustrates the One Welfare Plan (OPW), incorporating previous used symbols from **Figure 1**, Chapter 1. These symbols include the tree of life, representing the integration of the WAZA Animal Welfare Strategy (2015) and the SSC's Species Conservation Planning Principles and Steps (Byers et al., 2022). Additionally, the figure depicts both the ex situ and in situ population within the circle of life, and highlighting the balance between these populations and the species' resilience symbolized by the Yin and Yang.

A notable difference in **Figure 26** is the central placement of the human being is centralised within the "Mother Earth", underscoring humanity's role in improving welfare conditions and taking responsibility for ensuring species survival across all ecosystems. This emphasized the necessity of a global initiative, such as the "Reserve the Red" campaign, to protect and restore our planet. Although this model is adaptable to all taxa, the thesis specifically provides an example using Western Lowland Gorillas (WLGs) within the OWP.

Figure 26 *One Welfare Plan: image representation*

6.3 Recommendations

Below are some recommendations for how my research on personality and SWB can contribute to the OWP in numerous ways, particularly in the context of species conservation and welfare promotion. Understanding the personality and behaviours of individual animals within a species (proximate level) and across (ultimate level) can provide insights that enhance conservation, management and welfare strategies and overall effectiveness. Here's how personality and SWB research can contribute to the OWP:

Tailored In Situ Conservation Strategies. Personality traits can influence how animals respond to various environmental stressors, human interactions, and changes in their habitats. By understanding these traits, conservationists can tailor management and reintroduction strategies to minimize stress and maximize adaptation for different individuals (Brooker et al., 2016; Merrick & Koprowski, 2017; Mittelbach et al., 2014; Wolf & Weissing, 2012, López 2020) .

Reintroduction Success. When reintroducing animals, considering their individual personalities can improve success rates. Animals with specific traits, such as boldness or adaptability, might have a higher chance of thriving in certain environments. Matching individual personalities to suitable release sites can increase the likelihood of successful reintroduction (Coleman & Wilson, 1998; Coss & Biardi, 1997; Dingemanse et al., 2003; Drent et al., 2003; D. Fraser, 2001; Godin & Davis, 1995).

Human-Wildlife Conflict Mitigation. Personality traits might influence how animals interact with humans and human-modified landscapes. Understanding which individuals are more likely to venture into human settlements or cause conflicts can inform strategies to mitigate such interactions.

Mitigating Invasive Species Impacts. In cases where invasive species threaten native wildlife, understanding the behavioural tendencies of both invaders and natives can aid in designing effective control strategies that target specific behaviours.

Ex situ Management and Wellbeing. Zoos are increasingly dedicated to providing the highest standards of care for their animals, aiming to promote not only their physical health but also their psychological and emotional wellbeing. This approach resonates with my recommendation to promote positive psychology for animals and enhance the quality of life for ex situ gorillas. Understanding the personalities of individual animals can help create enriched environments tailored to their needs thereby reducing stress and improving the overall wellbeing of ex situ animals (King & Landau, 2003; Robinson, Morton, et al., 2016; Robinson, Waran, et al., 2016; Weiss et al., 2006; Weiss, King, et al., 2011).

Behavioural Monitoring and Management. Personality traits can affect animal behaviours, including social interactions, foraging patterns, and responses to threats. Monitoring these behaviours can provide insights into how populations are adapting to changing conditions and can guide management decisions (Best et al., 2015; Blumstein et al., 2018; Croft et al., 2009; Freeman & Gosling, 2010; Gold & Maple, 1994; Gosling, 2001; Herrelko et al., 2020; Krause et al., 2010; Kuhar et al., 2006; López, 2020; Massen & Koski, 2014; Morton et al., 2015; Pike et al., 2008; Tetley & O'Hara, 2012; Sih et al., 2004; Weiss, Adams, & Johnson, 2011; Wolf & Weissing, 2010, Weinstein & Capitanio, 2008).

Informed Breeding Programs. Personality traits can have genetic components. Incorporating knowledge of personalities into breeding programs can help maintain or select for desirable traits that contribute to population viability (reproduction: e.g., mate choice, Bergmüller & Taborsky, 2010; Seyfarth et al., 2012; Weiss et al., 2023; Wolf et al., 2008), fitness success (Réale et al., 2009: Smith and Blumstein, 2008), life-history strategies (Réale et al., 2009; Stamps, 2007; Wolf et al., 2007)).

Collaborative Research and Holistic Approach. Collaborating with experts in personality research can enrich the holistic understanding of species' behaviours, needs, and interactions with their environment. This interdisciplinary approach aligns with the collaborative nature of the OWP. Zoos often collaborate with conservation organizations, researchers, and governmental agencies to support in situ conservation efforts. By facilitating collaboration and supplying a collective understanding of gorilla behaviour and personality can help bridge the gap between ex situ and in situ conservation initiatives.

Research and Data Sharing. Zoos are hubs of research and data collection. They can contribute to the understanding of gorilla behaviour, health, and social dynamics, both in situ and ex situ context. Data can be shared with in situ conservation teams, enhancing the collective knowledge of gorilla populations and helping to inform conservation strategies.

Education and Advocacy. Zoos can engage the public and raise awareness about gorilla conservation. The knowledge of individual gorilla personalities can be a powerful tool for educating visitors and creating emotional connections with the local animals. By showcasing gorillas as individuals with distinct personalities, zoos can inspire support for conservation initiatives and advocate for the OWP.

This study on gorilla personalities, conducted in both ex situ and in situ settings, underscores the crucial role that zoos can play in the OWP. Therefore, zoos and other institutions have the potential to contribute significantly to conservation. By integrating personality research into conservation strategies, the OWP can become even more comprehensive and effective. It acknowledges the individuality of animals within a population and harnesses this knowledge to create tailored, adaptive, and successful conservation efforts.

By recognizing and comprehending the diverse range of individual variability within a species, we can create a future in which each animal, whole populations (whether in captivity or in the wild), and humankind as a whole may flourish. The One Welfare Plan has the genuine potential to ensure that conservation initiatives fully acknowledge and address the distinct requirements of each and every species we want to save, therefore promising a future where these efforts are realized. By doing so, we not only protect the invaluable marvels of the natural world, but also secure the foundation for our own welfare.

6.4 Conclusion

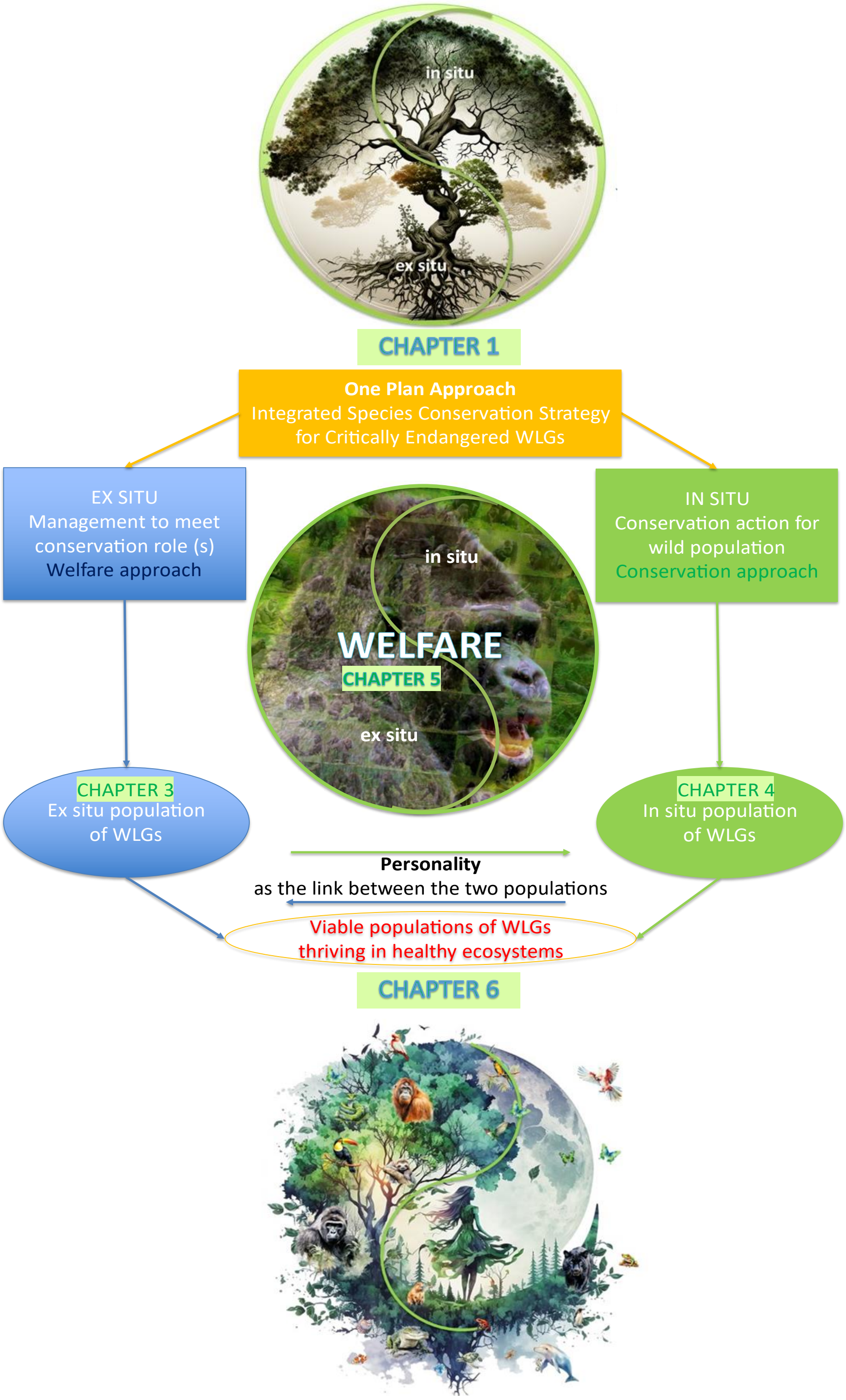

Figure 27 *Road Map for the Approach carried out in the Thesis to achieve the One Welfare Plan*

Figure 27 shows the road Map of my thesis, here below, I will summarise the different steps I took to achieve the integration of personality and wellbeing within the One Welfare Plan:

The One Plan Approach (OPA) is a comprehensive strategy for animal conservation that integrates both in situ and ex situ techniques, with an emphasis on conservation biodiversity through collaborative initiatives across several sectors. Zoos play a crucial role in this endeavour by engaging in diverse activities such as breeding and reintroduction programmes or by understanding and providing social and physical environmental conditions to promote individuals' wellbeing. Gaining insight into the unique characteristics and gorillas' personality is crucial in promoting wellbeing and facilitating efforts to protect and preserve them. To this end, I conducted a study on the personality of ex situ and in situ Western lowland gorillas (WLG) and bridged the gap by integrating this as a novel toolkit – personality and subjective wellbeing (SWB) - within the OPA. The aim was to compare the personality in both WLG populations. The findings illustrate how socio-ecological factors, such as habitat, food, social organisation, and life history, impact the formation of personality development. The observed differences between the in situ and ex situ WLGs demonstrate the complex interaction between environmental dynamics, adaptability, and the evolution of personality. This research not only advances our understanding of gorilla personality and its evolution but also underscores its pivotal role in shaping the wellbeing and adaptive strategies of gorilla populations, with sociability to be key for both, personality, and wellbeing.

Integrated within the One Welfare Plan (OWP), this research offers a holistic new framework for conservation, management, and wellbeing (long-term and short-term happiness) of gorillas in diverse contexts by addressing the five needs/ domains: biological, social, emotional, cognitive and goes beyond the individual needs. It aligns with the principles of Maslow's "Hierarchy of Needs" (1943) updated in WAZA Animal Welfare Strategy (2015), and the "Five Domain Model" (Mellor, 2016; Mellor et al., 2020). It is also based on the concept dealing with a continuum reaching from in situ to ex situ (Veasey, 2017), the "bifocal view" with a balanced approach between the populations (ex and in situ, Keulartz, 2017, 2023), and "The 24/7 Across the lifespan" (Brando and Buchanan-Smith, 2018) to ensure that conservation efforts prioritize optimal welfare and quality of life of animals across different contexts and species.

Additionally, a practical application of positive psychology in conservation can be seen in the efforts to protect and rehabilitate critically endangered WLGs. By adopting this integrated positive psychology insights, we can create conditions that not only prevent extinction but also enable wildlife to thrive, thereby fulfilling our ethical obligation to preserve the rich diversity of life on Earth. This positive psychology framework offers a promising avenue for future conservation efforts, fostering a more sustainable and compassionate relationship between humans and the natural world, with humans being central for the fulfilling of “The Needs/ domains” and beyond. Incorporating insights from this research into the OWP can enhance the conservation efforts for gorillas and can be applied to other species as well.

Our ethical obligation to manage, protect, and conserve wildlife is based on recognizing the intrinsic value of all living organisms and the importance of maintaining ecological balance and diversity. Different ethical approaches, including my positive psychology approach, an optimistic approach to conservation, offer various perspectives on how to fulfil this obligation. This aligns with the ethical principles and conservation objectives of the OWP and holds the potential to enhance the lives of gorillas living in various settings. By addressing their needs on the diverse levels - ex situ, in situ and within the OWP with humans as being central - each providing unique insights into the best practices and opportunities for positive welfare and survival of wildlife, we can strive to fulfil the goals of this comprehensive optimistic conservation strategy. Further research in this area holds the potential to unlock new avenues for enhancing conservation, welfare and managment across different species and environments, ensuring these remarkable primates thrive for generations to come.

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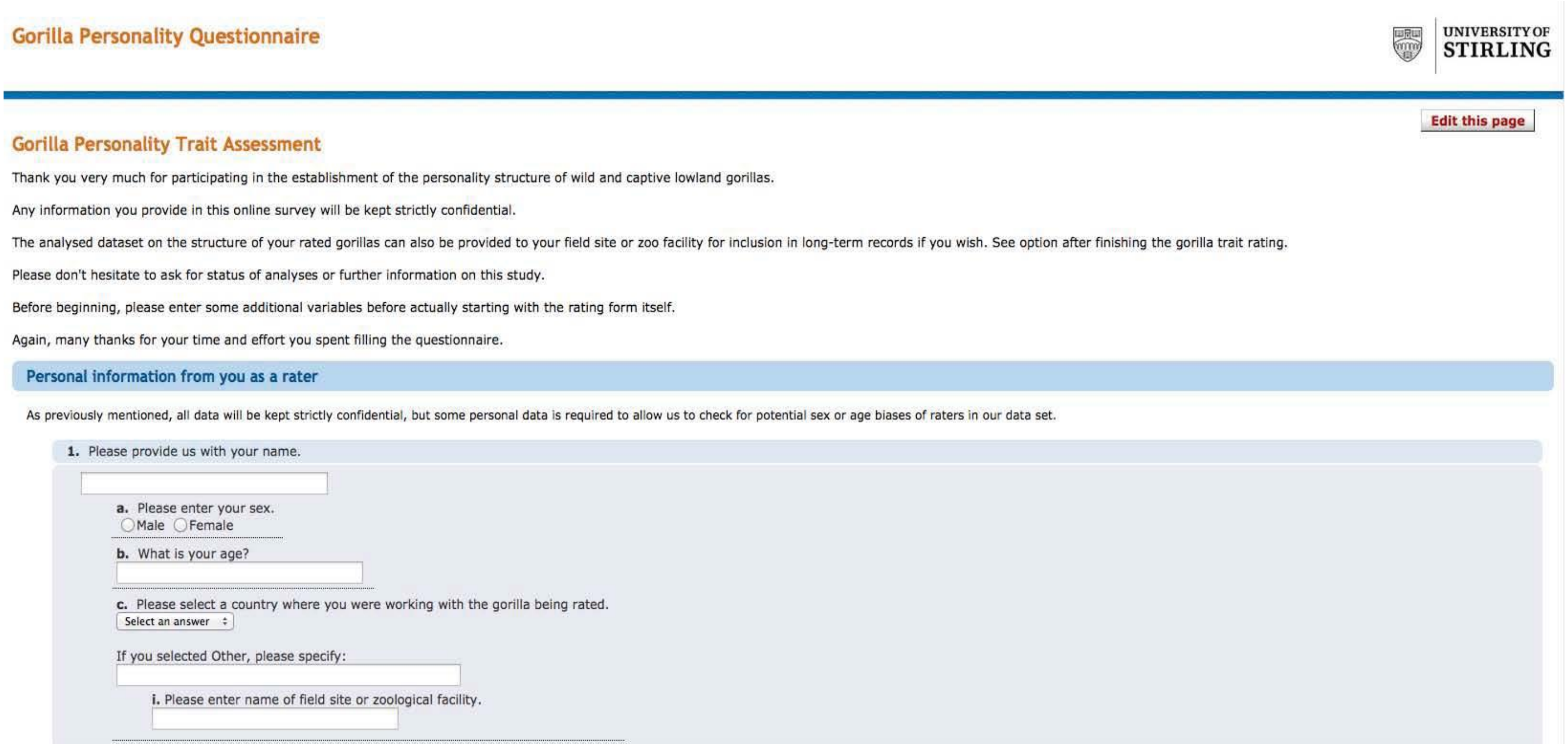
Appendix

TableAPP 1 *Example Gorilla Personality Questionnaire*



Gorilla Personality Trait Assessment

Thank you very much for participating in the establishment of the personality structure of wild and captive lowland gorillas.

Any information you provide in this online survey will be kept strictly confidential.

The analysed dataset on the structure of your rated gorillas can also be provided to your field site or zoo facility for inclusion in long-term records if you wish. See option after finishing the gorilla trait rating.

Please don't hesitate to ask for status of analyses or further information on this study.

Before beginning, please enter some additional variables before actually starting with the rating form itself.

Again, many thanks for your time and effort you spent filling the questionnaire.

Personal information from you as a rater

As previously mentioned, all data will be kept strictly confidential, but some personal data is required to allow us to check for potential sex or age biases of raters in our data set.

1. Please provide us with your name.

a. Please enter your sex.
○ Male ○ Female

b. What is your age?

c. Please select a country where you were working with the gorilla being rated.
Select an answer

If you selected Other, please specify:

i. Please enter name of field site or zoological facility.

Additional information on the gorilla individual being rated

Now we would like to ask you to fill addtional information on the rated gorilla before filling the personality questionnaire.

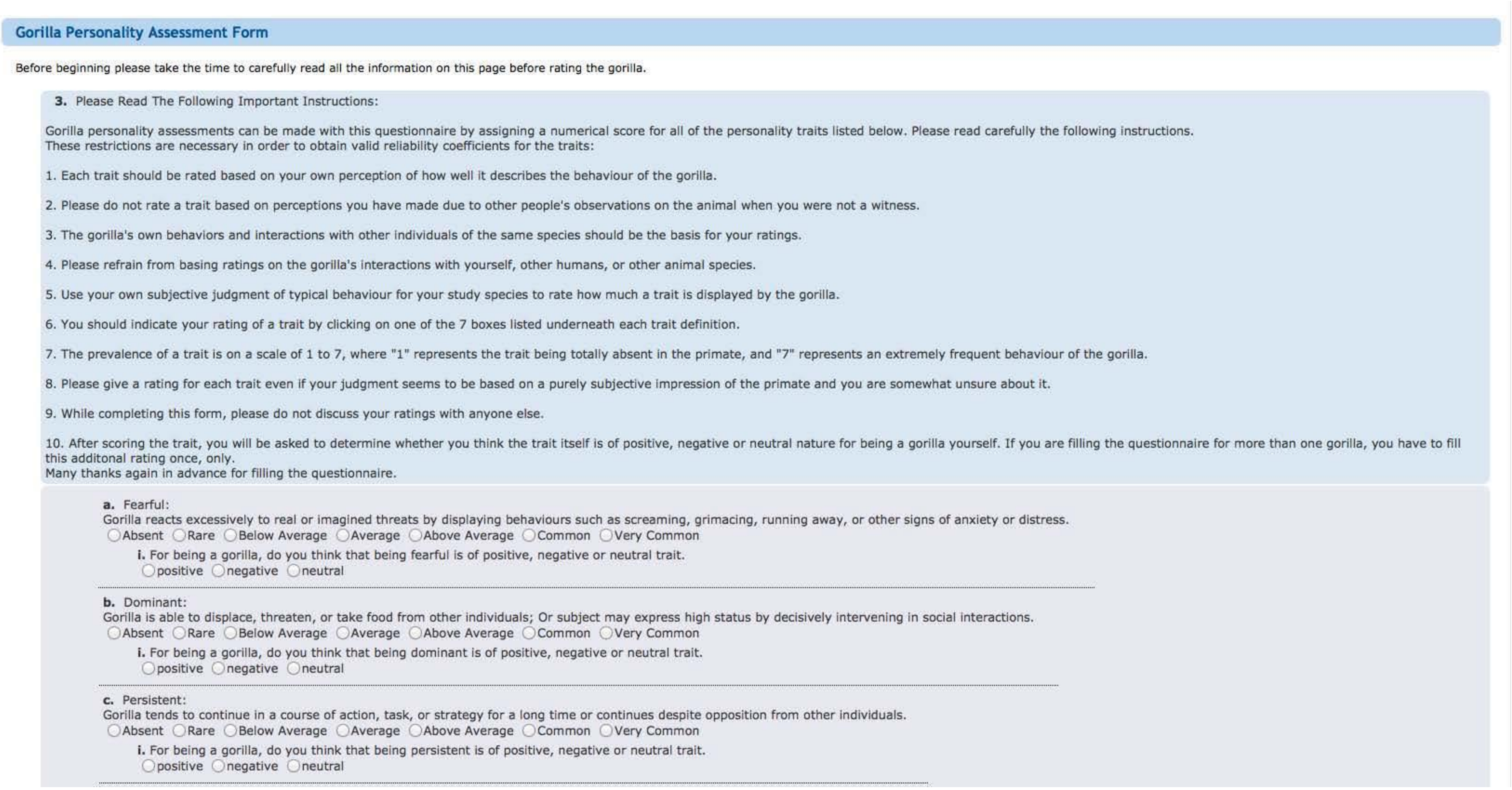
2. Please enter the name of the gorilla who will be rated on this questionnaire

a. How old is the gorilla at the time of the rating?

b. Is the group in which the gorilla is living their natal group (born in this group)?
○ yes
○ no

c. Is the gorilla living solitary or in a group (breeding or all male)?
○ solitary living animal
○ breeding group
○ bachelor group

d. Please enter the social rank of the gorilla in their current group.
○ High ranking male
○ High ranking female
○ Mid ranking male
○ Mid ranking female
○ Low ranking male
○ Low ranking female



Gorilla Personality Assessment Form

Before beginning please take the time to carefully read all the information on this page before rating the gorilla.

3. Please Read The Following Important Instructions:

Gorilla personality assessments can be made with this questionnaire by assigning a numerical score for all of the personality traits listed below. Please read carefully the following instructions.
These restrictions are necessary in order to obtain valid reliability coefficients for the traits:

1. Each trait should be rated based on your own perception of how well it describes the behaviour of the gorilla.

2. Please do not rate a trait based on perceptions you have made due to other people's observations on the animal when you were not a witness.

3. The gorilla's own behaviors and interactions with other individuals of the same species should be the basis for your ratings.

4. Please refrain from basing ratings on the gorilla's interactions with yourself, other humans, or other animal species.

5. Use your own subjective judgment of typical behaviour for your study species to rate how much a trait is displayed by the gorilla.

6. You should indicate your rating of a trait by clicking on one of the 7 boxes listed underneath each trait definition.

7. The prevalence of a trait is on a scale of 1 to 7, where "1" represents the trait being totally absent in the primate, and "7" represents an extremely frequent behaviour of the gorilla.

8. Please give a rating for each trait even if your judgment seems to be based on a purely subjective impression of the primate and you are somewhat unsure about it.

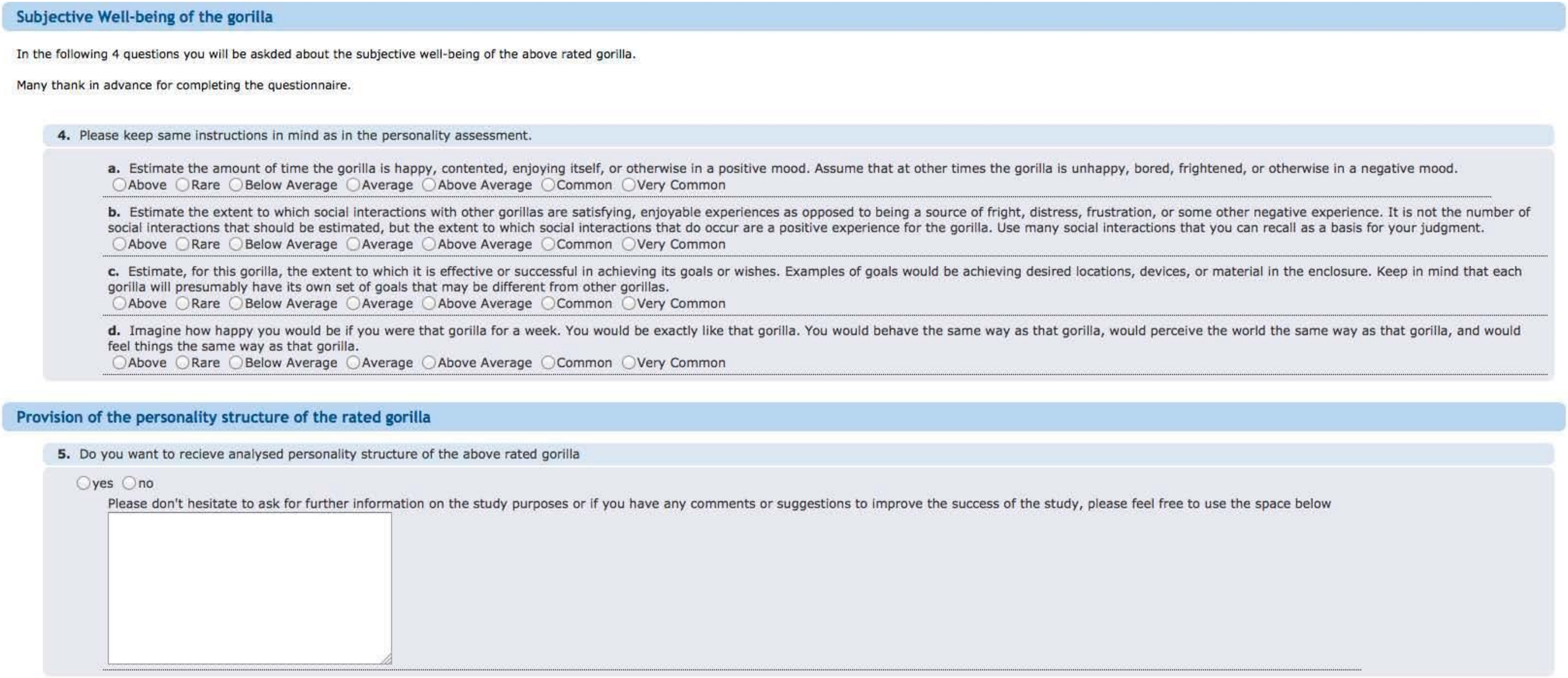
9. While completing this form, please do not discuss your ratings with anyone else.

10. After scoring the trait, you will be asked to determine whether you think the trait itself is of positive, negative or neutral nature for being a gorilla yourself. If you are filling the questionnaire for more than one gorilla, you have to fill this additonal rating once, only.
Many thanks again in advance for filling the questionnaire.

a. Fearful:
Gorilla reacts excessively to real or imagined threats by displaying behaviours such as screaming, grimacing, running away, or other signs of anxiety or distress.
○Absent ○Rare ○Below Average ○Average ○Above Average ○Common ○Very Common
i. For being a gorilla, do you think that being fearful is of positive, negative or neutral trait.
○positive ○negative ○neutral

b. Dominant:
Gorilla is able to displace, threaten, or take food from other individuals; Or subject may express high status by decisively intervening in social interactions.
○Absent ○Rare ○Below Average ○Average ○Above Average ○Common ○Very Common
i. For being a gorilla, do you think that being dominant is of positive, negative or neutral trait.
○positive ○negative ○neutral

c. Persistent:
Gorilla tends to continue in a course of action, task, or strategy for a long time or continues despite opposition from other individuals.
○Absent ○Rare ○Below Average ○Average ○Above Average ○Common ○Very Common
i. For being a gorilla, do you think that being persistent is of positive, negative or neutral trait.
○positive ○negative ○neutral



Subjective Well-being of the gorilla

In the following 4 questions you will be askded about the subjective well-being of the above rated gorilla.

Many thank in advance for completing the questionnaire.

4. Please keep same instructions in mind as in the personality assessment.

a. Estimate the amount of time the gorilla is happy, contented, enjoying itself, or otherwise in a positive mood. Assume that at other times the gorilla is unhappy, bored, frightened, or otherwise in a negative mood.
○Above ○Rare ○Below Average ○Average ○Above Average ○Common ○Very Common

b. Estimate the extent to which social interactions with other gorillas are satisfying, enjoyable experiences as opposed to being a source of fright, distress, frustration, or some other negative experience. It is not the number of social interactions that should be estimated, but the extent to which social interactions that do occur are a positive experience for the gorilla. Use many social interactions that you can recall as a basis for your judgment.
○Above ○Rare ○Below Average ○Average ○Above Average ○Common ○Very Common

c. Estimate, for this gorilla, the extent to which it is effective or successful in achieving its goals or wishes. Examples of goals would be achieving desired locations, devices, or material in the enclosure. Keep in mind that each gorilla will presumably have its own set of goals that may be different from other gorillas.
○Above ○Rare ○Below Average ○Average ○Above Average ○Common ○Very Common

d. Imagine how happy you would be if you were that gorilla for a week. You would be exactly like that gorilla. You would behave the same way as that gorilla, would perceive the world the same way as that gorilla, and would feel things the same way as that gorilla.
○Above ○Rare ○Below Average ○Average ○Above Average ○Common ○Very Common

Provision of the personality structure of the rated gorilla

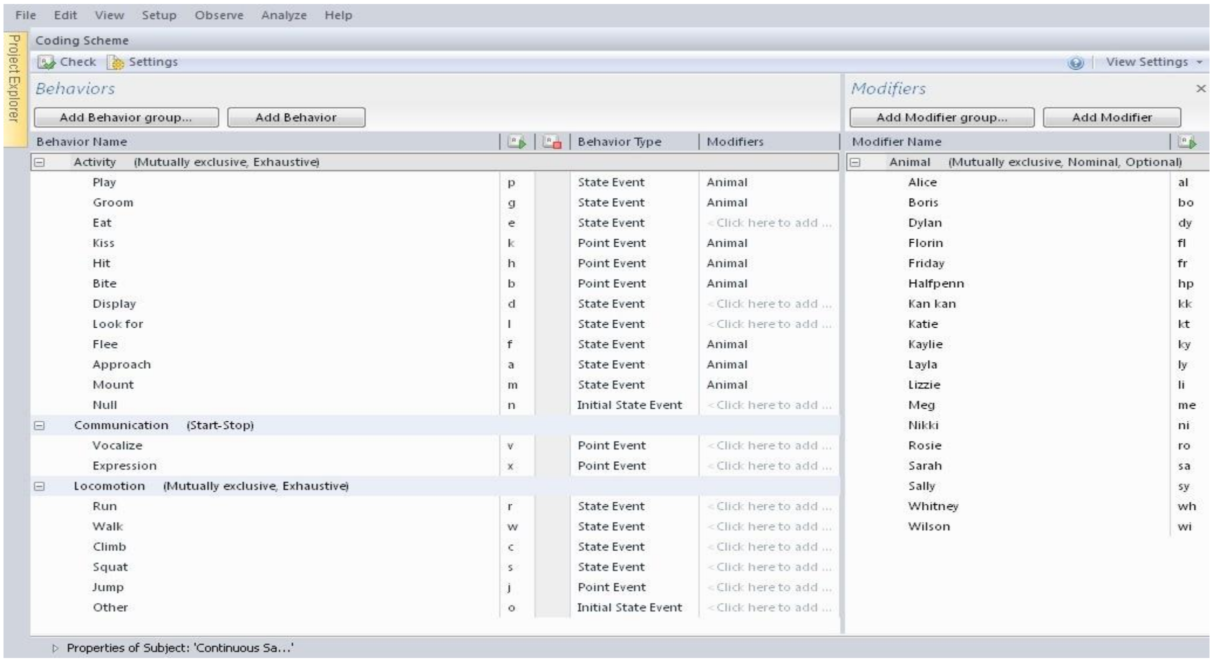
5. Do you want to recieve analysed personality structure of the above rated gorilla

○yes ○no

Please don't hesitate to ask for further information on the study purposes or if you have any comments or suggestions to improve the success of the study, please feel free to use the space below

TableAPP 2 *Ethogram*

Observation_ Noldus: Mood – state dependent behavioural responses



Behavior Name			Behavior Type	Modifiers
Activity (Mutually exclusive, Exhaustive)				
Play	p		State Event	Animal
Groom	g		State Event	Animal
Eat	e		State Event	<Click here to add ...
Kiss	k		Point Event	Animal
Hit	h		Point Event	Animal
Bite	b		Point Event	Animal
Display	d		State Event	<Click here to add ...
Look for	l		State Event	<Click here to add ...
Flee	f		State Event	Animal
Approach	a		State Event	Animal
Mount	m		State Event	Animal
Null	n		Initial State Event	<Click here to add ...
Communication (Start-Stop)				
Vocalize	v		Point Event	<Click here to add ...
Expression	x		Point Event	<Click here to add ...
Locomotion (Mutually exclusive, Exhaustive)				
Run	r		State Event	<Click here to add ...
Walk	w		State Event	<Click here to add ...
Climb	c		State Event	<Click here to add ...
Squat	s		State Event	<Click here to add ...
Jump	j		Point Event	<Click here to add ...
Other	o		Initial State Event	<Click here to add ...

Modifier Name	
Animal (Mutually exclusive, Nominal, Optional)	
Alice	al
Boris	bo
Dylan	dy
Florin	fl
Friday	fr
Halfpenn	hp
Kan kan	kk
Katie	kt
Kaylie	ky
Layla	ly
Lizzie	li
Meg	me
Nikki	ni
Rosie	ro
Sarah	sa
Sally	sy
Whitney	wh
Wilson	wi

FEEDING	**Remark type of food**
Forage/Feed	Actively examining exhibit for forage/browse material. Scanning ground for food, stripping browse, etc. Individual may be sitting, standing, shuffling, or walking. Food directed activity such as eating.
Drink	Individual is ingesting water. Does not include ingestion of urine

Category	**Definition**

SOCIAL CONTACT	**Interaction & Proximity, if in contact with others**
Alone/solitary Social	No other gorilla in view
Out of sight	When the individual that is observed is partly or completely invisible, i.e. when a behaviour could be missed because of lack of sight

ACTION BEHAVIOUR	**(active/ passive), DIRECTION**
Inactive	Inactive behaviour: sitting, lying down, sleeping, hanging, relaxing with eyes open or closed, standing or standing upright
Locomotion	Moving: walking, running, hanging, jumping, sliding, climbing, following, … Social locomotor: Involves travel while in contact with another. Buddywalk: Animals walking tripedally or bipedally while holding each other across the shoulder or on the hips. This form of travel could involve more than one other individual.
Walking together Contact resting Sitting together, touching	Focal individual walks with one or more other individuals, following each other and/or walking next to each other Sitting next to each other and bodies touch each other
Nest building	Subject construct a platform for sleep or rest by bending branches or other materials (f.e. blankets, woodwool) over each other. Behaviour includes bending, transporting it, sitting, and standing bipedally or lying on it

PLAY	P	(active/passive), DIRECTION
Object play		
Om	Object Manipulation	Manipulation on an object or attempts to manipulate a fixed object with concentrated attention—this includes touching, pulling, lifting with mouth, hand, or foot; it may also include some patterns typical for play fighting
Oa	Object transporting	A gorilla carries an object, steadily concentrates on the object watching it or repeatedly looking at it
	Object carrying	A gorilla holds or carries an object during locomotor or social play, does not steadily concentrate on the object, object is not crucial for the progression of play
	Own-body-part play Play sitting on Play jumping on	A gorilla plays with a part of its own body, foot, hand, or fingers A playful gorilla target sits on a distinct object A playful gorilla target jumps on an object and then it either stays on it or continues in locomotion
	Play throwing object	A playful gorilla throws an external object
	Play climbing on Play swinning on Play wave	A playful gorilla climbs on external object A playful gorilla swings an external object A playful gorilla waves an external object
	Play with water	
	Play rubbing	A gorilla rubs an object with palms of its hands against a tree trunk, floor, or other substrate
Play (Solitary, social and locomotion play)		
	Acrobatic Play Pirouetting	An animal climbs, jumps, and dangles from supports in its environment (e.g., branches, ropes, etc.) in solitary or social way (animals climb, jump, and dangle together and concurrently often on the same support) An animal performs rolling over either on the ground or on vertical supports in solitary or social way (animals roll in contact hanging on the same vertical support)
	Play recovering a thing Play running Play chase	Animal chases playmate and attempts to grab object carried by it Animal runs alone (solitary play) A playful gorilla chases another one or is being chased
	Somersault	An animal flips over either on the ground or on vertical supports in solitary or social way (animals flip in contact)
	Jumping	An animal jumps on equipment present in its environment
	Rolling	Turning the body from side to side while supine; can be complete or incomplete rotation
	Dangling	An animal holds an infant by its hands and allow it to dangle in the air
	Airplain	An adult lies on its back and rises an infant up with its hands and feet
	Gentle wrestling	Limbs entwined while sitting or laying; gorillas roll/twist together placing open mouths on each other
	Climbing or standing on another	An animal climbs or stands on the body of a conspecific
	Play bite Play kick	An animal bites gently bites a playmate The partner's body is kicked either with the with the hands or feet
	Play pull	An animal pulls a playmate
	Play push	An animal gently pushes a playmate either with its hands or feet
	Play retrieve Play slap	An animal holds a playmate to avoid its flight An animal slaps any part of the fellow's body
	Rough and tumble (rough wrestling)	Vigorous bipedal wrestling. Typically consisted of chasing, lunging, tackling, vigorous wrestling, falling on the other, and vigorous mock biting
	Tickle Play brusque rush	An animal contacts the partner's body with its mouth or hands An animal jumps with its four limbs onto a playmate
	Play stamping	An animal jumps on a play partner with its feet
	Flip	An animal jumps over the head or back of another ('leapfrog')
	Play fight	Playful gorillas fight together but with no obvious intention to hurt each other seriously; it resembles agonistic combats
	play clapping	hands or drumming on the floor or other substrate
	play rolling	
	play sliding Chest beating	Sliding down from hill, tree or other external equipment An animal repetitively strikes the chest or belly area with outstretched or cupped hands (used generally to invite to play)
	piggy back ride Peek-a-boo	

MOTHER-INFANT INTERACTIONS **MOTHER POSITIVE**	**(active/ passive,both), DIRECTION**
M psychological availability	M looks at infant, directs her face towards her infant
M look	M is attentive when gorilla infant communicates (e.g., looks at them);
M attention	M modifies her position to have better eye contact, to watch communication given by the infant or play of infant;
M surveillance	M joins an infant who is engaged/busy in something (e.g. enrichment), makes herself available.
M available	
M responds to gorilla infant M adapt	M paces caregiving to match infants's behavior (e.g., waits for infant when moving), is patient during eating or playing; M responds to infant's behavior, signals, and communication attempts; in a positive way, encouragement
M response	M and infant communication, exchange
M communication	
M directs behaviors towards the infant M tickles	M tickles M lets infant lead and she doesn't mind (e.g., allowing the infant to do something to the caregiver such as pulling hair or touching),
M let infant lead	M tolerates food stealing (running away) from infant
M tolerate food taking	M initiates social interaction (engage in interaction with infant e.g. communication).
M initiate interaction	Mother initiates social play (e.g. Chasing, wrestling or slapping of an individual by another, without agonistic elements, often accompanied by a play face) with the infant.
M initiate play	M appropriately allows infant to "do their own thing."
M allow	
M support, empathy, guidance M guide	M changes infant behavior in a positive and supportive way by providing "guidance"

MOTHER NEGATIVE	(active/ passive,both), DIRECTION
M detachment M ignores infant	in the presence of a infant, mother does not make eye contact; mother does not react to infant in a social way; mother does not engage infant when that would be possible, mother ignores them when they are feeding, playing;
M busy M drops food	in the presence of a infant, mother does other tasks during free time, such as responding to other caregivers, takes a "break" or groom herself, drops food instead of feeding the infant or does not nurse
M failure to respond	
	M responds but in a nonsocial, mechanical manner.
M control movement of the infant	M fails to share enthusiasm, joy, or excitement of infant;
M block I M interrupts I	Mother prevents the infant from leaving using physical restraint (e.g. by pulling the infant by the arm or leg or by holding the infant firmly in her arm M interrupts infant activity to get the infant to do something else
MI rejects	Mother prevent the infant from making contact or suckling by holding the infant at a distance with the arm, by blocking her chest with her arm, or by avoiding the infant
M punishes an I M grabs	M physically and negatively grabs a child to move

INFANT POSITIVE	(active/ passive,both), DIRECTION
Infant responsiveness and anticipation	
Infant look	Infant actively looks at caregiver,
Infant initiate interaction	I attempts to engage interaction with caregiver
Infant anticipate	I anticipates mother engagement by a change of behavior (e.g. smiling, showing excitement)
Infant response I engage play	I responds to mother's behavior, signals, and communication attempts I tries to get mother to play
I watch	I watches caregiver intently
Infant imitate	I imitates behaviour of mother or caregiver
I seek security I check	infant seeks caregiver when experiencing stress or is upset; Infant uses caregiver as a "secure base" (e.g. by looking at the caregiver to share a positive or negative experience)
I stress when left	infant shows separation anxiety or distress when caregiver leaves or turns head away, infant attempts to re-engage caregiver;
I cautious I beg	infant shows wariness of strangers and may cling to caregiver or hold on to her. infant begging for food or object from mother

INFANT NEGATIVE **I detachment**	(active/ passive,both), DIRECTION
I no anticipation	I does not smile or get "excited" with anticipation of caregiving
I I failure to respone	
I no response to positive I no response to negative	I seems unresponsive emotionally and physically to appropriate and positive caregiver behavior and caregiver attempts to engage the infant (e.g., attempts to get the infant to smile or laugh); I seems unresponsive emotionally to negative caregiver behavior or harsh handling;

NEUTRAL MI INTERACTION **no neutral iinteraction**	(active/ passive,both), DIRECTION
MI neutral	
MI inspection	Mother visually or manually inspects the infant's body without grooming (include smelling)
manipulation	M or I manipulates (rub, rock, scratch, turn, bounce) I or M excluding play behavior
I carrying MI supports carrying M crutch walk	Supported by the mother with one or both arms (supported); infant on mother's lap, M move using arms as crutches
I ventral	the offspring clings unaided to the ventrum (clinging ventral);
I on M	offspring on mother other than ventral or dorsal
I dorsal	the offspring sits on, or clings to the mother's back (dorsal);
I travels independent	travel independent of the mother (independent)

POSITIVE AFFECT	(active/ passive,both), DIRECTION
positive affect	
Smile	Grin
Laugh	facial expression of laughing face, often together with verbal expression, such as giggeling
Rock	M rocking infant
Breast feeding	nurse
Embrace	M hugs (embrace)
Kiss	puts mouth on body part of individual
Tenderness	holds in an affectionate way
Hold hands	MI holding hands
Nuzzle	M nudge infant with the nose
Caress	gently rubs mouth or hand over body (head)
Social lick	puts mouth on body part of individual
Muzzle-muzzle	face to face with individual (less than 15cm)
watch attentively	
Greet	(e.g. Raise hand to individual)

AFFILITIVE BEHAVIOUR (active)	B	DIRECTION/Laterality
Affiliative behaviour	Implies all kind of friendly/prosocial behavior (f.e. embraze, nuzzle, hug, hand contact, kiss, reconsiliation after aggression, play)	
Allogrooming	One animal manipulates the fur, extremity, or orifice of another. During a grooming episode, the groomer often looks intently at the portion of the body which is being manipulated. Grooming may include both manual and oral components. (Manual: Individuals use the fingers and whole hand to manipulate and remove materials; Oral: use of mouth and lips to manipulate and/or remove materials)	
Self-grooming	The animal is grooming itself	

SEXUAL BEHAVIOR	(active/ passive), DIRECTION
Sniff	
Precopulatory behaviour	sexual behavior which occurs prior to copulatory mounting, like presenting
Mount solicitation	Hind quarters oriented toward partner with tail up
Inspect genitals	Close visual, tactile, or olfactory scrutiny of the own genitalia or genital region of another
Mounting	Hands on partner's hips and double foot clasp
Rape	
Incomplete mount	Hands on partner's hips or double foot clasp

AGONISTIC	(active/ passive), DIRECTION, Attack or Threaten
Contact aggression	Physical contact between individuals, includes all forms of agonistic behaviour like grabbing, shaking, attack wrestling, crouching, aggressive biting, pushing, pulling, finger-fighting, hitting, slapping, kicking, dragging, grappling,
Non-contact aggression	No physical contact between individuals or an object, includes f.e. supplanting, presenting, threating leap, threating present, fleeing, chasing, drumming, fear grimacing, lunging, staring, hiding, displaying (charging), cage-shaking, or submissive behaviour like moving out of the way of another individual to avoid aggression (detour) or other submissive gestures (appeasement) directed towards a dominant individual after aggression, or in an attempt to prevent aggression. It includes pant-grunts, crouching, touch, kiss, embrace, present, brief grooming, creeping
Intimidation	Also known as pilo-erection. The hairs stand on end, erect fur, to look bigger, to intimidate or impress
Submission	Avoid gaze, move away, avoid

OTHER BEHAVIOUR	
Snout brushing	Repetitive brushing of the nose by hand or food
Single nose touch	A single touch of the nose with one finger
Wipe	Use of leaves, straw, paper, etc. to wipe dirt (faeces, urine, mud, ejaculate, etc.) from self or others
Scratching	A single scratch or repetitive scratching the body but belonging to one stroke/movement
Body shake	(short) shake of the entire body
Missed/error	Not yet defined behaviour
Adduct penis	Erect penis spasmodically jerks
Cough	Coughing or sneezing which belongs to a cold or and cough
Other remainder	All other behaviours not definied in above mentioned descriptions
Yawning	Yawn, opening mouth and showing teeth

ABNORMAL BEHAVIOUR	
Splash water	
Hair plucking	
Rocking	
Urophagy	Ingesting urine
Coprophagy	Ingestion of feces
Eating salvia	Repetitive depositing and sucking up one´s own saliva
Eating vomit	Ingestion of own vomit
Ingestion other (vomit)	Ingesting another individual's vomit
Manipulation feces	Manipulating feces with the hands and/ or the mouth
Smearing feces	Smearing feces on a surface with the hands and/ or the mouth
Sucking on others/ objects	Non nutritive sucking on objects or others, not associated with foraging
Licking on objects/ others	Non nutritive licking on objects or others, not associated with foraging
R/R	
Hand in the mouth	putting own hand in mouth to initiate/which results in vomiting
Licking hands	Non nutritive licking of hand or fingers, associated with regurgitation/reingestion, often following ingestion of own vomit
Stamping	repetitive stamping of the feet while seated, associated with regurgitation/reingestion
Weaving	Seated making (slow) movements with the upperbody from left to right, often with both hands on the floor next to the body, associated with regurgitation/reingestion
R/R Head shake	A single or multiple head shake to initiate/which results in vomitting, associated with regurgitation/reingestion
bottom up	repetitive moving the bottom up to initiate/which results in vomitting, not associated with foraging
Abnomal behavior in interchange	Any abnormal behaviour which is adressed towards keepers, other groups or observer. Includes social affiliative as well as agonistic behavior. F.e., Eye flashing, warning growl, beg, splash with water..

Emotions	Definition
Anger (revenge)	A Gorilla might be blocked from pursuing a goal and/or has the feeling of being treated unfairly. They express a form of unhappiness, frustration and is often connected to violence. They can show strong dislike or impatience about something and is mad about the situation.
Anxiety	Gorilla seems uneasy, solicitude and/ or apprehensive about an uncertain event or matter; gorilla expresses fearfulness, might be frightened, scared or worried, insecure to express or continue with a certain behaviour or another individual
Boredom	Gorilla is lacking the joy or need to interfere with others or the surrounding, uninspired, down, no arousal
Contentedness	Gorilla expresses the feeling or showing satisfaction with their possessions, behaviour, or situation, synonym for satisfaction
Curiosity, attention	Gorilla tries to see or know objects, other individuals, novel situations
Empathy	Gorilla shows the tendency to understand and shar the feelings of another gorilla or the situation in which the gorilla is in
Excitement	A gorilla is highly positive aroused by a situation, object or what another gorilla or individual is doing in his surroundings. He shows great enthusiasm, is aroused and reactive
Fear	Gorilla is afraid or expresses a feeling of worry, being concerned or insecure, synonym for terrified, scared, afraid, frightened
Frustration	Gorilla expresses the feeling of being upset or annoyed as a result of being unable to change or achieve something. It seems that the prevention of the progress, success of a goal or fulfilment of something makes him feel annoyed, angry or bitter
Gentle	Gorilla is showing a mild, kind or tender behaviour towards on object, or another gorilla, they are moderate in action, effect and degree
Gratitude	Gorilla shows a form of appreciation or thankfulness to another gorilla.
Inspiration	Gorilla is highly aroused, animated or guided by his surrounding, an object, another gorilla or event, synonym for inspirited, animated, influenced, roused
Jealous	Gorilla attempts to disrupt activities between other gorillas or is troubled by others who are in a preferable position (food, location)
Joy	Gorilla expresses pleasure or being in good fortune, synonyms for happy, enjoying, being satisfied, cheerful
Love	Gorilla shows an intense feeling of deep affection, a great interest and pleasure with something they do or with another gorilla,
Pride	A gorilla is expressing a feeling of deep pleasure or satisfaction derived from the own achievements of the gorilla, the achievements of those with whom they are closely associated.
Sadness	Gorilla is experiencing or showing sorrow or unhappiness, synonym for unhappy, sorrowful, distressed
Sensitive	Gorilla is experiences sensitivity towards another event, object or individual in a form of deeper connection, compassion or sensibility with their senses
Sympathy	Gorilla is expressing the feeling of pity or sorrow for another gorilla's misfortune, synonyms are
Tenderness	Gorilla shows a strong sensitivity towards pain, soreness or expresses another deep affection towards himself, another gorilla or surrounding
Restless	Gorilla looks unable to rest or relax, this could be in form of physical or emotional rest, involving constant activity
no emotion recognizable	
other positive	
other negative	

Modifier

Pr	Inter-primate proximity
0	in contact, body parts touching
1	1.5 meter of another
2	1.5 meters but > 5 meter of another
3	> 5 meter of another

D		**directed to itself, cage partner, caretaker or observer**
R		**Receiving from cage partner, caretaker**
	J	Jambo
	Mi	Mintha
	Ma	Mandji
	N	Nemsi
	L	Lobo
	G	Gyasi
	K	Kisiwa
	C	Chama
	W	Wimbé
	T	Tayari
	Mp	Mapasa
	I	Iriki
	Mu	M'fungajii
	Mz	M'Zungu
	S	Itself
	C	Caretaker
	O	Observer
	V	Visitor

TableAPP 3 *Reliabilities of Personality Traits in eWLGs (intraclass co-efficients)*

Trait	**ICC(3,1)**	**ICC(3,k)**	**Trait**	**ICC(3,1)**	**ICC(3,k)**	**Trait**	**ICC(3,1)**	**ICC(3,k)**
Submissive	.64	.86	Friendly	.45	.75	Conventional	.31	.62
Playful	.64	.86	Inquisitive	.45	.74	Individualistic	.31	.61
Dominant	.63	.86	Vulnerable	.44	.74	Sympathetic	.30	.61
Active	.63	.86	Anxious	.43	.73	Impulsive	.30	.61
Autistic	.57	.83	Imitative	.43	.73	Manipulative	.30	.60
Lazy	.55	.81	Jealous	.38	.68	Erratic	.30	.60
Bullying	.54	.80	Fearful	.37	.67	Stable	.30	.60
Innovative	.53	.80	Cool	.36	.67	Distractible	.30	.60
Social	.52	.80	Depressed	.36	.67	Sensitive	.29	.60
Solitary	.52	.79	Persistent	.36	.67	Unemotional	.28	.58
Stingy/Greedy	.51	.78	Defiant	.36	.66	Predictable	.27	.57
Inventive	.50	.78	Gentle	.35	.66	Cautious	.25	.55
Dependent	.49	.77	Independent	.34	.65	Decisive	.24	.53
Affectionate	.48	.77	Helpful	.34	.65	Disorganized	.24	.53
Aggressive	.48	.77	Excitable	.34	.65	Clumsy	.22	.50
Timid	.46	.75	Reckless	.33	.63	Quitting	.20	.46
Irritative	.46	.75	Protective	.32	.63	Thoughtless	.19	.45
Curious	.46	.75	Intelligent	.31	.62	Unperceptive	.18	.44

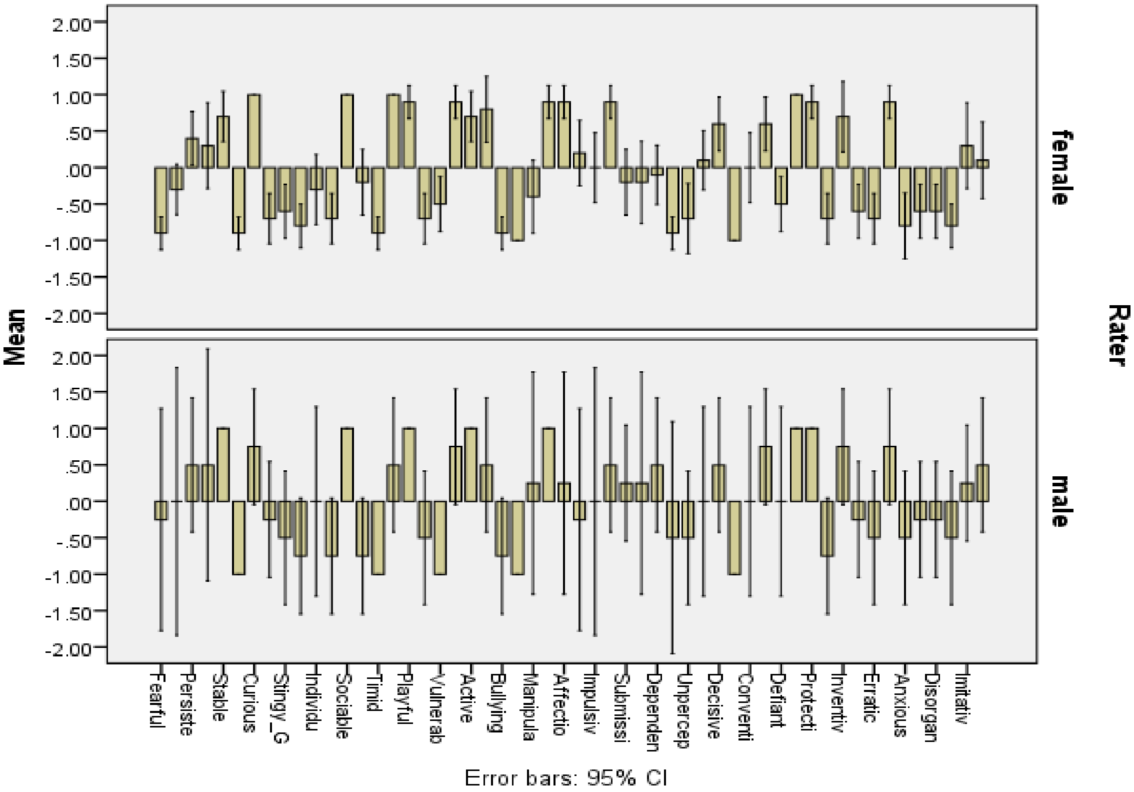
Note.
1= individual ratings; k = the mean number of raters per subject (k=3.54). Data are based on 184 individuals, 90 raters and 652 ratings.

TableAPP 4 *Reliabilities of the personality factors of eWLGs (intraclass co-efficients and Cronbach's alpha)*

Factors	ICC(3,1)	ICC(3,k)	Cronbach's alpha
Dominance	.67	.88	.87
Openness	.71	.90	.89
Conscientiousness	.47	.76	.70
Agreeableness	.54	.81	.86
Neuroticism	.55	.81	.78
Extraversion	.53	.80	.66

Note.
1= individual ratings; k = the mean number of raters per subject.
Data are based on 184 individuals, 90 raters and 652 ratings.

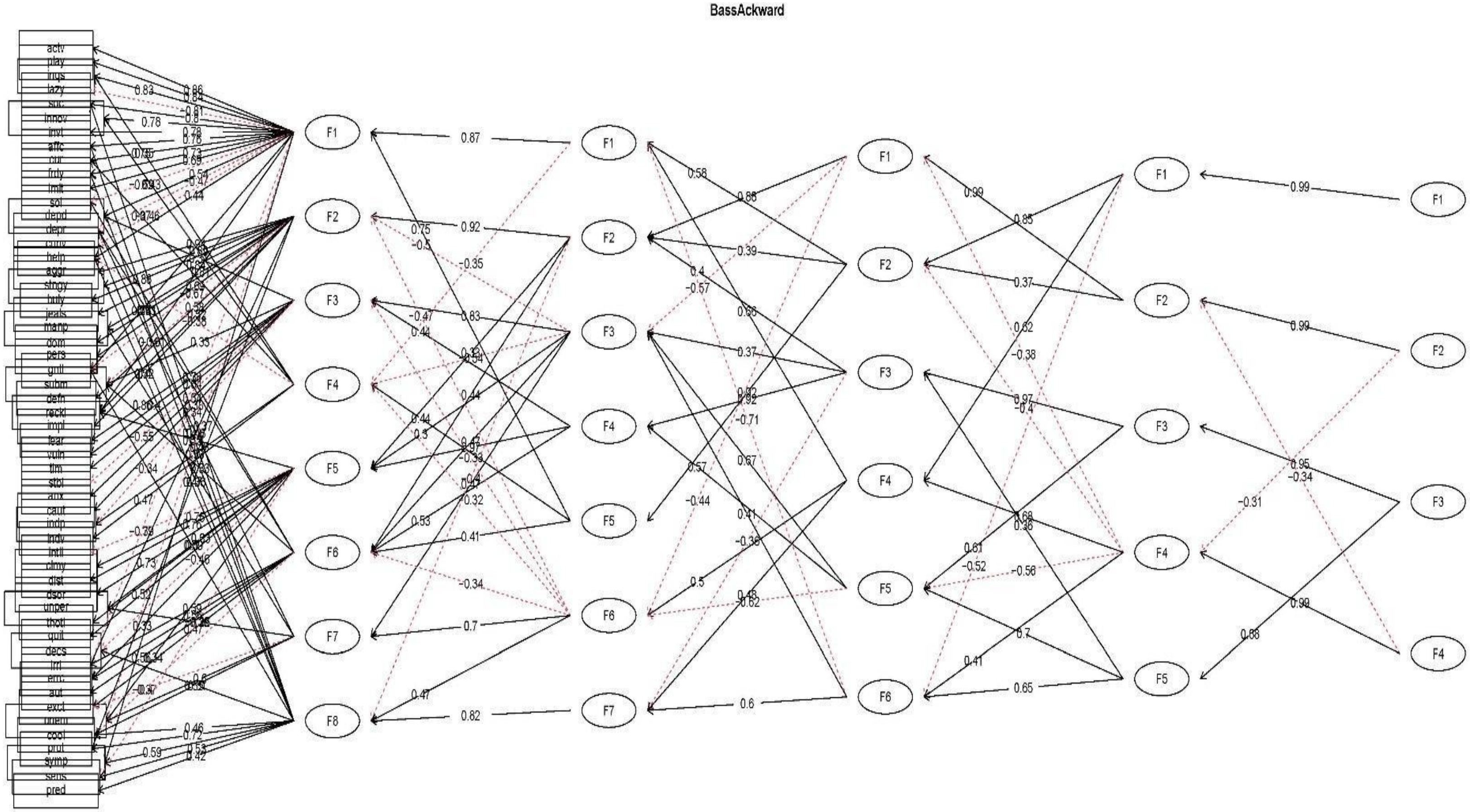
TableAPP 5 *Human gender Differences in the personality questionnaire.*



TableAPP 5 shows the mean and standard deviation of each rated personality trait sorted by gender of human rater. Gender-differences have been found for the following traits;

Mean and standard deviation of each rated personality trait according to raters (N = 15 females, N = 10 males)

TableAPP 6 *Distribution of traits across different number of factors (from 8 to 4) according to the Bass-Ackward factoring algorithm*



Notes: The provided diagram shows a Bass-Ackward factoring model applied to the set of 54 personality traits from the GPQ.
The traits (listed on the left) are grouped into factors (F1 to F8). The number of factors is reduced from 8 to 4.
E.g. Eight-Factor Model (F1 to F8): Each trait is associated with one or more factors. Factor loadings indicate the strength of the relationship between each trait and the factor.
Factors that persist across multiple levels (e.g., F1) are considered more stable and significant in explaining the underlying structure of the personality factor. Stability is indicated by strong factor loadings that remain consistent despite the reduction in the number of factors.

TableAPP 7 *Reliabilities of Personality Traits in iWLGs (intraclass co-efficients)*

Item	**ICC(3,1)**	**ICC(3,*k*)**	**Item**	**ICC(3,1)**	**ICC(3,*k*)**	**Item**	**ICC(3,1)**	**ICC(3,*k*)**
Dependent	.58	.79	Gentle	.37	.62	Lazy	.22	.44
Playful	.52	.75	Cautious	.36	.61	Persistent	.20	.42
Dominant	.50	.73	Anxious	.35	.60	Erratic	.20	.42
Submissive	.47	.71	Affectionate	.35	.60	Decisive	.19	.40
Aggressive	.44	.68	Active	.34	.59	Thoughtless	.19	.39
Distractible	.43	.68	Cool	.34	.59	Helpful	.18	.39
Inquisitive	.42	.67	Jealous	.33	.58	Clumsy	.18	.37
Protective	.42	.67	Independent	.33	.58	Disorganized	.17	.36
Curious	.42	.67	Stingy	.31	.56	Sympathetic	.16	.35
Impulsive	.41	.66	Irritable	.30	.54	Defiant	.16	.35
Imitative	.41	.66	Depressed	.30	.54	Autistic	.13	.29
Solitary	.40	.65	Quitting	.30	.54	Predictable	.11	.26
Excitable	.40	.65	Conventional	.27	.51	Innovative	.11	.25
Fearful	.39	.64	Manipulative	.26	.49	Individualistic	.08	.19
Vulnerable	.38	.63	Inventive	.25	.49	Sensitive	.07	.17
Sociable	.38	.63	Friendly	.24	.47	Unemotional	.04	.10
Timid	.37	.62	Stable	.24	.47	Intelligent	.03	.08
Bullying	.37	.62	Reckless	.23	.46	Unperceptive	.01	.02

Note.
1= individual ratings; k = the mean number of raters per subject (k=2.8). Data are based on 167 individuals, 25 raters and 468 ratings

TableAPP 8 *Reliabilities of Personality Dimensions in iWLGs (intraclass co-efficients and Cronbach's alpha)*

Factor	ICC(3,1)	ICC(3,k)	Cronbach's alpha
Neuroticism	.36	.58	.95
Sociability	.42	.68	.94
Dominance	.60	.79	.94
Tolerance/ Self-Control	.41	.64	.81

Note.
1= individual ratings; k = the mean number of raters per subject. Data are based on 198 individuals, 25 raters and 499 ratings.

TableAPP 9 *Cut-off points for the sociality personality construct analysed via fuzzy set analysis*

Trait	Trait [a,b,c,d,e,f,g]	Trait [a,b,c,d,e,f,g]	Cut-off point	Trait [a,b,c,d,e,f,g]	Cut-off point
Activity	.08	Erratic	.18	Persistent	.05
Affectionate	.03	Excitable	.03	Playful	.05
Aggressive	.05	Fearful	.05	Predictable	.15
Anxious	.06	Friendly	.22	Protective	.11
Autistic	0	Gentle	.06	Quitting	0
Bullying	.05	Helpful	.14	Reckless	.08
Cautious	.16	Initiative	.16	Sensitive	.09
Clumsy	.04	Impulsive	.12	Social	.05
Conventional	0	Independent	.13	Solitary	.10
Cool	0	Individual	0	Stable	.09
Curious	0	Innovative	0	Stingy	.05
Decisive	.10	Inquisitive	.09	Submissive	.17
Defiant	.08	Intelligent	.08	Sympathetic	.12
Dependent	.19	Inventive	.08	Thoughtless	0
Depressed	.07	Irritable	.08	Timid	.5
Disorganised	0	Jealous	.07	Unemotional	0
Distractible	.10	Lazy	.06	Unperceptive	0
Dominant	.12	Manipulative	.10	Vulnerable	0

Note.
Bold faced traits are missing traits in some of the questionnaires involved.
a traits and their classification in ex situ bonobos (Weiss et al., 2015), 51 traits.
b traits and their classification in ex situ orangutans (Weiss et al., 2006), 47 traits.
c traits and their classification in ex situ chimpanzees (Weiss et al., 2009), 54 traits.
d traits and their classification in humans (Weiss et al., 2022), 46 traits.
e traits and their classification in iVMGs (Eckhardt et al., 2015), 51 traits.
f traits and their classification in eWLGs 54 traits.
g traits and their classification in iWLGs (analysed in Chapter 5), 54 traits.

TableAPP 10 *Sociality personality construct analysed via fuzzy set analysis in pre-finalised stage*

DOM$_{soc}$	Dom.	Jeal.	Aggress.	Stingy	Bully.	Irritable	Reckl.	Manip.	Def.
	.88	.73	-.71	-.68	-.57	.52	-.50	. 49	.47
	Persis.	Excit.	Impul.	Prot.	Caut.	Submis.	Erratic	Depend.	Indep.
	-.47	-.37	-.35	.30	-.28	.28	-.27	.25	-.24
SOC$_{soc}$	Affec.	Friendly	Social	Symp.	Gentle	Solitary	Depend.	Imitative	Playful
	.74	.70	.69	.63	.57	-.46	.40	.39	.35
	Inquis.	Helpful	Stable	Manip.	Sensitiv	Indep.	Curious	Invent	Active
	.31	.29	.29	.28	.27	.-26	.25	.22	.21
CON$_{soc}$	Pred.	Thought.	Reckl.	Impul.	Sens.	Stable	Erratic	Defiant	Conv.
	-.48	-.46	-.45	-.37	.35	.26	-.24	.23	.19
NEU$_{soc}$	Fearful	Anxious	Vuln.	Timid	Subm.	Indep.	Depen	Dom.	Quit.
	.62	.58	-.53	.50	.47	-.46	.39	-.33	.28
OPN$_{soc}$	Curious	Inventive	Active	Inquis.	Innov.	Playful	Imitative	Impul.	Reckl.
	.73	.70	.68	.68	.62	.62	.45	.36	.33
Proto-AGR$_{soc}$	Dom.	Reckl.	Impul.	Defiant	Erratic	Depend.	Independ.	Fearful	Dec.
	.88	-.45	-.35	-.27	-.45	.25	-.24	-.21	-.20

Note.
Dimensions are listed as following: DOMsoc = Dominance, SOCsoc = Sociability, CONsoc = Conscientiousness, NEUsoc = Neuroticism, OPNsoc = Openness, Proto-AGRsoc = Agreeableness.
Traits are listed to compare the membership between the personality dimensions (fuzzy sets). E.g., in AGR, the traits are shortcuts of the original trait, thus here the traits standing for: Helpful, Friendly, Gentle.
As more unique a trait itself is, as higher is the degree of membership of that trait.
Highlighted in green or red= trait is loaded in more than one factor; it will be decided on the trait in which dimension it fits best.
Green = will be loaded into this dimension, Red = it will be deleted from this dimension (mainly due to lower loading compared to the other loadinginto the other dimension.
'-' = negative loadings.

TableAPP 11 *Correlation between Emotion (1) and Mood (2, longer-term persistent behaviour) and SWB in eWLGs*

State-dep. beh. Response	Anger	Anxiety	Bore	Curious	Fear	Excit	Frust	Jealous	Joy	Love	Sensitive	Tender	Content	Sadness	Positive	Restless	SWB$_{Mean}$
Approach^{f}	.14	-.01	.12	-.03	.01	-.24	.27	-.29	-.14	.21	.32	-.35	-.06	.31	.00	.09	-.19
Approach^{g}	.11	.09	.20	.37	.00	.10	.20	.33	.10	.20	.08	.30	.20	.03	.28	.16	.36
Beg-For-Food	-.18	.10	-.29	.03	.03	.02	.36	.24	.15	.39	.11	.10	.04	.33	.11	.20	.20
Beg^{f}	-.12	.33	-.33	.26	.08	.07	-.50*	.12	.44*	.35	.26	.16	.18	.21	.28	.01	.06
Beg^{g}	-.11	.32	.09	.22	.19	.08	.09	.05	-.45*	.38	.11	.14	.07	.19	.16	.23	.04
Between	.29	.16	-.25	.42*	.19	.26	.33	.26	.10	.03	.20	.22	.27	.15	.37	.20	.57**
Chestbeat	-.13	.13	.13	.04	.24	.48*	.33	.24	.29	.05	.21	.11	.12	.08	.10	.08	.42*
Close	-.03	.03	.26	.52**	.27	.33	.11	.20	.38	.27	.08	.03	.27	.22	.40	.05	.78**
Contact	.26	.23	.07	.27	.03	.23	-.43*	.03	.03	.62**	.29	.13	.09	.03	.15	.31	.09
Contact-aggression -	.66**	.19	.00	.35	.32	.21	.11	.11	.15	.39	.06	.19	.07	.11	.16	.04	.05
Contact-rest^{f}	.21	-.46*	.26	.22	.05	.34	.08	.11	.66**	.17	.30	.12	.22	.23	.19	.17	.29
Contact-rest^{g}	.33	.34	.36	.31	.01	.38	.15	.02	.38	.10	.16	.00	.23	.01	.26	.40	.07
Displace^{f}	.08	.07	.20	.00	.14	.26	.10	.19	-.42*	.30	.08	.08	.06	.30	.23	.00	-.11
Displace^{g}	.11	.07	.12	.49*	.19	.09	.28	.19	.06	.02	.11	.11	.09	.19	.29	.01	.23
Drumming	.09	.34	.40	.05	.17	.34	.03	.15	.34	.16	.09	.28	.23	.17	.21	.20	-.07
Feeding	.08	.49*	.12	.03	.04	.41*	.55**	.18	.15	.26	.05	-.43*	.10	.04	.07	.38	.12
FF	.04	.21	.15	.30	.08	.14	.18	.08	.23	.13	.04	.21	.29	.08	.35	.18	-.23
Follow^{f}	.20	.11	.25	.31	.03	.14	-.43*	.01	.46*	.50*	.23	.09	.04	.28	.05	.04	.,46*
Follow^{g}	.17	.34	.44*	.36	.07	.00	.20	.18	.05	.01	.32	.15	.18	.00	.29	.28	.02
Foodman	.23	.31	.18	.16	.08	.47*	.06	.03	.78**	.14	.14	.08	.07	.10	.21	.16	.46*
Play	.26	.22	.03	.03	.25	.73**	.27	.03	.75**	.05	.23	.06	.16	.06	.07	.08	.56**

Grab	.35	.23	.45*	.26	.29	.16	.23	.07	.04	.19	.23	.15	-.47*	.03	-.54**	.00	-.27
Groom^{f}	.36	.21	.21	.02	.21	.13	.19	.04	.28	.45*	.16	.31	.34	.01	.31	.17	-.10
Groom^{g}	.14	.12	.16	.03	.01	.23	-.46*	.26	.43*	.43*	.23	.12	.25	.26	.18	.06	.08
Hold-on^{f}	.25	.30	.38	.09	.10	.24	.19	.36	.52**	.47*	.35	.03	.09	.14	.13	.16	.42*
Hold-on^{g}	.08	.55**	.13	.43*	.04	.18	.17	.07	.16	.25	.05	.35	.11	.35	.24	.32	.12
I-anticipation	.23	.08	.26	.17	.04	.32	-.49*	.19	.00	.43*	.33	.14	-.47*	.02	.36	.07	-.19
I-carrying	.27	.21	.08	.07	.23	.38	-.61**	.02	.04	.48*	.05	.06	.22	.11	.05	.24	-.09
I- seek-security	.32	.28	.25	.05	.03	.14	.00	.20	.18	.10	.13	.19	.31	.35	.06	.32	-.37
I -travel-indep.	.14	.15	.10	.21	.05	.27	.30	.20	.05	.45*	.20	.31	.10	.26	.08	.08	.02
I-anticipation^{f}	.13	.35	.01	-.46*	.24	.15	.17	.39	.35	.18	.39	.08	-.42*	.05	-.53**	.14	.06
I-anticipation^{g}	.09	.45*	.13	.02	.15	.31	.18	.17	-.50*	.08	.09	.05	.15	.15	.41*	.04	-.28
I-carry^{f}	.35	.44*	.20	.30	.19	-.47*	-.42*	.15	.35	.32	.17	.22	.05	.07	.17	.16	-.19
I-carry^{g}	.12	.31	.12	.31	.11	.05	.29	.03	.33	.40	.38	.00	-.42*	.01	-.43*	.11	.04
Inactive	.05	.21	.15	.04	.03	.51*	.35	.04	.49*	.01	.14	-.46*	.09	.02	.04	.13	.30
I-seek^{f}	.08	.03	.20	.16	.14	.16	.16	.25	.28	.05	.08	.24	-.47*	.22	.25	.10	.16
I-seek^{g}	.08	.06	.24	.24	.14	.26	.15	.14	.30	.31	.08	.03	.12	.63**	.28	.22	-.45*
I-trav^{f}	.09	.27	.23	.30	.21	.06	.39	.17	.26	.40	.44*	.07	.18	.17	.39	.23	-.12
I-trav^{g}	.11	.35	.14	.39	.19	.35	.09	.05	.30	.25	.11	.32	.13	.19	.11	.20	.04
Join-play	.16	.26	.06	.00	.02	.46*	.06	.12	.61**	.04	.26	.08	.23	.09	.15	.07	.36
Leave	.23	.33	.07	.48*	.21	.38	.04	.22	.16	.31	.08	-.56**	.12	.19	.08	.09	.42*
Leave^{f}	.05	.16	.07	.09	.15	.01	.17	.07	.17	.03	.35	.04	.27	.08	.35	.25	.28
Leave^{g}	.11	.05	.13	.17	.35	.13	.05	.08	.19	.05	.29	.25	.40	.15	.36	.03	.46*
Locomotion	.02	.22	.04	.02	.14	.46*	.14	.10	.57**	.02	.14	.32	.02	.12	.03	.06	.32

M-control	.12	.30	.18	.25	.08	.04	.09	.21	.08	.25	.12	.36	.13	.04	.12	.12	.17
M-detach	.34	.05	.25	.01	.12	.39	.27	.08	.19	.32	.15	.18	-.58**	.17	.40	.05	-.27
M-failure-to-rresponse	.11	.06	-.44*	.00	.08	.03	-.44*	.07	.37	.63**	.49*	.11	.20	.19	.13	.27	.15
manipulation	.19	.31	.05	.08	.35	.34	.24	.10	.66**	.10	.18	.16	.07	.13	.03	.18	.46*
M-control^{f}	.09	.42*	.16	.29	.13	.11	.16	.17	.14	.25	.09	.28	.16	.17	.20	.07	-.04
M-control^{g}	.04	.21	.34	.30	.08	.14	.38	.08	.03	.17	.04	.13	.21	.55**	.23	.18	.12
M-detach^{f}	.42*	.18	.16	.28	.11	.39	.10	.00	-.45*	.13	.12	.10	.38	.10	.03	.16	-.29
M-detach^{g}	.12	.25	.14	-.43*	.02	.01	.21	.12	.28	.18	.38	.05	.33	.11	-.54**	.24	-.08
M-direct^{f}	.04	.13	.31	.11	.08	.14	.23	.08	.03	.17	.04	.13	.23	.08	.05	.29	-.10
M-fail^{f}	.04	.17	.18	.08	.08	.14	.18	.08	.23	.39	.04	.13	.05	.08	.11	.29	.02
M-fail^{g}	.08	.21	.33	.19	.22	.02	.33	.21	.40	.39	.60**	.01	.06	.14	.27	.32	-.01
More	.08	.29	.02	.37	.26	.48*	.07	.08	.24	.16	.20	.07	.45*	.29	.53**	.08	.25
M-psy	.17	.08	.17	.27	.10	-.56**	-.49*	.08	.18	.34	.02	.04	.04	.04	.16	.25	-.01
M-psy^{f}	.27	.39	.31	.44*	.01	-.47*	.32	.06	-.57**	.20	.14	.07	.07	.03	.32	.17	-.14
M-psy^{g}	.14	-.41*	.09	.28	.08	.20	.24	.00	.33	.12	.27	.14	.02	.03	.17	.05	.11
Negative-emo	.05	.23	.20	.06	.07	.16	.04	.37	.05	.03	.08	.04	.17	.07	.21	.74**	.05
Negative-affect^{f}	.23	.53**	.35	.31	.21	.15	.14	.37	.15	.16	.11	-.46*	.17	.30	.06	.31	-.04
Negative-affect^{g}	.23	.27	.25	.16	.19	.00	.00	.16	.08	.01	.26	.00	.12	.11	.14	.13	.27
Nestbuilding	.06	.30	.26	.02	.11	.21	.02	.11	.13	.12	.06	.19	.10	.36	.10	.03	-.12
Nose-touch	.11	.06	.20	.59**	.19	.08	.23	.19	.17	.09	.11	.16	.39	.19	.48*	.32	.38
Objectmanipulation	.21	.03	.04	.00	.11	.55**	.23	.04	.61**	.08	.24	.28	.20	.15	.01	.18	.25
Passby	.35	.24	.23	.21	.17	.02	.16	.02	.13	.14	.32	.08	.16	.16	.23	.15	.16
Passby^{f}	.14	.31	.33	.08	.41*	.02	.24	.20	.04	.44*	.35	.19	.08	.19	.13	.11	-.20

Passby^{g}	.11	.03	.36	.13	.10	.08	.00	.34	.14	.09	.26	.00	.43*	.01	.46*	.03	.04
Positive-affect^{f}	.17	.20	.14	.12	.03	.00	.37	.36	.21	.01	.17	.03	.12	.11	.04	.17	-.11
Positive-affect^{g}	.12	.00	.22	.17	.22	.27	.21	.33	.24	.29	.12	.19	.36	.03	.15	.09	.35
Prosocial-positive^{f}	.23	.34	.05	.07	-.42*	.14	.01	.01	.41*	.00	.23	.02	.13	.02	.12	.37	.52*
Prosocial-positive^{g}	.21	.06	.37	.13	.37	.03	N/A	.01	.04	.19	.21	.15	.26	.07	.40	.73**	.06
proximity-till-1.5	.08	.11	.03	.41*	.28	.29	.17	.27	.25	.10	.05	.14	.24	.03	.39	.46*	.69**
proximity-till-5m	.11	.28	.18	.49*	.39	.14	.08	.21	.24	.10	.11	.23	.21	.02	.46*	.37	.76**
Pv	.09	.26	.20	.24	.07	.32	.09	.29	.31	.16	.17	.29	.05	.11	.37	.17	.18
RR	.04	.21	.11	.17	.08	.31	.35	.08	.17	.17	.04	.32	.35	.08	.20	.35	.35
Scratch	.26	.13	.18	.02	.15	.19	.02	.13	.29	.02	.02	.25	.14	.00	.26	.26	-.11
Selfdirected	.17	.00	.08	.48*	.30	.12	.01	.02	.14	.11	.29	.14	.34	.30	.37	.29	.46*
SelfGroom	.26	.13	.01	.28	.28	.17	.15	.16	.25	.20	.26	.19	.28	.13	.32	.03	.11
Shared-attention^{f}	.06	.06	.48*	.14	.11	.21	.44*	.11	.04	.24	.06	.19	.01	.34	.20	.08	.01
Shared-attention^{g}	.04	.21	.34	.30	.08	.14	.38	.08	.03	.17	.04	.13	.21	.55**	.23	.18	.12
Snoutbrush	.04	.21	.18	.11	.08	.14	.18	.52**	.14	.13	.04	.13	.08	.08	.20	.18	.06
Start^{f}	.13	.14	.27	.20	.02	.58**	.34	.13	.25	.24	.13	.20	.15	.08	.35	.34	.04
Start^{g}	.12	.16	.30	.30	.04	.48*	.20	.15	.27	.34	.12	.16	.19	.06	-.49*	.32	-.07
Touch^{f}	.19	.17	.04	.11	.07	.49*	.05	.03	.47*	.04	.19	.25	.17	.01	.29	.11	.38
Touch^{g}	.11	.19	.27	.06	.10	.14	.26	.17	.00	.23	.08	.22	.11	.30	.27	.57**	-.09
Watch-attentively	.17	.43*	.18	.61**	.08	.04	.21	.10	.35	.05	.14	.04	.05	.38	.19	.01	.14
Watch^{f}	.32	.39	.31	.64**	.07	.20	.16	.14	.15	.04	.14	.16	.06	.31	.20	.23	.01
Watch-other	.28	.12	.50*	.16	.27	.34	.12	.33	-.41*	.14	.18	.07	.19	.01	.15	.05	-.15
Watch^{g}	.17	.26	.23	.05	.30	.22	.03	.02	.08	.02	.29	.35	.07	.04	.05	.04	.05

Yawn	.13	.28	.09	.20	.24	.21	.10	.24	.40	.09	.13	.39	.10	.28	.45*	.23	.06

Note.
I=Infant, M=Mother.

TableAPP 12 *Cut-off points for the sociality personality construct across great apes species analysed via fuzzy set analysis*

Trait [a,b,c,d,e,f,g]	**Cut-off point**	**Trait** [a,b,c,d,e,f,g]	**Cut-off point**	**Trait** [a,b,c,d,e,f,g]	**Cut-off point**
Activity	.08	Erratic	.18	Persistent	.05
Affectionate	.03	Excitable	.03	Playful	.05
Aggressive	.05	Fearful	.05	Predictable	.15
Anxious	.06	Friendly	.22	Protective	.11
Autistic	0	Gentle	.06	Quitting	0
Bullying	.05	Helpful	.14	Reckless	.08
Cautious	.16	Initiative	.16	Sensitive	.09
Clumsy	.04	Impulsive	.12	Social	.05
Conventional	0	Independent	.13	Solitary	.10
Cool	0	Individual	0	Stable	.09
Curious	0	Innovative	0	Stingy	.05
Decisive	.10	Inquisitive	.09	Submissive	.17
Defiant	.08	Intelligent	.08	Sympathetic	.12
Dependent	.19	Inventive	.08	Thoughtless	0
Depressed	.07	Irritable	.08	Timid	.5
Disorganised	0	Jealous	.07	Unemotional	0
Distractible	.10	Lazy	.06	Unperceptive	0
Dominant	.12	Manipulative	.10	Vulnerable	0

Note.
Bold faced traits are missing traits in some of the questionnaires involved.
[a] traits and their classification in ex situ bonobos (Weiss et al., 2015), 51 traits.
[b] traits and their classification in orang-utans (Weiss et al., 2006), 47 traits.
[c] traits and their classification in chimpanzees (Weiss et al., 2009), 54 traits.
[d] traits and their classification in humans (Weiss, 2022), 46 traits.
[e] traits and their classification in Virunga mountain gorillas (Eckardt et al., 2015), 51 traits.
[f] traits and their classification in ex situ Western lowland gorillas, 54 traits.
[g] traits and their classification in in situ Western lowland gorillas (analysed in **Chapter 5**), 54 traits.