COGNITIVE CHALLENGES IN CAPTIVE CHIMPANZEES: BEHAVIORAL AND WELFARE IMPLICATIONS AND INFLUENCE OF PERSONALITY

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Universitat de Girona

DOCTORAL THESIS

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List of publications

This thesis is a compendium of the previously published research articles:

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Universitat
de Girona

Dr Miquel Llorente Espino, at Universitat de Girona, and Dr. Federica Amici, at University of Leipzig and Max Planck Institute for Evolutionary Anthropology

WE DECLARE:

That the thesis titled *Cognitive challenges in captive chimpanzees: behavioral and welfare implications and influence of personality*, presented by Maria Padrell Dalmau to obtain a doctoral degree, has been completed under my supervision and meets the requirements to opt for an International Doctorate.

For all intents and purposes, I hereby sign this document.

Signature

federica amici

Miquel Llorente | Federica Amici

Girona, 27 December 2023

Dr. David Riba, Dr. Yulán Úbeda, Dr. Miquel Llorente, Dr. Federica Amici, Ms. Maria Pau Córdoba, Mr. Albert Giberga, Mr. Antonio Broekman and Ms. Susana Almagro, as co-authors of the following articles:

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Accept that Ms. Maria Padrell presents the cited articles as the principal author and as part of his/her doctoral thesis and that said articles cannot, therefore, form part of any other doctoral thesis. And for all intents and purposes, hereby signs this document.

federica amici

David Riba   Yulán Úbeda   Miquel Llorente   Federica Amici

Maria Pau Córdoba   Albert Giberga   Antonio Broekman   Susana Almagro

Girona, 27 December 2023

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Leipzig, 15th November 2023

Confirmation of supervision

I hereby confirm that Ms. Maria Padrell Dalmau conducted a research stay from 16.09.2019 to 20.12.2019 at the Max Planck Institute for Evolutionary Anthropology (Department of Comparative Cultural Psychology) and Leipzig Zoo, under my co-supervision and in accordance with the doctoral regulations of the University of Girona. During her stay, she collected chimpanzee behavioural and personality data for her dissertation titled "Cognitive challenges in captive chimpanzees (*Pan troglodytes*): behavioral and welfare implications and influence of personality". She received a research grant from the German Academic Exchange Service (Deutscher Akademischer Austauschdienst - DAAD) (Funding programme: Research Grants - Short-Term Grants, 2019, ID: 57442045).

Dr. Federica Amici

Federica Amici

Note on personal pronouns usage

This doctoral thesis is a compendium of published research articles authored by a team of researchers. Therefore, to ensure alignment with the existing published literature and to acknowledge the collaborative nature of this work, the pronoun “we” rather than “I” is consistently employed throughout the thesis.

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Abstract

Cognitive challenges are frequently provided to captive non-human primates, either as enrichment activities or within an experimental framework. Nonetheless, little is known about the impact of these activities on animal behavior and welfare. Furthermore, the influence of individual characteristics such as sex, age or personality on subjects' interest and performance in cognitive activities is still poorly understood. This doctoral thesis aims to address these knowledge gaps by investigating the relationship between cognitive challenges, behavior, welfare and personality in captive chimpanzees (*Pan troglodytes*). In particular, the first two studies (Articles 1 and 2) assessed the association between cognitive challenges and welfare within the framework of enrichment activities, whereas in the following studies (Articles 3 and 4) we evaluated chimpanzee personality with a questionnaire based on Eysenck's Psychoticism-Extraversion-Neuroticism (PEN) model and investigated the link between personality traits and cognitive performance in a non-invasive research context.

The study sample consisted of 37 chimpanzees housed at two different institutions, Fundació Mona (Girona, Spain) and the Leipzig Zoo (Leipzig, Germany). Data on cognitive performance, behavior and welfare were collected in the subsample of 14 chimpanzees from Fundació Mona, whereas personality data encompassed all subjects. Cognitive enrichment activities assessed at Fundació Mona included an artificial termite-fishing task and a double-sided food maze filled with food rewards. The association between personality and cognitive performance was assessed through a set of puzzle boxes that required the chimpanzees to employ problem-solving skills to access food rewards.

Throughout the first three studies (Articles 1, 2 and 3), we found that most of the chimpanzees participated in the cognitive challenges (termite-fishing task, double-sided food maze and puzzle boxes), but with considerable variation across individuals. The high proportion of success in the puzzle boxes and the artificial termite-fishing task suggests that

these tasks presented an appropriate level of challenge. By contrast, only two individuals were able to master the food maze. Sex and age did not predict differences in participation in any of the cognitive tasks, except for the food maze, in which females were more likely to participate than males. Additionally, the two only individuals that were successful at retrieving food rewards from the food maze were females, in line with previous findings showing a female-bias in tool-use behavior in chimpanzees. Personality did not predict differences in participation in the puzzle boxes. In contrast, lower Extraversion and lower Dominance were linked to a higher probability of success in both sexes, and higher Neuropsychoticism predicted higher probability of success in females. We also observed that the probability of losing contact with the puzzle boxes (a measure of motivation) was higher in younger chimpanzees and in those rated higher on Neuropsychoticism.

Articles 1 and 2 also investigated the impact of cognitive enrichment activities on chimpanzee behavior and welfare. In line with our predictions, both tasks consistently promoted species-typical behaviors (e.g., tool use and foraging) while reducing undesirable behaviors (e.g., inactivity) across sessions. However, in contrast to our predictions, participation in these activities was not linked to a reduction in the occurrence of abnormal behaviors or the rate of self-directed behaviors. Although the rate of self-directed behaviors was not affected by the presence of cognitive enrichment tasks, these behaviors increased as function of participation in the food maze, possibly due to heightened emotional arousal. In general, participating in the enrichment activities did not have significant effects on chimpanzee social behavior. However, the occurrence of aggression-related behaviors increased as a function of participation in the food maze, possibly due to intragroup competition.

In Articles 3 and 4 we used a 12-item questionnaire including Eysenck's primary scales to assess chimpanzee personality. Our results highlighted the potential of this model, but also its limitations. For example, we obtained good levels of inter-rater reliability both when assessing the subsample of chimpanzees from Fundació Mona (Article 3) and when evaluating a larger sample including the chimpanzees from the Leipzig Zoo (Article 4). Furthermore, in Article 3, several personality traits correlated with chimpanzee behavioral observations conducted over an 11-year period, providing some evidence for convergent validity. However, some traits correlated with more than one behavior, indicating limited discriminant validity. The factorial analyses in Article 4 yielded a three-factor personality structure closely resembling the one previously reported in chimpanzees assessed with the same questionnaire, including the traits Extraversion, Dominance/Fearless Dominance and Neuropsychoticism.

Concerning our main hypotheses, we concluded that: (1) chimpanzees show differences in interest and performance in cognitive tasks, both in enrichment and research contexts; (2) some of this variation is predicted by sex and personality; (3) cognitive enrichment activities increase animal welfare by providing animals with opportunities to engage in challenges, while promoting species-typical behaviors and reducing some undesirable behaviors; and (4) while Eysenck's model offers an alternative approach to assess chimpanzee personality, further research is required to validate its applicability in this species and other non-human primates.

Resum

Els reptes cognitius són sovint proporcionats a primats no humans en captivitat, ja sigui com activitats d'enriquiment o dins d'un marc experimental. No obstant això, es coneix poc sobre l'impacte d'aquestes activitats en el comportament i el benestar dels animals. A més, encara es té un coneixement limitat sobre la influència de les característiques individuals com el sexe, l'edat o la personalitat en l'interès i el rendiment dels subjectes en les activitats cognitives. Aquesta tesi doctoral té com a objectiu abordar aquestes mancances de coneixement investigant la relació entre els reptes cognitius, el comportament, el benestar i la personalitat en ximpanzés (*Pan troglodytes*) en captivitat. En particular, en els dos primers estudis (Articles 1 i 2) es va avaluar l'associació entre els reptes cognitius i el benestar en un context d'enriquiment, mentre que en els estudis següents (Articles 3 i 4) es va avaluar la personalitat dels ximpanzés amb un qüestionari basat en el model de Psicoticisme-Extraversió-Neuroticisme (PEN) d'Eysenck i es va investigar la relació entre els trets de personalitat i el rendiment cognitiu en un context experimental no invasiu.

La mostra d'estudi consistí en 37 ximpanzés allotjats en dues institucions diferents, la Fundació Mona (Girona, Espanya) i el Zoo de Leipzig (Leipzig, Alemanya). Les dades sobre el rendiment cognitiu, el comportament i el benestar es van recollir en la submostra de 14 ximpanzés de la Fundació Mona, mentre que les dades de personalitat van abastar tots els subjectes. Les activitats d'enriquiment cognitiu avaluades a la Fundació Mona incloïen una tasca que simulava la pesca de tèrmits i un laberint de doble cara que contenia recompenses alimentàries. L'associació entre la personalitat i el rendiment cognitiu es va avaluar mitjançant un conjunt de caixes trencaclosques que requerien que els ximpanzés utilitzessin habilitats de resolució de problemes per accedir a les recompenses alimentàries.

Al llarg dels tres primers estudis (Articles 1, 2 i 3), vam observar que la majoria dels ximpanzés participaven en els reptes cognitius (pesca de tèrmits, laberint alimentari de doble

cara i caixes trecaclosques), però amb una variació considerable entre els individus. L'alta proporció d'èxit en les caixes trencaclosques i en la tasca de pesca de tèrmits suggereix que aquestes tasques presentaven un nivell adequat de desafiament. En canvi, només dos individus van ser capaços d'extreure correctamente les recompenses del laberint alimentari. El sexe i l'edat no van predir diferències en la participació en cap de les tasques cognitives, excepte en el laberint alimentari, on les femelles mostraren més probabilitat de participar que els mascles. A més, els dos únics individus que aconseguiren extreure correctament recompenses del laberint alimentari eren femelles, en línia amb investigacions prèvies que mostren un biaix femení en l'ús d'eines en els ximpanzés. La personalitat no va predir diferències en la participació en les caixes trencaclosques. En canvi, valors més baixos d'Extraversió i de Dominància es van relacionar amb una major probabilitat d'èxit en ambdós sexes, i valors més alts de Neuropsicoticisme van predir una probabilitat més alta d'èxit en les femelles. També vam observar que la probabilitat de perdre el contacte amb les caixes trencaclosques (una mesura de la motivació) era més alta en ximpanzés més joves i en aquells que tenien una puntuació més alta en Neuropsicoticisme.

En els Articles 1 i 2 també es va investigar l'impacte de les activitats d'enriquiment cognitiu en el comportament i el benestar dels ximpanzés. En línia amb les nostres prediccions, ambdues tasques van promoure de manera consistent comportaments propis de l'espècie (per exemple, l'ús d'eines i la cerca d'aliments) mentre reduïen comportaments indesitjats (per exemple, la inactivitat) al llarg de les diverses sessions d'enriquiment. No obstant això, en contra de les nostres prediccions, la participació en aquestes activitats no es va relacionar amb una reducció de l'ocurrència de comportaments anormals o auto-dirigits. Tot i que l'ocurrència de comportaments auto-dirigits no es veié afectada per la presència de les tasques d'enriquiment cognitiu, aquests comportaments van augmentar durant la participació en el laberint alimentari, possiblement a causa de l'elevada estimulació. En general, participar en les activitats d'enriquiment no va tenir efectes significatius en el comportament social dels ximpanzés. No obstant això, la participació en el laberint alimentari es relacionà amb un augment en l'ocurrència de comportaments relacionats amb l'agressió, possiblement a causa de la competència dins del grup.

En els Articles 3 i 4 es va utilitzar un qüestionari de 12 ítems que incloïa les escales primàries d’Eysenck per avaluar la personalitat dels ximpanzés. Els nostres resultats van destacar el potencial d'aquest model, però també les seves limitacions. Per exemple, es van obtenir bons nivells de fiabilitat entre observadors, tant en l'avaluació de la submostra de ximpanzés de la Fundació Mona (Article 3) com en l'avaluació d'una mostra més gran que incloïa els ximpanzés del Zoo de Leipzig (Article 4). A més, en l’Article 3, diversos trets de personalitat van correlacionar amb observacions de comportament dels ximpanzés realitzades al llarg d'un període d’11 anys, proporcionant evidència de validesa convergent. No obstant això, alguns trets van correlacionar-se amb més d'un comportament, indicant una validesa discriminant limitada. Les anàlisis factorials a l’Article 4 van donar lloc a una estructura de personalitat de tres factors molt similar a la prèviament reportada en ximpanzés avaluats amb el mateix qüestionari, incloent els trets d'Extraversió, Dominància/Dominància sense por i Neuropsicoticisme.

En relació amb les nostres hipòtesis principals, vam concloure que: (1) els ximpanzés mostren diferències en l'interès i el rendiment en tasques cognitives, tant en contextos d'enriquiment com de recerca; (2) una part d'aquesta variació està relacionada amb el sexe i la personalitat; (3) les activitats d'enriquiment cognitiu milloren el benestar dels animals proporcionant oportunitats per afrontar reptes, alhora que fomenten comportaments propis de l'espècie i redueixen alguns comportaments indesitjats; i (4) tot i que el model d'Eysenck ofereix una alternativa per avaluar la personalitat dels ximpanzés, és necessari continuar investigant per tal de validar-ne l'aplicabilitat en aquesta espècie i en altres primats no humans.

Resumen

Los desafíos cognitivos son proporcionados con frecuencia a primates no humanos en cautiverio, ya sea como actividades de enriquecimiento o dentro de un marco experimental. Sin embargo, se sabe poco sobre el impacto de estas actividades en el comportamiento y el bienestar animal. Además, todavía hay un conocimiento limitado sobre la influencia de características individuales como el sexo, la edad o la personalidad en el interés y el rendimiento de los sujetos en actividades cognitivas. Esta tesis doctoral tiene como objetivo abordar estas lagunas de conocimiento investigando la relación entre desafíos cognitivos, comportamiento, bienestar y personalidad en chimpancés (*Pan troglodytes*) en cautiverio. En particular, en los dos primeros estudios (Artículos 1 y 2) se evaluó la asociación entre desafíos cognitivos y bienestar en un contexto de enriquecimiento, mientras que en los estudios siguientes (Artículos 3 y 4) se evaluó la personalidad de los chimpancés mediante un cuestionario basado en el modelo de Psicoticismo-Extraversión-Neuroticismo (PEN) de Eysenck y se investigó la relación entre rasgos de personalidad y rendimiento cognitivo en un contexto experimental no invasivo.

La muestra de estudio consistió en 37 chimpancés alojados en dos instituciones diferentes, Fundació Mona (Girona, España) y el Zoo de Leipzig (Leipzig, Alemania). Los datos sobre rendimiento cognitivo, comportamiento y bienestar se recopilaron en la submuestra de 14 chimpancés de Fundació Mona, mientras que los datos de personalidad abarcaron a todos los sujetos. Las actividades de enriquecimiento cognitivo evaluadas en Fundació Mona incluyeron una tarea que simulaba la pesca de termitas y un laberinto de doble cara que contenía recompensas alimenticias. La asociación entre personalidad y rendimiento cognitivo se evaluó a través de una serie de cajas rompecabezas que requerían que los chimpancés emplearan habilidades de resolución de problemas para acceder a recompensas alimenticias.

A lo largo de los primeros tres estudios (Artículos 1, 2 y 3), se observó que la mayoría de los chimpancés participaron en los desafíos cognitivos (tarea de pesca de termitas, laberinto de alimentos y cajas rompecabezas), pero con considerable variación entre individuos. La alta proporción de éxito en las cajas rompecabezas y en la tarea de pesca de termitas sugiere que estas tareas presentaron un nivel apropiado de desafío. En cambio, solo dos individuos fueron capaces de extraer correctamente los alimentos del laberinto de alimentos. El sexo y la edad no predijeron diferencias en la participación en ninguna de las tareas cognitivas, excepto en el laberinto de alimentos, en el cual las hembras fueron más propensas a participar que los machos. Además, los dos únicos sujetos que obtuvieron recompensas de forma exitosa en el laberinto de alimentos eran hembras, en línea con hallazgos previos que muestran un sesgo femenino en el comportamiento de uso de herramientas en los chimpancés. La personalidad no predijo diferencias en la participación en las cajas rompecabezas. En cambio, valores más bajos de Extraversión y de Dominancia se asociaron con una mayor probabilidad de éxito en ambos sexos, y valores más altos de Neuropsicoticismo predijeron una mayor probabilidad de éxito en las hembras. También observamos que la probabilidad de perder el contacto con las cajas rompecabezas (una medida de la motivación) era mayor en chimpancés más jóvenes y en aquellos con una puntuación más alta en Neuropsicoticismo.

Los Artículos 3 y 4 también investigaron el impacto de las actividades de enriquecimiento cognitivo en el comportamiento y el bienestar de los chimpancés. De acuerdo con nuestras predicciones, ambas tareas promovieron consistentemente comportamientos típicos de la especie (por ejemplo, uso de herramientas y búsqueda de alimentos) al tiempo que redujeron comportamientos indeseables (por ejemplo, inactividad) a lo largo de las sesiones de enriquecimiento. Sin embargo, contrariamente a nuestras predicciones, la participación en estas actividades no se asoció con una reducción en la ocurrencia de comportamientos anormales o autodirigidos. Aunque la ocurrencia de comportamientos autodirigidos no se vio afectada por la presencia de las tareas de enriquecimiento cognitivo, estos comportamientos aumentaron durante la participación en el laberinto de alimentos, posiblemente debido a una mayor excitación emocional. En general, participar en las actividades de enriquecimiento no tuvo efectos significativos en el comportamiento social de los chimpancés. Sin embargo, la ocurrencia de comportamientos relacionados con la agresión aumentó en función de la participación en el laberinto de alimentos, posiblemente debido a la competencia intragrupal.

En los Artículos 3 y 4 utilizamos un cuestionario de 12 ítems que incluía las escalas primarias de Eysenck para evaluar la personalidad de los chimpancés. Nuestros resultados resaltaron el potencial de este modelo, pero también sus limitaciones. Por ejemplo, obtuvimos buenos niveles de fiabilidad entre evaluadores, tanto al evaluar la submuestra de chimpancés de Fundació Mona (Artículo 3) como al evaluar una muestra más grande que incluía a los chimpancés del Zoo de Leipzig (Artículo 4). Además, en el Artículo 3, varios rasgos de personalidad correlacionaron con observaciones de comportamiento de los chimpancés realizadas a lo largo de un período de 11 años, proporcionando cierta evidencia de validez convergente. Sin embargo, algunos rasgos correlacionaron con más de un comportamiento, indicando una validez discriminante limitada. Los análisis factoriales en el Artículo 4 revelaron una estructura de personalidad de tres factores que se asemejaba estrechamente a la reportada previamente en chimpancés evaluados con el mismo cuestionario, incluyendo los rasgos de Extraversión, Dominancia/Dominancia sin miedo y Neuropsicoticismo.

En relación con nuestras hipótesis principales, concluimos que: (1) los chimpancés muestran diferencias en el interés y el desempeño en tareas cognitivas, tanto en contextos de enriquecimiento como de experimentación; (2) parte de esta variación está relacionada con el sexo y la personalidad; (3) las actividades de enriquecimiento cognitivo aumentan el bienestar animal, proporcionando oportunidades para que los animales se involucren en desafíos, así como promoviendo conductas típicas de la especie y reduciendo algunas conductas indeseables; y (4) aunque el modelo de Eysenck ofrece un enfoque alternativo para evaluar la personalidad de los chimpancés, se requiere investigación adicional para validar su aplicabilidad en esta especie y en otros primates no humanos.

Chapter 1. General introduction and objectives

Photograph taken by author

1.1. The welfare of captive animals

Despite the ongoing discrepancies regarding whether animals should have moral status (i.e., being considered entities deserving of moral considerations; Janssens, 2021; Warren, 1997; Banwell, 2023; Padrell et al., 2021) evidence from multiple studies suggests that a wide range of taxa are sentient beings, capable of experiencing positive and negative affective states such as happiness, pleasure, pain, or fear (Duncan, 2006; Panksepp, 2011). Therefore, ensuring a good quality of life to those who live under human care is our ethical responsibility (Gruen, 2021). For this reason, legislations, guidelines and codes of ethics have been developed worldwide to improve the welfare of captive animals. Firstly, these publications have focused on farm animals (Directive 98/58/EC; Regulation 1/2005) and those used for scientific purposes (Directive 86/609/EEC; Directive 2010/63/EU), but more recently they have also included animals kept in zoological institutions (Directive 1999/22/EC; Mellor et al., 2015; World Association of Zoos and Aquariums [WAZA], 2023). In fact, over the past few decades, animal welfare has become a topic of major concern in zoos and other facilities potentially exhibiting animals (e.g., animal sanctuaries and wildlife rescue and rehabilitation centers[1]), as shown by the increasing recent literature on the topic (Binding et al., 2020; Cole & Fraser, 2018; DiVincenti et al., 2023; Fultz, 2017; Kagan et al., 2015; Learmonth, 2019; Maple & Bloomsmith, 2018; Maple & Perdue, 2013; Perdue et al., 2020; Rose & Riley, 2019; Sherwen et al., 2018; Wolfensohn et al., 2018). This growing interest on animal welfare coincides with a progressive shift in public attitudes toward keeping animals in captivity (Doyle, 2017; Naylor & Parsons, 2019), which has led to a change in the concept and role of zoological institutions

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[1] Animal sanctuaries and wildlife rescue and rehabilitation centers share the purpose of rescuing and rehabilitating animals that have been abused, injured or abandoned. The distinction between these two entities remains ambiguous, without clear legal or official definitions. However, the Global Federation of Animal Sanctuaries (GFAS), functioning as an accrediting organization, defines a sanctuary as a non-profit organization committed to providing lifetime care for animals without engaging in intentional captive breeding, commercial exploitation, or direct public interaction with them (Fultz, 2017). In contrast, wildlife rescue and rehabilitation centers typically focus on reintroducing animals back to their natural habitats.

(Roe et al., 2014; Sampaio et al., 2020; Ward et al., 2018). Specifically, modern zoos have progressively moved away from the mere purpose of entertainment to focus on conservation (Conde et al., 2011; Routman & Khalil, 2022; Tribe & Booth, 2003), education and public engagement (Godinez & Fernandez, 2019; Kleespies et al., 2022; Nygren & Ojalammi, 2018; Patrick et al., 2007), and on conducting non-invasive research (Rose & Riley, 2021) that ultimately improves animal welfare (Binding et al., 2020), increases species' knowledge (Garcia-Pelegrin et al., 2022), and creates opportunities for public engagement while promoting positive attitudes toward conservation (Craig & Vick, 2021; Hopper, 2017).

Defining and assessing animal welfare has proved to be a challenging endeavor. Historically, there have been different scientific approaches to the study of animal welfare, depending on the criteria used to define the concepts of well-being, welfare and quality of life (Fraser, 2009; McMillan & Yeates, 2020). The first and most traditional view focuses on basic health and proper functioning of animals, so that welfare was considered as the absence of disease and injury (Sainsbury, 1986) and measured through parameters such as growth rate and reproductive success (Broom, 1986), that is, «fitness» state. In contrast, the second approach gives relevance to the affective states of animals, prioritizing not only the absence of pain and suffering, but also the presence of pleasure (Balcombe, 2009; Boissy et al., 2007; Duncan & Petherick, 1991; Mellor & Beausoleil, 2015). Finally, the third approach emphasizes the importance for captive animals to develop species-typical behaviors, also known as ethological needs (Brambell, 1965; Kiley-Worthington, 1989) or natural behaviors (Bracke & Hopster, 2006). The notion of ethological needs implies that welfare in captive animals is poor if their environment does not allow for opportunities to express the behaviors they would exhibit in the wild (Hughes & Duncan, 1988). Nonetheless, some researchers have questioned the accuracy of using the behavior of wild-living counterparts as a baseline to assess animal welfare in captivity (Learmonth, 2019; Veasey et al., 1996; Wolfensohn et al., 2018).

In recent years, the concept of animal welfare has broadened to include considerations of their emotional states (Duncan, 2004; Hemsworth et al., 2015; Veasey, 2017). Whether and to what extent different animals experience emotions is a fundamental question for advancing our understanding of animal welfare. However, there is yet no consensus on the definition and application of the concept of emotion in non-human animals (Adolphs, Mlodinow, & Barret, 2019; de Vere & Kuczaj, 2016; Izard, 2010; Malezieux, Klein & Gogolla, 2023; Paul & Mendl, 2018). Researchers in the field of emotions commonly distinguish between feelings and emotions. Feelings are private and conscious states that are not observable, whereas emotions are measurable physiological or neural responses, often reflected in behavior (de Waal & Andrews, 2022). Thus, although emotions cannot be directly measured, they can be indirectly assessed, for example, through physiological and behavioral indicators (Hemsworth et al., 2015). For instance, great apes express alleged emotional states through various channels, including facial expressions, body cues or vocalizations (Heesen et al., 2024; Kret et al., 2020). These emotional expressions can be either involuntary, thus serving as immediate reflections of inner states, or intentional, acting as indicators of forthcoming actions (Kret et al, 2020).

Understanding emotions also involves considering their connections with motivation and reward (Rolls, 2007). Emotions are considered evolved aspects of brain processes that drive behavioral responses to different types of stimuli, which can be rewarding (pleasurable) or punishing (unpleasant) experiences (Boissy et al., 2007; Rolls, 2007). Regarding the experience of reward, evidence suggests that dopamine circuits in the brain play a crucial role in generating the desire and anticipation for rewards, while opioid circuits, interacting with dopamine circuits, contribute to the pleasurable feeling of enjoying rewards (Berridge & Robinson, 2003; Boissy et al. 2007). Furthermore, neuroscience has also shown that behaviors like exploration, foraging and affiliative interactions are particularly rewarding for individuals and trigger positive affective states (Mellor, 2015a, 2015b; Panksepp, 2005). In line with these assumptions, welfare has been conceptualized as the state of an individual in relation to its attempts to cope with and adapt to the demands of the environment (Broom, 2001; Broom, 1986, 1991; Hill & Broom, 2009). That is, an animal achieves a positive welfare state when it has the ability and opportunity to appropriately respond to positive and negative internal and external stimuli and conditions (Arndt et al., 2022). However, to achieve an optimal level of welfare, animals do not only need to endure the challenges of their environment, but also to thrive (Maple & Bloomsmith, 2018; Maple & Perdue, 2013). To this end, the objective is not only to minimize their negative experiences but also to provide them with opportunities to engage in highly-motivated and highly-rewarding behaviors that trigger positive affective states, contributing to a life that is truly "worth living" (Mellor, 2015a; Mellor, 2016; Mellor & Beausoleil, 2015; Whitham & Wielebnowski, 2013). Examples of rewarding behaviors include activities that promote food acquisition and exploration of the environment (Mellor, 2016), but also provide challenges that cognitively stimulate animals and allow them to make choices (Clark, 2011; Whitham & Wielebnowski, 2013). In fact, a certain degree of choice and control over the environment is considered fundamental to achieve good welfare (Badihi, 2006; Dawkins, 2003; Morgan & Tromborg, 2007; Sambrook & Buchanan-Smith, 1997; Whitham & Wielebnowski, 2013).

Overall, welfare is therefore a complex concept that encompasses multiple aspects of animals' life, from biological functioning to their subjective experiences. As a consequence, an optimal assessment of welfare should be interdisciplinary (Siegford, 2013), integrating behavioral, physiological and biological indicators (e.g., exploratory behaviors, hormonal measurements, immunological markers) to provide a holistic evaluation (Broom, 2014; Whitham & Wielebnowski, 2013). In both humans and other animals there is evidence that these types of measurements can provide insight on subjects' emotional states (reviewed in Broom, 2014). Nonetheless, such approach is not always feasible in zoological institutions and other captive environments for at least two reasons. First, caretakers and other staff usually lack the time or the professional training to effectively assess welfare (Brent, 2007). Second, these institutions have limited financial resources, especially wildlife rescue and rehabilitation centers and sanctuaries, which are typically non-profit organizations that mostly receive funding from private sources (Hirata et al., 2020).

1.2. Chimpanzee behavior and welfare

1.2.1. Chimpanzees in captivity

In the wild, chimpanzees (*Pan troglodytes*) are the most numerous and widely distributed among great ape species. Their home range covers over 2.6 million km^2, with a discontinuous distribution from southern Senegal and Guinea in the west and the western borders of the United Republic of Tanzania in the east (Humle et al., 2016). While chimpanzee taxonomy remains a topic of ongoing debate, current genetic data provides evidence for the recognition of four subspecies: the Western Chimpanzee (*P. troglodytes verus*); the Nigeria-Cameroon Chimpanzee (*P. t. ellioti*); the Central Chimpanzee (*P. t. troglodytes*); and the Eastern Chimpanzee (*P. t. schweinfurthii*). A detailed description of the distribution of the different subspecies is provided by Caldecott and Miles (2005).

The global population of wild chimpanzees is currently estimated to range between 345,000 and 470,000 individuals (Carlsen et al., 2022; Great Apes Survival Partnership [GRASP] & IUCN, 2018). Nonetheless, this species faces multiple threats, including poaching, bushmeat trade, infectious diseases and loss of habitat due to human actives. These factors have led to a significant population decline over the past 20-30 years, which is expected to persist in the near future (Humle et al., 2016). Consequently, chimpanzees meet the criteria for being considered as an endangered species (Oates, 2006).

Regarding the chimpanzees living under human care, there is currently no reliable estimate of the total captive chimpanzee population worldwide. In Europe, a significant proportion of great apes live in zoos affiliated with the European Association of Zoos and Aquaria (EAZA), where they are subjected to population management programmes (Ex situ Programmes, EEPs) designed to maintain genetic diversity of threatened species. At the end of 2021, the Chimpanzee EEP consisted of 782 individuals distributed among 94 institutions (EAZA, 2021). Furthermore, according to the European Studbook for the Chimpanzee (Carlsen & De Jongh, 2015), by the end of 2014 an additional 291 individuals were housed in 31 non-EAZA European facilities, such as unaccredited zoos, animal parks and sanctuaries. Thus, considering both EAZA and non-EAZA institutions, the latest figures estimate that approximately 1073 captive chimpanzees live across 125 European facilities.

In the US, there are approximately 1300 captive chimpanzees living in a variety of facilities, including zoological parks accredited by the Association of Zoos and Aquariums (AZA), sanctuaries accredited by the Global Federation of Animal Sanctuaries (GFAS), unaccredited animal parks, research laboratories and those that are kept as pets and performers for the entertainment industry (ChimpCARE, 2020). Although the US National Institutes of Health now prohibits biomedical research on chimpanzees, some of the animals that were used for this purpose are still kept in these facilities. Furthermore, although the possession and use of great apes is banned in many states, there is no federal legislation prohibiting the ownership of chimpanzees in the US (ChimpCARE, 2020).

According to the Great Ape Information Network (GAIN), an open-access nationwide database containing the detailed life history information of all apes who have lived or currently reside in Japan (Matsuzawa, 2016), the country is currently home to 291 chimpanzees distributed in 45 facilities (GAIN, 2015). Chimpanzee population management in Japan is subjected to a conservation program, the Japanese Species Management Program by the

Japanese Association of Zoos and Aquariums (JAZA). Similarly, all chimpanzees living in the Australasian region (Australia and New Zealand) are managed under the Australian Species Management Program by the Zoo and Aquarium Association (ZAA). By 2016, Australia held a captive chimpanzee population of 52 individuals distributed in 5 facilities (Fisken et al., 2018).

Recently, the Ape Alliance published a report (Ape Alliance, 2018) focusing on the captive chimpanzee population in China. The report identified 51 facilities housing a total of 187 chimpanzees. Nonetheless, it also raised concern about disparities between the number of chimpanzees officially declared by the Chinese government and the actual number observed on public displays in zoos, wildlife parks and shows throughout the country.

In Africa, the Pan African Sanctuary Alliance (PASA) unites a total of 23 primate centers across the continent that rescue and rehabilitate primates and other wildlife that are often victims of illegal wildlife trade (Farmer, 2002). This organization works with local and international NGOs, experts and volunteers with the objective of protecting African primates while supporting local communities (Ferrie et al., 2014). The 23 facilities are distributed over 13 African countries, which collectively care for approximately 1300 great apes, including 1158 chimpanzees (PASA, 2021). Only during 2021, PASA members rescued a total of 400 animals, comprising 182 primates. Furthermore, in 2021 PASA released 413 animals to the wild, including 73 primates (PASA, 2021). Nonetheless, reintroduction is a complex and expensive process and only a small fraction of the great apes at PASA sanctuaries can be returned to their natural habitat (Speiran et al., 2023). Animals who have spent several years in captivity may be too traumatized and unable to develop the necessary skills to survive in the wild (PASA, 2021). Thus, considering that most of these animals will spend the rest of their lives in captivity, it is crucial to provide them with the best care possible to ensure their optimal welfare.

Official information on chimpanzee population in other world regions is difficult to access. Fisken and colleagues (2018) published a report providing data for the 2016 global great ape populations that are under conservation programs in accredited zoos around the world. The report details the number of chimpanzees in European, North American, Japanese, African and Australian zoological institutions. Nonetheless, this report does not include global estimates for chimpanzees outside these conservation programs. This excludes chimpanzees residing in regions such as South America or South East Asia, where there are facilities housing chimpanzees and other great apes, yet actual population figures are difficult to estimate.

1.2.2. Behavioral, cognitive and social complexity of chimpanzees

Non-human primates are among the most challenging animals to keep in optimal captive conditions due to their behavioral, cognitive and social complexity (Talbot et al., 2023). This is especially true for our closest living relatives, chimpanzees (Suntsova & Buzdin, 2020), because many aspects of their lives are particularly complex (Ross, 2020). In the wild, chimpanzees live in multi-male, multi-female groups characterized by high levels of fission-fusion dynamics, with females transferring across groups upon reaching sexual maturity (Arcadi, 2018; Symington, 1990). In contrast to other primate species, the members of a group do not always remain together, but rather split in small «parties» of variable size and composition that repeatedly meet (i.e., fusion) and part (i.e., fission) during the course of the day (Hanamura, 2015). Furthermore, chimpanzees have the ability to adapt to a variety of complex and multidimensional habitats, from tropical forests to savannahs (Hunt, 2020), which makes it very difficult to reproduce their environmental needs in captive settings (Ross, 2020). Some of these habitat types are highly variable in terms of climate fluctuations and resource availability, leading to high behavioral diversity in the communities that live in them (Kalan et al., 2020).

In the wild, chimpanzees interact in complex ways with their environment, exhibiting a wide range of behaviors and displaying advanced cognitive abilities (Gilby & Machanda, 2022). For example, they can use spatial memory to recall the location of large fruit trees across seasons (Janmaat et al., 2013) or to revisit previous nest sites of army ants upon which they pray (Schöning et al., 2007). Moreover, research conducted in captivity suggests that chimpanzees have long-term memories that may allow them to recall specific past events (Lewis et al., 2019). There is also evidence that chimpanzees have planning abilities that allow them to anticipate future events, for example by gathering objects for later use (Mulcahy & Call, 2006; Osvath, 2009). Similar to many other non-human primates, chimpanzees also have a complex understanding of the objects that surround them and of their properties. For instance, they can track the displacement of an invisible object that is hidden in a container which changes locations (Barth & Call, 2006) and, to some degree, they understand causal relationships (Cacchione & Rakoczy, 2017; Hanus & Call, 2011; Völter et al., 2016). Furthermore, like other non-human primates, chimpanzees share some numerical processing mechanisms with humans, such as the ability to represent numerical values (see Cantlon, 2012). Wild chimpanzees, for example, use these numerical abilities to decide whether to participate or not in conflicts with other groups (Wilson et al., 2001).

Chimpanzees are also renowned for their advanced problem-solving skills. In the wild, they are continuously exposed to complex ecological and social challenges that are better dealt with understanding and decision-making skills (Morimura, 2006). They show high cognitive flexibility, being able to innovate and adapt their behavior to changing conditions (Bandini & Harrison, 2020; Cantwell et al., 2022). Research in captivity has shown that chimpanzees are able to master complex tasks, such as the floating peanut task, which requires using water as a tool to access a peanut in a container (Ebel et al., 2019; Hanus et al., 2011). Chimpanzees are flexible tool-users, which means that they have the ability to use or manufacture an external object to reach specific goals, finding innovative solutions in novel situations (Call, 2013; Hunt et al., 2013). Additionally, they can successfully manipulate tools in hierarchical and sequential manners (Hayashi & Takeshita, 2022; Martin-Ordas et al., 2012). In their natural habitat, tool-use behavior is typically associated with access to specific food resources, including termite-fishing (Boesch & Boesch, 1990; Goodall, 1986; Jones & Sabater Pi, 1969), nut-cracking (Boesch & Boesch, 1983; Inoue-Nakamura & Matsuzawa, 1997) and even hunting (Pruetz et al., 2020), but it has also been described in non-foraging contexts, during aggression, sexual displays and for hygiene purposes (Micheletti et al., 2022; Pal & Sinha, 2022). Furthermore, compelling evidence indicates a cultural component in chimpanzee tool-use, as different chimpanzee communities display distinct types of tools and techniques (Koops et al., 2015; Lycett et al., 2010; McGrew & McGrew, 1992). This suggests that social learning mechanisms are usually involved in the acquisition of tool-use behaviors (Hobaiter et al., 2014; Whiten et al., 2022).

Like most primates, chimpanzees also exhibit a broad range of social behaviors. They form strong and long-lasting social bonds (Mitani, 2009) and establish complex associations with their conspecifics (Bray et al., 2021; de Waal, 2007; Massen & Koski, 2014; Samuni et al., 2018; Silk, 2002; Surbeck et al., 2017). It has also been suggested that these strong social relationships between individuals facilitate group-level cooperation (Samuni et al., 2021). In fact, it is well known that chimpanzees can coordinate their actions and cooperate to solve problems. In the wild, they engage in complex cooperative behaviors such as cooperative hunting, meat sharing or the formation of coalitions (Boesch, 1994; Gilby & Machanda, 2022). In addition, numerous studies in captivity support that, when exposed to experimental tasks, chimpanzees also spontaneously tend to cooperate with their conspecifics (Hirata & Fuwa, 2007; Rosati et al., 2018; Schmelz et al., 2017; Suchak et al., 2016). Experimental cooperative tasks also revealed that chimpanzees use gestural and vocal communication to coordinate their actions (Melis & Rossano, 2022; Voinov et al., 2020). Recent work has shown that chimpanzees have remarkable communicative skills, being able to combine calls to produce an extensive repertoire of structured vocal sequences (Bortolato et al., 2023; Girard-Buttoz et al., 2022). Thus, gestures and vocal communication play an important role in the lives of wild and captive chimpanzees (Call & Tomasello, 2007; Slocombe et al., 2022). For example, wild chimpanzees use vocalizations to increase social cohesion (Bouchard & Zuberbühler, 2022) or to facilitate cooperative hunting (Mine et al., 2022), and gestures to initiate play behavior (Fröhlich et al., 2016) or drawn others' attention towards specific targets (Wilke et al., 2022).

Like humans, chimpanzees have slow life histories, characterized by slow growth and late weaning, delayed maturity and long lifespan (Davison & Gurven, 2021). Therefore, infants form strong and long-lasting affective bonds with their mothers (Reddy & Sandel, 2020), who play a crucial role in their development of social and cognitive skills and provide them with important opportunities for social learning (Bründl et al., 2022; Hayashi & Matsuzawa, 2017; Hirata, 2009; Lonsdorf, 2006, 2013; Maestripieri, 2018). For example, captive mother-reared chimpanzees are more likely to engage in species-typical behaviors, such as grooming, nest building or copulation, as compared to hand-reared individuals (Clay et al., 2023). In wild chimpanzees, maternal care has been associated with higher reproductive success (Crockford et al., 2020), whereas maternal loss has been linked to reduced growth and survival (Nakamura et al., 2014; Samuni et al., 2020; Stanton et al., 2020). Similarly, studies with captive chimpanzees have shown that early maternal separation can have negative long-term effects on their social skills and welfare (Chernus, 2008; Kalcher-Sommersguter et al., 2015; Martin, 2023). Chimpanzees are also sensitive to others' emotional states (Koski & Sterck, 2010) and exhibit empathy-related behaviors (Clay, 2022; Brooker et al., 2024). Like humans, primates can establish emotional and non-emotional connections with others through behaviors like mimicry, behavioral contagion, and emotional contagion. Furthermore, current evidence suggest that great apes show more sophisticated forms of empathic responses, such as targeted help and consolation (Brooker, Webb & Clay, 2022). For instance, they can show affiliative interactions towards recipients of aggression (i.e., consolation), thus reducing their levels of stress (Fraser et al., 2008; Webb et al., 2017). Research in captivity has also shown that chimpanzees engage in cognitively complex prosocial behaviors, such as spontaneous altruism (Melis et al., 2011; Warneken et al., 2007; Warneken & Tomasello, 2006). These altruism-like behaviors have also been documented in wild settings (Boesch et al., 2010). Furthermore, chimpanzee responses to injured and dead conspecifics resembles those shown by humans, as they show signs of emotional distress and their reaction to death appears to be mediated by social bonds with the deceased individual (Anderson, Gillies & Lock., 2010; de Marco et al., 2022; van Leeuwen et al., 2016). Finally, reassurance behaviors toward a bereaved mother following the loss of her infant have been observed in zoo-housed chimpanzees (Goldsborough et al., 2020).

Another expression of chimpanzee psychological complexity is their display of behavioral abnormalities that resemble symptoms of compromised mental health observed in humans. Increasing evidence suggests that, in great apes, early adverse experiences are associated with long-term alterations in coping style, emotional and behavioral regulation, brain morphology, and even in the expression of nervous system genes related to anxiety and mood disorders (Sánchez et al., 2001). Chimpanzees often develop behavioral abnormalities, including stereotypes, self-mutilation, excessive aggression, fear, or withdrawal, which can detrimentally impact their social skills and ability to integrate in a group (Bruene et al., 2006). Notably, chimpanzees that have been used in research, kept as pets, or involved in the entertainment industry may endure long-term consequences from these traumatic experiences. This can lead to the development of behavioral phenotypes resembling psychological disorders found in humans, such as depression, anxiety disorders, or post-traumatic stress disorder

(Bradshaw et al., 2008; Ferdowsian et al., 2011; Lopresti-Goodman et al., 2015; Sánchez et al., 2001; Úbeda et al., 2021).

Finally, it is well-known that chimpanzees and other non-human primates show high inter-individual differences in temperament or personality (Freeman & Gosling, 2010). In chimpanzees, in particular, personality has been studied for decades using personality questionnaires based on human models (King & Figueredo, 1997; Weiss et al., 2009; Weiss et al., 2011), which have proved that chimpanzee personality traits are similar or comparable to those describing human personality (Weiss, 2017b, 2018), Furthermore, individual differences in chimpanzee personality have been linked to crucial aspects of their life, including welfare (Robinson et al., 2017), longevity (Altschul et al., 2018), rank and reproductive success (Weiss et al., 2023), and cognitive performance (Altschul et al., 2017; Herrelko et al., 2012; Reamer et al., 2014).

Overall, it seems obvious that reproducing the environmental needs of non-human primates and providing them with an optimal level of welfare in a captive setting is extremely challenging, especially for a species that shows sophisticated behaviors and advanced cognitive, emotional and social skills, like chimpanzees. Therefore, research focused on the behavior and welfare of captive chimpanzees is crucial to better understand the needs of this species in a captive environment and to identify those aspects that most need improvement (Ross, 2020). Only by doing so, shall we be able to implement the necessary measures to guarantee chimpanzees a life “worth living”.

1.2.3. Assessment of chimpanzee welfare through behavioral observations

Behavioral observations constitute an accurate, cost-effective and non-invasive method to assess welfare in non-human primates (Lutz & Baker, 2023; Whitham et al., 2023). Negative behavioral indicators, such as atypical or abnormal behaviors, have been extensively studied in captive chimpanzees (Baker & Easley, 1996; Bloomsmith et al., 2020; Jacobson et al., 2016), possibly because they are more evident and easier to identify than positive behavioral indicators (Clay et al., 2023). Abnormal behaviors in primates have been defined as behaviors that differ in kind or degree from the natural behaviors of the species in the wild (Erwin et al., 1979; Walsh et al., 1982). Traditionally, the presence of abnormal behaviors has been considered an indicator of poor welfare due to its association with animals living in physically and socially impoverished environments and experiencing inadequate management practices (Baker, 1997; Brent, 1992; Maki et al., 1993; Martin, 2023; Turner et al., 1969). However, several authors have questioned the relationship between abnormal behaviors and welfare in captive chimpanzees and in non-human primates in general. For instance, it has been showed that coprophagy, a frequent abnormal behavior in captive chimpanzees, might be socially-learned and should not be necessarily considered an indicator of poor welfare (Hopper et al., 2016).

Other researchers claim that, to some degree, abnormal behaviors may be endemic to captive populations and very difficult to eradicate despite efforts of improving their living environment (Birkett & Newton-Fisher, 2011). Furthermore, some abnormal behaviors can also develop in welfare-promoting environments and in the absence of any psychological distress, as a result of an animal's coping mechanisms (Lutz & Coleman, 2022). Indeed, whether animals develop abnormal behaviors depends not only on the environment in which they are living, but also on multiple factors, including sex, age, early rearing history, genetic predisposition and personality (Bloomsmith et al., 2020; Lutz & Coleman, 2022).

In addition to abnormal behaviors, self-directed behaviors (e.g., touching, rubbing or scratching one's body or face) have traditionally been proposed as indicators of poor welfare in non-human primates, because they have been linked to negative emotional states like increased tension or anxiety (Baker & Aureli, 1997; Maestripieri et al., 1992). In line with this, several studies have reported an increase in self-directed behaviors following changes in non-human primates’ environments (Bonnie et al., 2016; Lukas et al., 2003). Furthermore, self-directed behaviors appear to increase when primates are exposed to challenges or novel situations (Elder & Menzel, 2001; Itakura, 1993; Leavens et al., 2004; Leavens et al., 2001; Meyer & Hamel, 2014), but not necessarily in a negative context (Laméris et al., 2022; Neal & Caine, 2016).

In recent years, there has been a growing interest in establishing measures of good quality of life and considering positive behavioral indicators of welfare, moving beyond the traditional focus on negative markers (Mellor, 2016; Whitham & Wielebnowski, 2013; Wolfensohn et al., 2018). Understanding the natural repertoire of a species and how individuals live in the wild becomes crucial when using behavior as a measure of welfare (Lutz & Baker, 2023). One of the first attempts to describe the welfare needs of chimpanzees was developed by Pruetz and McGrew (2001) and is based on this natural-based approach. In their review, the authors provide recommendations for chimpanzee captive care, based on how chimpanzees live and behave in the wild. Following this natural-based approach, several studies have assessed welfare by comparing different features between captive and wild chimpanzees, including activity budgets (Inoue & Shimada, 2020; Yamanashi & Hayashi, 2011), social interactions and social structure (Inoue & Shimada, 2020), diet and foraging activity (Gerstner & Pruetz, 2022) or nesting behavior (Anderson et al., 2019). Similarly, the presence (or absence) of species-typical behaviors exhibited by wild-living counterparts has often been evaluated as a measure of welfare (Browning, 2019; Hughes & Duncan, 1988; Novak & Suomi, 1988). For example, in a recent survey assessing welfare in chimpanzees across various institutions in the United States, including zoos, sanctuaries, and research facilities, Clay and colleagues (2023) collected behavioral data on 1122 individuals from 35 different institutions. The study focused on the occurrence of four species-typical behaviors: tool use, nest-building, social grooming, and copulation. The findings revealed that tool-use was observed in 94.3% of the sample, active grooming in 85.7%, copulation in 68.3%, and nest-building in 58.9%. However, the study highlighted that less than half of the chimpanzees (45.6%) exhibited all four behaviors, underscoring the need for additional measures to increase the opportunities for the expression of species-typical behaviors.

Some researchers have criticized the use of wild baselines to define how chimpanzees should live and behave in captivity (Cronin & Ross, 2020; Hosey, 2005; Neal Webb et al., 2019) because, similar to abnormal behaviors, the association between the presence (or absence) of species-typical behaviors and welfare in chimpanzees is not straightforward (see Clay, 2023). Nonetheless, despite the limitations of undesirable (e.g., abnormal, self-directed behaviors) and species-typical behaviors as measures of welfare, studies assessing these behaviors in chimpanzees from different captive environments and with diverse life histories have provided valuable information about their prevalence and their possible relationship with welfare (Bloomsmith et al., 2020; Bloomsmith et al., 2019; Clay et al., 2023; Jacobson et al., 2016). In other words, monitoring the behavior of captive chimpanzees is crucial to fully understand the species' needs in captivity and to successfully establish welfare standards (Ross, 2020). In line with this, Whitham and colleagues (2023) conducted a study in which they monitored behavioral data in chimpanzees from 16 different facilities in order to establish reference intervals for behavioral and physiological measures of welfare. These reference intervals are ranges of values for variables of interest (i.e., grooming, feeding, locomotion, etc.) calculated by collecting data on physically healthy animals with no welfare concerns. The authors suggest that these reference intervals can be used by animal caregivers to make decisions regarding husbandry practices and management. Similarly, taking into consideration the increasing literature on captive chimpanzees, Ross (2020) provides a recent review of the most important welfare considerations according to experts in the field of captive chimpanzee care and management, including recommendations for topics such as social housing, facilities, diet, environmental enrichment or the relationship with humans. He concludes that more space, larger groups and more choices and control over the environment are some potential improvements that can help increase chimpanzee welfare in captivity (Ross, 2020).

1.3. Personality in non-human primates

1.3.1. Animal personality: Foundations, applications and assessment

In the field of animal science, personality refers to the existence of behavioral and physiological differences among individuals of the same species, which are consistent over time and across different contexts (Carere & Maestripieri, 2013; Réale et al., 2007). In an attempt to differentiate it from human personality, animal personalities have also been referred to as temperament, behavioral syndromes, coping styles or behavioral predisposition (Gosling, 2001; Gosling & John, 1999; Koolhaas et al., 1999; Reber et al., 2021; Sih et al., 2004; Wilson et al., 1994); but nowadays, the term personality is widely accepted. Animal personality is a relatively new area of research, although the first studies providing empirical evidence date back to the early 1900s (Lorenz, 1935; Pavlov, 1906, 1941). Mostly, seminal research in this area has been conducted with primates (Buirski et al., 1978; Crawford, 1938; Chamove, 1974; Chamove et al., 1972; Hebb, 1949; Nash & Chamove, 1981; Yerkes & Yerkes, 1936). This is not surprising, considering that their phylogenetic closeness with humans, as well as their complex social lives, intelligence and emotions, make non-human primates an ideal model for personality research (Figueredo et al., 2015; Michalski & Shackelford, 2010). However, it was not until the 1990s that research on animal personality, in general, and on primate personality, in particular, gained in popularity. Since then, numerous studies aimed to describe species-specific personality structures and/or provide insights into how to measure personality traits across a wide range of taxa, including invertebrates (Kralj-Fišer & Schuett, 2014), fish (Castanheira et al., 2013), reptiles (Waters et al., 2017), birds (van Oers & Naguib, 2013), and mammals (Ciardelli et al., 2017; Highfill & Kuczaj, 2007; Menzies et al., 2013; Úbeda et al., 2019). In non-human primates, personality research has been conducted in large and diverse samples of subjects living in laboratories, zoos and in the wild (Freeman and Gosling 2010; Gartner and Weiss 2018). Additionally, there has been a growing interest in studying personality in animal sanctuaries (Chotard et al., 2023; King et al., 2005; Úbeda & Llorente, 2015).

Currently, animal personality has become a prolific and interdisciplinary area of research, with numerous contributions from the fields of ethology, psychology, genetics, neuroscience and endocrinology, among others (Carere & Maestripieri, 2013). From a theoretical point of view, the study of animal personality and its underlying mechanisms can provide insights about the nature and evolution of human personality (Gosling, 2001; Nettle & Penke, 2010; Weinstein et al., 2008). In fact, current evidence suggests that personality traits in non-human animals resemble those describing human personality (Gosling, 2001; Sih & Giudice, 2012) and that some of these traits share a common neurobiological basis (Carere et al., 2010; Koolhaas et al., 2010; Lages & McNaughton, 2022), especially in non-human primates (Fritz et al., 2020; Latzman et al., 2018; Latzman et al., 2015). From an applied perspective, understanding inter-individual differences in animals kept under human care may have important implications for animal welfare and management (Gartner & Weiss, 2018; Norman et al., 2021; Powell & Gartner, 2011). For example, individuals with different personalities may react differently to similar environments or experimental conditions (Carere & Maestripieri, 2013), or be more or less likely to suffer stress in a captive setting (Adams & Huntingford, 2005; Cussen & Mench, 2015). The assessment of personality could prove a particularly relevant tool in environments such as zoos and other captive settings, for the optimization of husbandry practices and environmental enrichment strategies customized to meet the requirements of each individual (Baker, 2012; Goswami et al., 2020; Quintavalle

Pastorino et al., 2019). Furthermore, knowledge about animal personality could improve the success of conservation and re-introduction programs, as it may aid in the selection of the most suitable individuals (e.g., those with bolder and more explorative traits) to be released into the wild (de Azevedo & Young, 2021).

Historically, two main theoretical and methodological approaches have been used to study animal personality: one is rooted in ethology and behavioral ecology and the other one is based on human comparative psychology. Individual variation in behavior (i.e., personality) can generate differences in terms of biological efficiency or fitness and therefore is subjected to selection pressure (Smith & Blumstein, 2008). Thus, behavioral ecologists seek to comprehend the evolutionary processes that have preserved these variations in individual behavior among populations (Réale et al., 2010). Conversely, comparative psychologists usually seek to identify the underlying dimensions or traits that reflect behavioral variation, with an emphasis on understanding the genetic and environmental influences and their implications for fitness (Gartner & Weiss, 2018). When assessing animal personality, behavioral ecologists have traditionally used a coding methodology, which usually implies measuring the animals' responses to the introduction of novel objects or other changes in their environments (Massen et al., 2013; Spencer-Booth & Hinde, 1969; Yerkes & Yerkes, 1936). Behavioral coding can also involve observing subjects' spontaneous behavior (Brandão et al., 2019; Koski, 2011). This methodology typically focuses on traits such as boldness, exploration tendency, aggressiveness, activity, or sociability (Koski, 2014). In contrast, comparative psychologists primarily rely on subjective trait ratings obtained through questionnaires containing a list of attributes or adjectives. These questionnaires are filled by raters who are familiar with the animals (Vazire et al., 2007). After collecting the data, researchers use data reduction techniques, such as exploratory factorial analysis, principal component analysis or cluster analysis to identify underlying constructs or groups that represent higher-order personality traits (Fernández-Lázaro et al., 2019; Weiss & Adams, 2013).

Both methodologies, coding and rating, have been extensively used to assess personality in non-human primates (Blaszczyk, 2020; Freeman et al., 2011; Gosling et al., 2003a; Highfill et al., 2010), and they both have advantages and limitations. For example, behavioral coding would seem to be more objective, but studies in humans have shown that it does not always provide reliable estimates (Borkenau, 1992; Gosling et al., 1998), because behavioral observations tend to focus on single measures of specific behaviors in a particular context, while ratings provide a more global perspective, as they encompass the experience of the raters across time and situations (Gosling et al., 2003a). Behavioral measures, particularly those assessed in an experimental context, offer other advantages, as outlined in Weiss and Adams (2013). These advantages include high replicability within and across species, as the experimental procedures can be easily reproduced. Additionally, contrary to ratings, researchers do not necessary need extensive familiarity with the animals. Nonetheless, a significant drawback of behavioral measures is their tendency to assume a direct link between a specific behavior and a particular trait, with a consistent function across species, which may not always be the case. In contrast, ratings use several measures of multiple personality traits, providing a clearer understanding of trait meanings and allowing fair comparisons across species. (Weiss & Adams, 2013). Finally, questionnaires also provide some practical benefits, such as being less time-consuming for both the raters and the researchers, facilitating more efficient data collection (Freeman et al., 2011).

1.3.2. Applying human models to study non-human primates' personality

Researchers have long tried to demonstrate the biological basis of human personality by studying the psychological, neuroanatomical, hormonal and genetic mechanisms that determine behavioral patterns (Eysenck, 1963; Khatibi & Khormaei, 2016; Sanchez-Roige et al., 2018; Sellers et al., 2007). If human personality indeed has a biological foundation, it is expected that at least some human traits would also be observed in our closest relatives. Thus, applying human personality models to non-human primates offers an opportunity to trace the evolutionary development of these traits and gain deeper insights into the underlying behavioral associations (King & Weiss, 2011). Following this approach, comparative psychologists have used several human models to assess personality in non-human primates, including the Five Factor Model or Big Five (Goldberg, 1990), Eysenck's Psychoticism-Extraversion-Neuroticism (PEN) model (Eysenck, 1967; Eysenck & Eysenck, 1964), or Cattell's 16 PF (Cattell & Mead, 2008). In order to achieve this, they have selected representative clusters of adjectives from the original human items, which describe behaviors that can be successfully identified in a species or taxonomic group, and they have disregarded those that are not relevant.

The ongoing debate over the optimal methodology for assessing non-human primates' personality (behavioral coding or trait rating), has witnessed substantial research supporting the use of human models, particularly when using a rating approach. Firstly, the close phylogenetic relationship between humans and non-human primates, especially great apes, provides a basis for better understanding and rating their personality characteristics (Weiss & Adams, 2013). Anthropomorphism —attributing human traits to animals— is a frequent criticism of employing human models (Weiss et al., 2011). Nonetheless, several studies in the wild and in captivity have demonstrated that great apes exhibit inherent personality structures specific to their species, and any similarities with human personality can be attributed to genetic and phylogenetic proximity rather than anthropomorphism (King et al., 2005; Weiss et al., 2012; Weiss et al., 2017). Another critical aspect when applying questionnaires is inter-rater reliability (i.e., consensus between raters). In primate personality research there is evidence suggesting that the level of reliability obtained when applying human models to non-human primates is similar to that observed in human studies (see Weiss 2017). Finally, various researchers have questioned the validity of trait rating (Šlipogor et al., 2021; Uher & Asendorpf, 2008; Uher & Visalberghi, 2016), claiming that traits obtained through this method may not accurately describe actual behaviors. However, associations between traits obtained from questionnaires based on human models and observed behaviors have been reported in several primate species, including monkeys (Ebenau et al., 2020; Iwanicki & Lehmann, 2015) and great apes (Eckardt et al., 2015; Konečná et al., 2008; Murray, 2011; Pederson et al., 2005; Schaefer & Steklis, 2014; Vazire et al., 2007). This suggest that, to some extent, ratings can effectively predict behavior.

1.3.3. Eysenck's biological theory of personality

Hans Eysenck (1916-1997) was one of the first researchers who applied statistical reduction methods to condense the complexity of personality in a few basic dimensions, which he referred to as higher-order traits (Eysenck, 1941, 1947). In an attempt to describe the biological basis of these traits, Eysenck also developed his arousal theory of personality (Claridge, 1967) in which he provided experimental evidence of the relationship between personality traits and biological factors, such as genetics, brain structure and physiological processes.

Eysenck's first study was conducted on a large sample of soldiers (Eysenck, 1944), who were asked to rate themselves on a 39-item questionnaire describing personality characteristics. Later, he expanded this analysis to a much larger sample, including almost 10,000 subjects (Eysenck, 1947). From this early research, he identified two basic personality dimensions: Extraversion/Introversion and Neuroticism/Emotional Stability. Shortly after, he also described a third dimension (Eysenck, 1952), Psychoticism/Superego, but it was not until a few years later that Eysenck fully developed his theory of personality in his notorious book *The biological basis of personality* (Eysenck, 1967), in which he presented the Psychoticism-Extraversion-Neuroticism (PEN) model.

Eysenck (1967) associated Extraversion with a general tendency to experience positive emotions. Extraverts are characterized by high sociability, activity and assertiveness, whereas introverts are more reserved, reflective and introspective (Eysenck, 1967). According to his arousal theory, Extraversion/Introversion is linked to differences in the reticular activating system (RAS), a subcortical region of the brain that plays a significant role in the regulation of the sleep-wake cycle and wakefulness. Eysenck suggested that extraverts have lower baseline levels of cortical arousal and a less sensitive RAS, which means that they require more external stimulation to reach high levels of arousal. By contrast, introverts have a higher level of baseline levels of cortical arousal and a more sensitive RAS, which makes them more reactive to external stimuli (Claridge, 1967; Eysenck & Furnham, 1993).

According to Eysenck's theory, Neuroticism is associated with a general tendency to experience negative emotions, including high levels of anxiety, irritability and sadness. In contrast individuals high in Emotional Stability exhibit traits of calmness, even-temperament, and resilience. In his arousal theory, Neuroticism/Emotional Stability is linked to the reactivity of the sympathetic nervous system, a region of the brain that plays a role in the response to stressful or potentially dangerous situations. Specifically, he claims that higher scores on this trait (i.e., more neurotic individuals) are related to strong physiological responses to stress (Claridge, 1967; Eysenck & Furnham, 1993).

The third major dimension incorporated in Eysenck's theory was Psychoticism, as described in his work *Psychoticism as dimension of personality* (Eysenck & Eysenck, 1976) and later revisions (Eysenck et al., 1985). According to Eysenck's description, people scoring high on this trait (i.e., more psychotic individuals) are cold, egocentric, hostile, suspicious, impersonal and aggressive (Eysenck & Furnham, 1993). The opposite pole of this dimension has been called "superego", following Freud's personality theory. Eysenck suggested that this trait was related to certain hormonal and biochemical secretions, such as serotonin and dopamine metabolites, and to sex hormones (Eysenck & Furnham, 1993). In particular, he observed that increased testosterone levels were linked to higher scores on this trait (i.e., more psychotic individuals). While Extraversion and Neuroticism have been extensively validated, clinically and psychometrically, Psychoticism is the most heterogeneous and less clearly defined dimension (Bech, 2020). Furthermore, it has also proven to be the less heritable trait (Heath & Martin, 1990). Nonetheless, several studies have provided evidence of the biological basis of Psychoticism (Claridge & Birchall, 1973; Claridge & Chappa, 1973; Colzato et al., 2009; Krishnadas et al., 2014; Loehlin et al., 2005; Turakulov et al., 2004).

In human personality research, Eysenck's model was eventually substituted by the Five Factor Model (FFM) or the Big Five (Goldberg, 1990), which is nowadays the dominant model used to assess human personality. This model describes five broad personality traits: Neuroticism, Extraversion, Agreeableness, Conscientiousness and Openness (to Experience). Critics of Eysenck's model claim that the five dimensions proposed in the Five Factor Model better capture the complexity of human personality (Costa & McCrae, 1992, 1995a, 1995b). Possibly for the same reason, most personality studies in chimpanzees and other non-human primates have also used adjective ratings based on items from the human Five Factor Model (Freeman & Gosling, 2010; King & Figueredo, 1997; Weiss, 2017a; Weiss et al., 2009). By contrast, Eysenck's model has been rarely used to assess primate personality, with only one study in macaques (Chamove et al., 1972) and one in chimpanzees (Úbeda & Llorente, 2015). Nonetheless, despite the limitations of Eysenck's model to assess human personality, there might be important applications to the study of non-human primates, as discussed in the following lines.

The key findings of Eysenck regarding the biological basis of his model have been extensively validated over the years (Ergüneş, 2018; Hagemann et al., 2009; Khatibi & Khormaei, 2016; Mitchell & Kumari, 2016; Soliemanifar et al., 2018), and similar validation has been demonstrated for the dimensions of the Five Factor Model (Alkalay et al., 2022; DeYoung, 2014; DeYoung et al., 2010; Jang, Livesley & Vernon, 1996; Ormel et al., 2013; Zuckermann, 1993). These associations between personality traits and neurobiological and genetic factors contribute to a better understanding of non-human primate personality from an evolutionary perspective. Furthermore, Eysenck's model and the Five Factor Model share two common traits (Neuroticism and Extraversion), which exhibit high levels of similarity across models (McCrae & Costa, 1985). Additionally, Eysenck hypothesized that Agreeableness and Conscientiousness in the Five Factor Model are facets of the trait Psychoticism (Eysenck et al., 1985), an assumption which has been partially supported by other authors (Draycott & Kline, 1995; Goldberg & Rosolack, 1994; Heaven et al., 2013; Ruch et al., 2020; Saggino, 2000).

Regarding its applicability to non-human primates, it is worth noting that Extraversion and Neuroticism are traits easy to identify and interpret in primate species. For instance, Extraversion is linked to high levels of inter-rater reliability across different studies on primate personality, while reliability across raters is lower for Agreeableness and Conscientiousness (Freeman & Gosling, 2010). Although Neuroticism usually shows lower inter-rater reliability (Dutton, 2008; Freeman & Gosling, 2010), this trait has been described in a wide range of primate species (Gosling, 2001; Iwanicki & Lehmann, 2015; Morton et al., 2013b; Wilson et al., 2018). In fact, the behavioral indicators of Neuroticism, such as fearfulness and reactivity towards novel stimuli or conspecifics, have been extensively studied in non-human primates (Locurto, 2007; Suomi et al., 2011). Finally, some of the characteristics that define Eysenck's Psychoticism, such as aggressiveness and impulsivity, are commonly displayed also by non-human primates, especially in competitive contexts and in dominance-related interactions (de

Almeida et al., 2015; Fairbanks et al., 2004; Higley et al., 2011). Similarly, the association between higher scores in Psychoticism and dominant, violent and unempathetic behavior in humans has been well-documented (see Cravens-Brown, 2002). It is also worth highlighting that several authors have attempted to describe psychopathic personality construct in chimpanzees (Latzman et al., 2016; Lilienfeld et al., 1999). Lilienfeld and colleagues (1999) developed the Chimpanzee Psychopathy Measure (CMP), a 34-item questionnaire, derived from previous personality inventories used in non-human primates, supplemented with items relevant to human psychopathy (e.g., "boredom prone," "fails to learn from punishment"). The Chimpanzee Psychopathy Measure demonstrated acceptable inter-rater reliability and internal consistency, along with expected correlations with behavioral measures such as agonism, sexual activity, daring behaviors, and teasing. More recently, Latzman and colleagues (2016) applied scale measures based on the triarchic psychopathology model in humans. This model encompasses three distinct phenotypic constructs: boldness, meanness and disinhibition (Patrick et al., 2009). Their findings support the application of this triarchic model as a basis for defining psychopathy-relevant dimensions in chimpanzees. Furthermore, additional research employing this model suggests that psychopathic tendencies in chimpanzees and humans share a common neurobehavioral and genetic basis (Latzman et al., 2017).

1.4. Cognitive challenges in non-human primates

1.4.1. Welfare implications

Captive animals offer an ideal opportunity to conduct non-invasive experimental research to measure their cognitive abilities and provide insight into the evolution of our own cognitive skills. In fact, a comparative perspective is nowadays considered crucial for our understanding of human cognition (Call, 2017). Given their phylogenetic closeness to humans, therefore, it is not surprising that non-human primates and great apes, in particular, have been the object of cognitive experiments for almost a century (reviewed by Clark, 2011). Studies assessing primate cognitive abilities have long been conducted in laboratories, followed by zoological institutions and, more recently, animal sanctuaries (McEwen et al., 2022; Ross & Leinwand, 2020; Schwartz & Beran, 2022). From a scientific perspective, non-laboratory settings offer some advantages, such as larger and more naturalistic environments, with animals housed in social groups and socio-ecological conditions that more closely resemble the ones they would experience in the wild (Cronin, 2017; Ross & Leinwand, 2020). Moreover, in zoos and primate sanctuaries cognitive research can also serve an educational purpose, by creating an opportunity to enhance the engagement of the general public with science and by potentially increasing visitors' knowledge and respect for a species (Egelkamp & Ross, 2019; Hopper, 2017).

Moreover, the introduction of problem-solving opportunities has the potential to enhance the welfare of captive great apes (Clark, 2011, 2017; Meehan & Mench, 2007). This hypothesis arises from the fact that, in the wild, great apes face complex problems related to their environment and therefore their need to be challenged is inherent to their nature (Morimura, 2006). For example, chimpanzees engage in problem-solving activities even when the reward is a non-preferred food item (Brooks et al., 2021) or no reward is involved (Clark & Smith, 2013). Similarly, in an experimental context, some chimpanzees may choose to work for food, even when the same food is available without effort (Menzel, 1991). This phenomenon, known as contrafreeloading (Jensen, 1963). has also been described in Japanese macaques (Ogura, 2011) and rhesus macaques (Reinhardt, 1994), as well as in non-primate species (McGowan et al., 2010; Smith et al., 2022; Vasconcellos, Adania & Ades, 2012). Furthermore, providing the animals with challenges offers them the opportunity to make choices and increase their control over the environment (Whitham & Wielebnowski, 2013). In line with these assumptions, cognitive challenges have been developed as enrichment activities for captive animals, rather than simply as a means to measure the subjects' cognitive skills. This approach falls within the definition of cognitive enrichment, also called "goal-oriented" enrichment (Ross, 2020), which, according to Clark (2011, p.6): "1) engages evolved cognitive skills by providing opportunities to solve problems and control some aspect of the environment, and (2) is correlated to one or more validated measures of well-being".

Despite the growing concern for animal welfare in zoo-housed animals (Kagan et al., 2015), the impact of cognitive challenges on subjects has often been overlooked (Ross, 2010), leaving the question of how to effectively measure these effects unanswered. Recently, however, there has been an increasing interest in studying the welfare effects of cognitive testing in non-human primates housed at research facilities and zoos (Cronin, 2017; Herrelko et al., 2012; Ruby & Buchanan-Smith, 2015; Whitehouse et al., 2013; Yamanashi & Hayashi, 2011). Regarding cognitive enrichment, an increasing number of studies have assessed the impact of different types of activities on the welfare of great apes. These include puzzle strategies and tool-use-promoting tasks (Bloomstrand et al., 1986; Brent & Eichberg, 1991; Celli et al., 2003; Clark & Smith, 2013; Llorente & Campi, 2014; Morimura, 2003, 2006; Nash, 1982; Yamanashi et al., 2016; Zaragoza et al., 2011), and more recently computer-based tasks (Clark et al., 2019; Morimura et al., 2023; Perdue et al., 2012; Schmitt, 2018; Tarou et al., 2004). Tool-based enrichments are relatively common in chimpanzees, as they intend to simulate ant- or termite-fishing, a species-typical behavior frequently observed in the wild (Boesch & Boesch, 1990; Goodall, 1986; Jones & Sabater Pi, 1969). The ability to use tools requires complex cognitive skills such as information seeking and recombination (Call, 2013; Hunt et al., 2013). Thus, tool-use-promoting enrichments likely provide higher cognitive stimulation than simpler foraging devices or manipulative objects (Dutton et al., 2018).

A common and basic approach to assess the impact on welfare of a particular task or problem-solving activity is to use behavioral indicators, either positive or negative, that can be monitored during task exposure and/or that can be compared with a baseline or control condition. For example, in contexts where a task is presented to the subjects, and they have the choice of whether to engage with it or not, participation or time spent interacting with the task are usually considered positive indicators of interest or motivation (Dutton et al., 2018; Lutz & Novak, 2005; Schapiro & Lambeth, 2007). Similarly, while success in solving a particular task may not be directly related to welfare, it can serve as an indicator of the suitability of the challenge for the species and of whether the level of difficulty is adequate to stimulate the animals without generating excessive frustration (Meehan & Mench, 2007). Nonetheless, studies assessing cognitive challenges in chimpanzees show great variation in participation and success across subjects. This variability may be attributed to multiple factors, including inter-individual differences in sex, age, cognitive skills and personality (Altschul et al., 2017; Celli et al., 2003; Clark & Smith, 2013; Herrelko et al., 2012; Hopper et al., 2014). Additionally, research on enrichment activities in non-human primates have shown that the level of interest and the effects of the enrichment may differ considerably across subjects (Coleman & Novak, 2017; Costa et al., 2018; Izzo et al., 2011).

Like any other enrichment, cognitive challenges are likely to be effective if they are biologically relevant (Brereton & Rose, 2023; Newberry, 1995). For example, they may increase behavioral diversity and promote species-typical behaviors that animals would exhibit in their natural habitats, while also reducing undesirable or stress-related behaviors (Lutz & Novak, 2005; Mason et al., 2007; Nash et al., 2021; Swaisgood & Shepherdson, 2005; Woerle, 2020; Young, 2003). Thus, to assess the welfare effects of a particular enrichment, researchers usually compare the frequency or the duration of these behaviors across enrichment and baseline conditions (Bracke & Hopster, 2006; Hill & Broom, 2009). Following this methodology, numerous studies have reported an increase in species-typical behaviors, such as extractive foraging and tool use, when using cognitive enrichment devices in captive chimpanzees, and a decrease in abnormal behaviors and other negative indicators of welfare, such as inactivity and self-directed behaviors (Bloomstrand et al., 1986; Brent & Eichberg, 1991; Celli et al., 2003; Clark & Smith, 2013; Llorente & Campi, 2014; Morimura, 2003; Nash, 1982; Yamanashi et al., 2016; Zaragoza et al., 2011).

It is worth-noting, however, that the relationship between self-directed behaviors, welfare and cognitive challenges is complex and still not well understood. For instance, several studies have reported an increase in self-directed behaviors when non-human primates are exposed to novel or difficult tasks (Bonnie et al., 2016; Elder & Menzel, 2001; Itakura, 1993; Leavens et al., 2004; Leavens et al., 2001), especially when they provide incorrect responses (Leeds & Lukas, 2018; Wagner et al., 2016; Yamanashi & Matsuzawa, 2010). However, researchers evaluating self-directed behaviors in the context of cognitive enrichment, which is supposed to improve welfare, have reported contradictory results in chimpanzees. For instance, Yamanashi et al. (2016) found a decrease in self-directed behaviors when tool-based feeders were provided to captive chimpanzees, as compared to when the enrichment was absent. In contrast, Clark and Smith (2013) reported an increase in scratching in the presence of a cognitive enrichment device, whereas actively engaging with the device was linked to a decrease in scratching. Similarly, some authors have reported a link between the presence of enrichment activities and lower frequency of self-directed behaviors in other non-human primates (Brent & Belik, 1997; Costa et al., 2018), while others have found no significant link (Laméris et al., 2021). Therefore, this suggests that the effects of cognitive enrichment activities on primate self-directed behaviors is still poorly understood.

Cognitive challenges can be provided either to isolated subjects or in a social setting. On the one hand, separating animals from their social group avoids disturbances and provides more accurate information on the subject’s performance. On the other hand, implementing cognitive challenges in a social setting increases ecological validity and reduces animal distress due to human-induced separation, potentially improving welfare (Cronin, 2017; Drea, 2006). In this last case, assessing the impact of a particular task or device on social behaviors is crucial to fully understand the welfare effects at the group level. Nonetheless, studies addressing this issue have reported contradictory results, possibly due to differences in their methodology. For instance, several authors have observed increased aggression as a result of competition over access to the device or task, either in a testing context (Jacobson et al. 2019; Ruby and Buchanan-Smith 2015; Tarou et al. 2004) or when providing a cognitive enrichment (Maki et al., 1989; Sha et al., 2012). However, this may be avoided by providing multiple devices or by securing simultaneous access to various animals (Brent & Eichberg, 1991; Fagot & Bonté, 2010; Yamanashi et al., 2016). Similarly, cognitive challenges in socially-housed primates have been reported to enhance social play (Clark & Smith, 2013) and other prosocial behaviors (Ruby and Buchanan-Smith, 2015) and to increase group cohesion (Whitehouse et al. 2013), but also to reduce affiliative interactions (Brent & Eichberg, 1991; Sha et al., 2012) or not to affect them (Yamanashi et al., 2016).

1.4.2. Personality and cognitive performance

Interindividual variation in cognitive performance is widespread among species. Animals within the same species often show differences in how they learn, remember, and integrate information (Boogert et al., 2018). Likewise, research conducted in captive non-human primates has shown significant differences in cognitive abilities among individuals (Herrmann & Call, 2012; Herrmann et al., 2010; Vonk & Povinelli, 2011). This variation in cognitive performance may give rise to stable and heritable phenotypes that are linked to increased fitness, potentially evolving through natural selection (Boogert et al., 2018). Nonetheless, despite their potential adaptive value, differences in cognitive performance have been traditionally overlooked or treated as non-adaptive variation in studies on animals (Wilson, 1998).

Cognitive performance in animals can be influenced by factors such as age, sex, rearing conditions and previous experience (Thornton & Lukas, 2012). Additionally, personality is considered an important potential source of individual variation in performance (Boogert et al., 2018). While the relationship between personality and cognition has long been acknowledged in humans (Ackerman & Heggestad, 1997), this association is still poorly understood in animals. The first studies exploring this topic in non-human animals were conducted in the early twentieth century by Pavlov, who suggested that personality types in dogs were linked to differences in associative learning (Pavlov, 1906, 1941). However, it was not until 100 years later that research on the association between personality and cognition in animals gained popularity, especially in the field of behavioral ecology (for a review, see Dougherty and Guillette, 2018).

By definition, personality implies behavioral variability, which constitutes the basis for natural selection (Dingemanse & Réale, 2005). Thus, given that differences in performance impact subjects' fitness and are thus subjected to selection, personality traits and cognitive abilities might have co-evolved (Carere & Locurto, 2011). In fact, some researchers have suggested a direct link between personality traits and differences in how individuals gather, process and handle information, thus resulting in "cognitive styles" (Carere & Locurto, 2011; Sih & Giudice, 2012). This "cognitive styles" hypothesis is based on the trade-off between speed and accuracy which mainly focuses on the link between exploratory behavior or boldness and performance. In line with this, several studies assessing different tasks in a wide range of taxa have shown that more exploratory individuals learn faster, whereas those being more shy or inhibited are more accurate in their responses and show higher flexibility (Coleman et al., 2005; Fichtel et al., 2023; Finkemeier et al., 2022; Guenther et al., 2014; Herrmann et al., 2007; Jones et al., 2020; Matzel et al., 2003; Šlipogor et al., 2022).

In humans, the relationship between personality and cognition has been explored in several contexts, mostly using personality traits obtained from the Five Factor Model or from Eysenck's PEN model. For example, the dimension Openness from the Five Factor Model has been associated with general intelligence (Chamorro-Premuzic & Furnham, 2006, 2014) and Conscientiousness has been repeatedly linked to academic and job performance (Hurtz & Donovan, 2000; Mammadov, 2022; Noftle & Robins, 2007; von Stumm et al., 2011). Furthermore, individuals scoring high in both Conscientiousness and Agreeableness have been reported to show better performance at work, but only in jobs involving cooperative interactions with others (Witt et al., 2002).

Extraversion has also been related to performance and intelligence, but with inconsistencies across contexts. For example, it has been suggested that extraverts perform better in stimulating environments and in tasks that require short-term memory, whereas introverts are more successful at tasks that require higher concentration and have better long-term memory (Li et al., 2010; Matthews, 1999). In line with this, studies with Eysenck's model show that extraverts perform better in more demanding or stimulating tasks, because they provide the sufficient level of excitation in their cortex (Bentea & Anghelache, 2012; Cox-Fuenzalida et al., 2006; Shigehisa et al., 1973; Szymura & Nęcka, 1998).

Neuroticism, another trait described by both the Five Factor Model and Eysenck's model, has been negatively correlated with cognitive performance across multiple studies and contexts (Chamorro-Premuzic & Furnham, 2003; Debusscher et al., 2016; Dobson, 2000; Judge & Zapata, 2015; Reynolds et al., 2014), particularly in highly stimulating tasks (Szymura & Wodniecka, 2003). This could depend on the fact that neurotic individuals are more likely to suffer from anxiety when exposed to potentially stressful situations, such as a test-taking context, and that this would negatively impact their memory and attention skills (Chamorro-Premuzic & Furnham, 2014). Finally, Psychoticism has been related to poor academic performance, but also to increased creativity, a feature that would be desirable in testing or problem-solving contexts (Acar & Runco, 2012; Eysenck, 1995). Similarly to Extraversion and Neuroticism, the effect of Psychoticism on performance depends on the type of task and the level of attention involved, with individuals scoring higher on this trait showing a worse performance when more attentional control is required (Corr, 2003; Szymura et al., 2007).

Following a comparative approach, recent studies have also explored the association between personality and cognitive performance in several non-human primate species by using personality traits obtained from a questionnaire-based methodology. These studies have employed different types of experimental tasks. As in humans, the traits Openness and Conscientiousness from the Five Factor Model are the traits most commonly linked to differences in performance measures (i.e., success, participation) in both monkeys (Altschul et al., 2016; Morton et al., 2013a) and apes (Herrelko et al., 2012; Hopper et al., 2014; Reamer et al., 2014). Current data suggest that the role of Neuroticism on non-human primate performance is still unclear. Some studies have failed to find a link between this trait and cognitive performance in several species, including marmosets (*Callithrix jacchus;* Marciano, 2019), capuchin monkeys (*Sapajus apella;* Morton et al., 2013a) and chimpanzees (Altschul et al., 2017). However, features that define Neuroticism, such as level of anxiety or emotional reactivity, have been reported to have both negative and positive effects on task performance in monkeys (*Papio ursinus*, Carter et al. 2014; *Callithrix jacchus,* Schubiger et al. 2015). Furthermore, in chimpanzees high Neuroticism has been associated with higher levels of vigilance and self-directed behaviors when animals engage in cognitive research (Herrelko et al., 2012).

Similarly to Neuroticism, the relationship between Extraversion and cognitive performance in non-human primates has only been explored in few species, and current data does not indicate a straightforward relationship. For example, in a study with touchscreen tasks, Altschul and colleagues (2017) found that, in general, extraverted chimpanzees exhibited higher levels of participation, faster response times, and increased accuracy, although this trend was not consistent across all tasks. In another study with rhesus macaques (*Macaca mulatta*), Altschul and colleagues (2016) reported that individuals scoring higher on Friendliness, a dimension described in this species that could be compared to human Extraversion, were more successful in a serial learning task.

Finally, although human personality does not include a dominance factor (Weiss, 2022), Dominance and other dominance-related traits, such as Confidence or Assertiveness, have been described in several primate species (Freeman & Gosling, 2010; Weiss, 2018). Nonetheless, there is little evidence for a relationship between Dominance or similar personality traits and cognitive performance in non-human primates. For example, Hopper and collaborators (2014) found that performance in a foraging apparatus was positively associated with Dominance in male chimpanzees, but not in females. In their study assessing performance in touchscreen tasks in chimpanzees, Altschul and colleagues (2017) found no effect of Dominance on participation or performance.

Overall, we can conclude that it is only recently that researchers have started to study the link between personality and cognitive performance in non-human primates, using a comparative perspective, although this is crucial to better understand the evolutionary origins, development and function of the link between personality and cognitive performance. Furthermore, given that questionnaires are an effective and quick method to describe primate personality, they could be a simple manner to incorporate personality variables when conducting cognitive research in these species, to obtain more valid results. Thus, considering the scarce literature on the topic and the potential advantages of a comparative approach, future research should further explore the link between personality and cognition in non-human animals.

1.5. Objectives:

1.5.1. General objectives and hypotheses

The main objective of this thesis is to investigate the impact of cognitive challenges on the **behavior** and **welfare** of captive chimpanzees (*Pan troglodytes*), and to assess how individual differences, such as **personality**, may play a role in modulating the outcomes of these activities. These topics have been explored in two different but partially overlapping contexts: **cognitive enrichment** and **cognitive testing**. In particular, the relationship between cognitive challenges and welfare has been assessed in the context of enrichment and the link between personality and cognitive performance has been evaluated in a non-invasive research setting.

Given the behavioral and cognitive complexity of non-human primates, and more specifically great apes, we hypothesized that: (1) we would find individual variation in chimpanzees' interest and performance in cognitive challenges; (2) this variation would be linked to individual differences in sex, age and personality; and (3) exposing chimpanzees to tasks which require problem-solving abilities would enhance their level of welfare, by increasing the frequency of species-typical behaviors and reducing the frequency of undesirable behaviors. Finally, considering chimpanzee phylogenetic proximity to humans, we hypothesized that (4) Eysenck's model would be a suitable tool to assess personality in this species.

1.5.2. Specific objectives and thesis structure

This doctoral program has been mainly conducted at Fundació Mona (Girona, Spain), a center for rescuing and rehabilitating primates, which hosts a group of 14 chimpanzees (*Pan troglodytes*). The core of this thesis comprises four empirical studies (Articles 1-4). Firstly, we evaluated the behavioral and welfare effects of cognitive tasks specifically designed and implemented as environmental enrichment (Articles 1 and 2). Secondly, we reviewed previous non-invasive cognitive research conducted at Fundació Mona (Article 3). Additionally, to explore the link between personality and cognitive performance, we characterized chimpanzees according to a personality questionnaire based on Eysenck's model, a tool originally developed for humans that has been formerly used also in non-human primates (Articles 3 and 4). Finally, I carried out a research stay at the Max Planck Institute for Evolutionary Anthropology and at the Wolfgang Köhler Primate Research Centre (Leipzig, Germany), with the purpose of assessing the suitability of Eysenck's model in a larger sample of chimpanzees (Article 4). A general discussion in Chapter 4 summarizes and integrates the findings of all four studies, addresses their limitations and provides recommendations for future research directions.

The specific objectives of this thesis and their inclusion within the four studies are detailed below:

- Evaluate the effectiveness tool-based tasks as cognitive enrichment for captive chimpanzees (Articles 1 and 2).
    - Assess the effects of the presence and the use of an artificial termite-fishing task on the frequency of solitary and social behaviors (Article 1).
    - Assess the effects of using a novel tool-based cognitive enrichment on the frequency of solitary and social behaviors (Article 2).
    - Assess temporal variation in chimpanzees' participation in the cognitive enrichment activities and in their behavior, using both positive (i.e., species-

    - typical behaviors) and negative (i.e., abnormal and self-directed behaviors) behavioral indicators of welfare (Articles 1 and 2).
- Explore individual differences in chimpanzees' participation and performance in cognitive enrichment activities (Articles 1 and 2) and in cognitive tasks within a research context (Article 3).
    - Assess whether sex and age predict differences in participation and performance in both enrichment and research contexts (Articles 1, 2 and 3).
    - Evaluate whether chimpanzee personality (measured with Eysenck's model) predicts differences in participation and performance in cognitive tasks presented in a testing context (Article 3).
- Assess the suitability of a 12-item questionnaire based on Eysenck's model to describe chimpanzee personality (Articles 3 and 4).
    - Assess the correlation between personality traits based on Eysenck's model and chimpanzee spontaneous behavior (Article 3).
    - Extend previous research on this model by evaluating a larger and more diverse sample (Article 4).

Chapter 2. General methodology

Photograph taken by author

2.1. Subjects and study sites

The study sample of this thesis consists of a total of 37 chimpanzees (*Pan troglodytes*) housed at two different institutions. Nonetheless, most of the data was collected in a subsample of 14 chimpanzees and only one article (Article 4) included personality data from all 37 subjects. Further details regarding group compositions and housing conditions are described below. Additionally, biographical information on all chimpanzees is provided in Article 4 (Table 1).

Fundació Mona (Girona, Spain): 14 individuals, 9 males and 5 females, that ranged in age from 15 to 38 years (mean = 20.1 years, SD = 8.4 years) at the beginning of the study and were divided into two mixed-sex groups of 7 individuals each (Mutamba and Bilinga groups). They were housed at Fundació Mona, an institution dedicated to the rescue, rehabilitation and re-socialization of primates that were formerly used as pets or in the entertainment industry. Despite lacking official accreditation, Fundació Mona aligns with the essential principles of an animal sanctuary: it is a non-profit organization that does not engage in intentional captive breeding and commercial exploitation, and does not allow direct public contact with animals (Fultz, 2017; Ross & Leinwand, 2020). The chimpanzees spent their daytime hours in a 5640 m^2 outdoor enclosure, divided into two areas (2420 m^2 and 3220 m^2), both covered by natural vegetation and containing wooden platforms, towers and ropes (Figure 1). The animals also had 140 m^2 of indoor facilities or bedrooms where they spent the nights and rainy/cold days.

Leipzig Zoo (Leipzig, Germany): 23 individuals, 8 males and 17 females, ranging in age from 3 to 53 years (mean = 28.3, SD = 13.7), living in two separate groups: a large group including 17 chimpanzees (6 males, 11 females) and a small group of 6 chimpanzees (1 male, 5 females). The large group also included two infants (<2 years) that, due to their young age, were excluded from our analyses. The chimpanzees were housed at the Wolfgang Köhler

Primate Research Center, also known as Pongoland, at the Leipzig Zoo (Germany), a large enclosure (30000 m^2), which is home to several species of great apes and is provided with natural and artificial elements that mimic their natural habitat. The chimpanzee outdoor facilities (Figure 2) comprise two different areas, one for each group (4000 m^2 for the large chimpanzee group, and 1400 m^2 for the small chimpanzee group), as well as separate indoor facilities (533 m^2 and 340 m^2) (Figure 3). Both facilities are covered with natural vegetation and include other elements such as rocks and streams. They also have trees, ropes and wooden platforms for climbing and shelter, and environmental enrichment devices, such as artificial termite mounds and food mazes.

Figure 1

Chimpanzee outdoor enclosures at Fundació Mona

(Photograph by Joan Brull)

Figure 2

Chimpanzee outdoor enclosures at Leipzig Zoo

(Photograph taken by author)

Figure 3

Chimpanzee indoor enclosures at Leipzig Zoo

(Photograph taken by author)

2.2. Brief description of the cognitive tasks and experimental procedures

2.2.1. Cognitive enrichment

The tasks proposed as cognitive enrichment were presented in a social context, in the outside enclosures of the two chimpanzee groups housed at Fundació Mona. They were designed to provide cognitive stimulation while also promoting a range of behaviors that belong to the species natural repertoire (e.g., tool use). A brief description of the two tasks used in this thesis (Articles 1 and 2) is provided below:

- Artificial termite-fishing tasks were structures constructed of cement and steel, simulating a termite mound, with holes in which removable PVC tubes could be inserted (Figure 4). The tubes were filled with preferred foods, such as honey or peanut butter. To successfully extract all the food from the tubes, the chimpanzees had to use branches or sticks that could be found in their enclosures.
- Food mazes were big rectangular structures (1m x 0.7m approx.) made of steel, with frontal transparent plastic panels (polycarbonate, 10mm thick) and wooden shelves with holes at the ends (Figure 5). The animals needed to move food items (dried fruits and nuts) through different levels using sticks.

At Fundació Mona the artificial termite-fishing tasks had been used as enrichment for several years, and therefore, the chimpanzees had previous experience with them. Nonetheless, before the study period, these devices had been largely inactive for approximately two years due to the necessity for maintenance and repair. Conversely, the food mazes were specifically designed for this thesis and therefore constituted a completely novel task for the chimpanzees. Each of the two chimpanzee groups had one enrichment device in their enclosure —one termite-fishing task and one food maze—. However, the food mazes were introduced later so that the termite-fishing tasks were assessed when no mazes were present in the enclosures. The termite-fishing tasks were evaluated between October and December 2018 (simultaneously in the two groups), and the food mazes between April and June 2019 (Mutamba group) and between June and September 2019 (Bilinga group).

For both cognitive enrichment tasks, we collected data in two conditions: baseline (i.e., enrichment devices did not contain food) and enrichment (i.e., enrichment devices were filled with food). In the study assessing the artificial termite-fishing tasks, we conducted a total of 8 sessions (8 days) for each condition, and in the study evaluating novel food mazes, we conducted a total of 12 sessions (12 days) for each condition. This difference depended on the fact that chimpanzees needed more time to learn how to use a novel and more complex device like the food maze. In both studies, baseline and enrichment days were randomly distributed over a 2- to 3-month period. Furthermore, in the study assessing the food mazes, we established a one-week habituation period before starting data collection. Thus, the chimpanzees were exposed to the empty devices during several days before starting with the enrichment sessions. This procedure was not conducted with the artificial termite-fishing tasks, as they were not new to the animals.

Figure 4

Artificial termite-fishing tasks

(Photographs taken by author)

Figure 5

Food mazes

(Photographs taken by author)

2.2.2. Cognitive research

Data on chimpanzee cognitive performance was obtained from previous non-invasive research conducted at Fundació Mona. This former research is described in detail in the study by Riba (2016). In a nutshell, this project, conducted between October 2009 and April 2013, investigated problem-solving skills and social learning in chimpanzees by exposing the subjects to puzzle boxes of different levels of complexity. The devices contained components such as doors, wooden bars, slides and tubes, which needed to be manipulated in a particular manner to obtain food rewards. To perform the experiments, chimpanzees entered an enclosure adjacent to their usual facilities, were they remained separated from their social group while performing the tasks. To ensure their collaboration, they were called by a familiar keeper, who also stayed in close proximity during the whole experimental sessions. The puzzle boxes were placed outside the enclosure, but the chimpanzees could manipulate them through the bars (Figure 6). The time that the chimpanzees were exposed to and engaged with the tasks varied depending on task complexity. Overall, each subject participated in 9 experimental sessions of 8 trials each, for a total of 72 trials: 24 trials for the simple tasks, 24 for the intermediate tasks and 24 for the complex tasks (see details in Supplemental Information Table S2, Article 3). Experimental sessions were videotaped and later coded by a single experimenter (David Riba) for the original study. Nonetheless, all sessions were recoded to evaluate inter-observer reliability for participation, success and latency (agreement between observers > 90%), and to assess an additional variable: the occurrence of losing contact with the task. We therefore used participation as a measure of interest, success and latency to solve the task as measures of actual performance, and losing contact with the task as an indicator of lack of motivation (see detailed descriptions of the variables in Article 3).

Figure 6

Chimpanzee engaging in the experimental sessions involving puzzle boxes

(Photograph by Miquel Llorente)

2.3. Behavioral observations

2.3.1. Cognitive enrichment

In the two studies assessing cognitive enrichment, for both baseline and enrichment conditions, we used two sampling methodologies: instantaneous scan sampling (every 2 min) and untimed-event focal sampling (10 min per subject) (Bakeman & Quera, 2011). Scan sampling allowed us to record mid- to long-duration behaviors, including solitary behaviors (i.e., participation in the enrichment, tool use, feeding, abnormal behaviors, inactivity) and social behaviors (i.e., social proximity, affiliation-related behaviors and aggression-related behaviors). Except for participation, these behaviors were selected from a behavioral catalogue that had been developed at Fundació Mona for a longitudinal study (see details in section 2.3.2). Contrary to instantaneous scan sampling, untimed-event focal sampling was used to detect self-directed behaviors, which are short-duration behaviors that occur very rarely. In particular, in our study we focused on rubs and scratches directed towards the face and body, as they have been consistently linked to associated with anxiety or arousal when chimpanzees are exposed to cognitive challenges (Clark & Smith, 2013; Leavens et al., 2001; Yamanashi & Matsuzawa, 2010). Although the behavioral catalogue used to assess both cognitive enrichment tasks was the same, the behaviors selected for the posterior analyses varied slightly, according to the specific objectives of each study. Descriptions of the behaviors included in each study can be found in Article 1 (Table 1) and Article 2 (Table 1).

2.3.2. Longitudinal study at Fundació Mona

Besides the behavioral observations conducted during the implementation of the two cognitive enrichment tasks, some articles of this thesis (Articles 1 and 3) also included additional behavioral data that had been collected at Fundació Mona as part of a longitudinal study (Crailsheim et al., 2020; Llorente et al., 2015). Specifically, this longitudinal study used the same methodology (2-min instantaneous scan sampling) and behavioral catalogue that we used for the behavioral observations conducted during the assessment of the two cognitive enrichment activities. Specifically, the behavioral catalogue of the longitudinal study included solitary activities (e.g., abnormal behaviors, locomotion, feeding, manipulation, inactivity, self-directed behaviors, and other solitary behavior), social interactions (e.g., grooming, dominance, submission, other agonistic behavior, social play, sexual behavior, proximity and other affiliative behavior), and interactions with humans (positive and negative). Detailed descriptions of these behaviors can be found in Supplemental Information Table S1, Article 3).

In Article 1 we used data from the longitudinal study to evaluate the long-term effects of the cognitive enrichment activity (i.e., the artificial termite-fishing task), by comparing the occurrence of both solitary and social behaviors before and after the introduction of the enrichment (i.e., pre- and post-treatment phases).

In Article 3, behavioral data from the longitudinal study was used to validate the personality traits obtained when assessing the chimpanzees with Eysenck's model. Particularly, we used behavioral data from an 11-year period and we performed Spearman correlations between personality traits and behaviors that matched the definitions of these traits.

2.3.3. Data collection software

Behavioral observations in the two studies assessing cognitive enrichment were collected using ZooMonitor, a software application developed by the Lincoln Park Zoo designed for monitoring the behavior of animals in zoological institutions, particularly behaviors relevant to welfare (Ross et al., 2016; Wark et al., 2019; https://zoomonitor.org). In recent years, software applications have become very popular in animal behavioral research, as they allow rapid real-time data collection which can be downloaded directly into electronic format, thus facilitating subsequent analyses (van der Marel et al., 2022). In this thesis, for example, we used tablet devices to collect data, which was then uploaded to a cloud server and finally exported into Excel (CSV files) to prepare data for the analyses.

Due to its multiple advantages, ZooMonitor has become the preferred data collection platform for many accredited zoos, aquariums, and sanctuaries (van der Marel et al., 2022). First, the ZooMonitor application is highly customizable, allowing users to add an unlimited number of behaviors to a project and organize them into different "behavior channels" (e.g., solitary behavior, social behavior, proximity), which can be used simultaneously. The duration of the session duration and length of intervals can also be customized to meet the project needs (Wark et al., 2019). ZooMonitor supports the common behavior sampling methods, including the ones selected in this thesis (scan sampling or interval recording, and untimed-focal event or "all occurrences"). These sampling methods are considered separate "channels" in ZooMonitor and can be used simultaneously when collecting data. Nonetheless, in this thesis, we used separate ZooMonitor projects for each sampling methodology (one for instantaneous scan sampling and one for untimed-focal event sampling), because recording self-directed behaviors, which were collected with untimed-focal event sampling, required the observer to be fully focused on one subject.

Another interesting feature of ZooMonitor is that it supports the use of behavioral modifiers, which provide additional and more detailed information for a behavior. These modifiers can be used, for instance, to record the sender and receiver of social behaviors, thus allowing the analysis of social relationships (Wark et al., 2019). After defining the channels and behaviors of a project, ZooMonitor also allows users to define additional questions that are answered before each observation session and that provide contextual information, such as weather or visitor presence. In this thesis, we used this feature to register whether the observation session was conducted in the enrichment or baseline condition. Another main advantage of ZooMonitor is that it is a very user-friendly application, meaning that users do not require a long training period. This is especially relevant for this thesis, as behavioral data was collected by several researchers. The application also allows users to perform automated reliability tests to check inter-observer reliability, which is fundamental when there are two or more observers collecting data. In this thesis, for example, researchers could only start collecting data after completing a training period and successfully passing the inter-observer reliability test (agreement between observers ≥ 85%). Finally, it is also worth noting that ZooMonitor is an accessible software application, which, for non-accredited AZA institutions zoological institutions, requires a low-cost annual subscription of 50US$.

2.4. Personality questionnaires and ratings

In both studies assessing chimpanzee personality (Articles 3 and 4), we used a questionnaire based on Eysenck's Psychoticism-Extraversion-Neuroticism (PEN) model of personality (Eysenck, 1967; Eysenck & Eysenck, 1964). This questionnaire was developed in a previous study, which evaluated some of the chimpanzees at Fundació Mona (Úbeda & Llorente, 2015). In this thesis, we (1) extended the sample by assessing new individuals at the Fundació Mona and at the Leipzig Zoo (Article 4), and (2) we tested the validity of this tool by performing correlations between behavioral measures and personality traits as obtained with Eysenck's model (Article 3).

The questionnaire contained 12 items, which corresponded to primary scales that are integrated in the three higher-order factors described by Eysenck (Eysenck and Eysenck, 1964, 1991; Eysenck et al., 1985). To select the items from the original human factors, the authors considered their suitability and relevance to describe chimpanzee personality. Each item was associated with two adjectives representing the two opposite poles of the trait, which raters scored using a 7-point Likert scale. For instance, for the item "aggressiveness", raters had to provide a score from (1) "pacific" to (7) "aggressive". Additionally, a brief definition for each trait was also provided. The original questionnaire was developed in Spanish, but it was translated (and back translated) to English and to German, to allow raters to complete it in their native language. The English version of the questionnaire can be found in Supplemental Information Questionnaire S1, Article 3.

All chimpanzees were assessed between 2012 and 2019 by a minimum of 6 raters who were highly familiar with the subjects, as they had worked as researchers, volunteers or keepers for a long time period (4 months to 18 years). While some authors have observed gradual shifts in chimpanzee personality traits over time (Rawlings et al., 2020), research employing both subjective ratings and behavioral observations suggest that, similarly to humans, chimpanzee personality remains fundamentally stable within individuals (Dutton, 2008; Massen et al., 2013; Weiss et al., 2017). Following previous research on personality, we calculated the reliability or consensus across raters using two intraclass correlation coefficients (ICC) (Shrout and Fleiss, 1979): ICC (3,1), which indicates the reliability of the scores for a single rater, and ICC (3, k), which indicates the reliability of scores based on the mean of the total number of raters.

2.5. Statistical analyses

2.5.1. Generalized Linear Mixed Models

Generalized linear mixed models (GLMMs; Stroup, 2016) comprise a class of statistical tools for experimental data analysis developed about a decade ago (Baayen, 2008; Barr, 2008), which, in recent years, have become widely used in psychology and behavioral sciences (Bono et al., 2021; Goldhammer et al., 2017; Moscatelli et al., 2012; Singmann & Kellen, 2019). GLMMs are an extension of generalized linear models (GLMs), which include both fixed and random effects (hence mixed models) into the linear predictor of a GLM. Thus, GLMMs include a response or dependent variable which is related to linear predictors (fixed effects) by a continuous function (e.g., logistic regression) and conditioned by additional factors that vary across the population sample (random effects). Both GLMs and GLMMs can be applied to response variables with different distributions, such as binary responses or counts. Moreover, the inclusion of random effects allows the modelling of non-independent data points, thus broadening the application of these models. For instance, GLMMs are particularly useful to analyze longitudinal data (i.e., repeated observations of the same variables over time) and grouped data, since group differences can be included as random effects. Furthermore, in an experimental design, GLMMs can include the experimental condition as a fixed effect while random effects can reflect the variability among subjects (He & Lee, 2022). We can therefore conclude that the possibilities and flexibility of GLMMs have contributed to their wide use among researchers.

In this thesis, GLMMs were used to (1) evaluate chimpanzee use of the cognitive enrichment devices over time and assess their link to subjects' behavior and welfare (Articles 1 and 2); and (2) investigate whether chimpanzee interest, motivation and performance in cognitive tasks were predicted by their personality traits (Article 3). All the analyses were conducted in R (R Core Team, versions 3.5.0 and 3.6.2). In Articles 1 and 2 we used the "glmmTMB" package (Brooks et al., 2017), which is particularly useful to fit count data that is zero-inflated (i.e., data containing more zeros than would be expected from the typical error distributions), which was the case for our behavioral data. In Article 3, we used the package "lme4" (version 1.1-17; Bates et al., 2015) and the functions "glmer" and "lmer", depending on the distribution of the response variables. Specifically, we used "glmer" for variables with binomial distribution (participation, success and losing contact with the task) and "lmer" for variables with a normal distribution (latency).

After defining the variables, the first step to fit a model is finding a suitable distribution for the response variable and choose the link function accordingly. If overdispersion (i.e., presence of more variance in the data than predicted by a statistical model) was detected in our models, data was refitted with an alternative distribution, which may have required transforming the predictor and, in few cases, both the predictor and the response variable. Then, to assess the adequacy of a particular model (i.e., the full model), one method is to compare it with a model which is identical, except that all the predictors have been removed (i.e., the null model). Thus, in our analyses we compared full models containing all predictors to null models containing only control predictors, using a likelihood ratio test (function ''anova'') (Dobson & Barnett, 2002). If full models significantly differed from null models ($p \leq 0.05$), we obtained the *p* values for each test predictor via single-term deletion using the R function drop1 (Barr et al., 2013). This function reveals which test predictors are significant based on AIC (Akaike information criterion) and LRT (likelihood ratio test) criteria. This stepwise procedure is broadly used in our area of research, as it strongly limits the number of statistic tests and thus the risk of getting false positives.

In general, our models contained two-way interactions as test predictors, which allowed us to better explore variation in our response. For example, in Articles 1 and 2, when assessing the effects of the cognitive enrichment tasks, participation was included in interaction with session number, to investigate possible differences in the outcome of enrichment tasks across sessions. In Article 3, when assessing the link between personality and performance, personality traits were included in interaction with sex, to explore possible sex differences in the link between personality and performance. When testing the models, if the two-way interactions (which always included their main effects) were not significant, we downgraded them and reran the models including only main effects (without the interaction). Furthermore, for categorical significant predictors with more than two levels, we conducted post-hoc tests with the "emmeans" package and Tukey corrections, to compare the different levels (Lenth, 2020). Finally, to rule out collinearity between variables, we calculated variance inflation factors (Field, 2009), ensuring they were sufficiently low. In our analyses, maximum variance inflation factors across all models were between 1.34 and 2.7, thus indicating low to moderate correlation between variables, which is considered acceptable (Daoud, 2017).

2.5.2. Factor analyses

Factor analysis is a statistical technique which aims to identify the underlying structure of a set of variables. Particularly, this tool summarizes the correlational relationship between and among variables accurately and concisely, thus facilitating its interpretation and conceptualization (Goldberg & Digman, 1994). This involves encompassing the maximum amount of information from the original variables into a smaller number of derived variables, namely factors (Gorsuch, 1983). In other words, these underlying factors explain the variance among the original variables. The amount of variance explained by a factor is expressed in an eigenvalue. Eigenvalues of 1 or above indicate that a factor accounts for more variance than a single variable and thus it should be retained in the analysis. The interpretation of a factor is then provided by the factor loadings, which are correlations of the original variables with the factors (Kline, 2014). Thus, factor loadings provide a quantitative measure of the degree to which a variable is related to a factor. Particularly, factor loadings closer to 1 reflect high significance of a variable within a factor, whereas those closer to 0 reveal lower weighting towards a factor (Gorsuch, 1983).

Since Cattell's first application of factor analysis to personality research (Cattell, 1945), this tool has been extensively used in the field (Chaplin, 2005; Kline, 1987; Lee & Ashton, 2007; Rothe, 2017; Russell, 2002), providing researchers with a deeper understanding of personality constructs and leading to the developments of personality theories (Luu & ElBassiouny, 2020). Personality questionnaires usually comprise large sets of items corresponding to adjectives or descriptors of personality features, which are assumed to cluster together revealing underlying constructs (factors) that correspond to personality traits. Thus, in this case each personality trait will be described by the amount of variance it accounts for (eigenvalue) and by the degree to which adjectives are related to it (loadings). In personality research, factor analyses can be used for different purposes: to conduct data reduction, to reveal the underlying factor structure (Exploratory Factor Analysis), to confirm a previous hypothesis (Confirmatory Factor Analyses) and to summarize the correlations between variables. Exploratory Factor Analysis provides a more general perspective, potentially assisting in identifying the underlaying factor structure that best explains the data. Thus, it is widely used by personality psychologists (Luu & ElBassiouny, 2020).

The Principal Component Analysis (PCA) is the most commonly used method for extracting factors in personality research, as well as in other disciplines (Russell, 2002). It involves decomposing the covariance (or correlation) matrix by identifying the variables which explain the higher amount of variance, as indicted by their respective eigenvalues (Hilbert & Bühner, 2020). Thus, the goal of this tool is capturing the greatest amount of variance with the smallest number of components (i.e., factors). Some authors prefer not to classify Principal Component Analysis as a type of factor analysis because these two statistical techniques differ in how they interpret the data (Kline, 1987). That is, factor analysis explicitly assumes the presence of an underlying factor structure within the data, whereas Principal Component Analysis provides a summary of the linear components of the original variables and their importance in terms of variance, without making prior assumptions (Hilbert & Bühner, 2020). This means that Principal Component Analysis uses the entire variance in the correlation matrix, including the error variance, while factor analysis excludes the error variance. Following human personality research, most studies in non-human primates have also used Principal Component Analysis to describe the personality structure of a particular species, including chimpanzees (*Pan troglodytes*; Weiss et al., 2009), bonobos (*Pan paniscus*, Weiss et al., 2015), mountain gorillas (*Gorilla beringei beringei*; Eckardt et al., 2015), langurs (*Semnopithecus entellus*; Konečná et al., 2008) capuchin monkeys (*Sapajus apella*; Morton et al., 2013b), marmosets (*Callithrix jacchus*; Šlipogor et al., 2022) and several macaque species (Adams et al., 2015; Robinson et al., 2018), to name a few.

An important issue in primate personality research is that, in general, researchers only have access to small sample sizes. To overcome this, there are types of exploratory factor analyses that have proved to be effective for small samples (<50 subjects), such as regularized exploratory factor analyses (REFA) and unweighted least squares factor analysis (ULS) (Jung, 2013; Jung & Lee, 2011; Jung et al., 2020). Regularized exploratory factor analyses, in particular, most likely constitutes the second more used alternative after Principal Component Analysis. This tool has been successfully applied to assess personality structure in chimpanzees

(*Pan troglodytes*; Úbeda and Llorente, 2015), bonobos (*Pan paniscus*; Garai et al., 2016), barbary macaques (*Macaca sylvanus*; Konečná et al., 2012), cotton-top tamarins (*Saguinus midas*; Masilkova et al., 2018) squirrel monkeys (*Saimiri sciureus and Saimiri boliviensis*; Wilson et al., 2018) and marmosets (*Callithrix jacchus*; Šlipogor et al., 2021). According to some authors, Regularized Exploratory Factor Analysis is generally recommended over unweighted least squares, unless a small number of factors is expected (Jung, 2013).

In Article 3 of this thesis, we compared personality traits obtained through questionnaires with behavioral measures and we assessed whether these traits could predict differences in cognitive performance. Personality data was obtained from a previous study conducted at Fundació Mona, in which Úbeda and Llorente (2015) used a questionnaire based on Eysenck's model and performed both principal component analyses and regularized exploratory factor analysis to determine the chimpanzee personality structure. The results of both methods were very similar, but due to the fact that they were performed using a small sample (N=11), we selected the structure described by the regularized exploratory factor analysis to calculate personality scores (i.e., a numerical value for each personality trait) used in Article 3.

In Article 4 we used the same questionnaire described by Úbeda and Llorente (2015) to test the suitability of Eysenck's model in a larger sample of chimpanzees (N=37), including individuals from Fundació Mona and from the Leipzig Zoo. To determine the personality structure, we conducted a Principal Component Analysis and a Robust Unweighted Least Squares factor analysis using FACTOR 12.04.0 (Ferrando & Lorenzo-Seva, 2017; Lorenzo-Seva & Ferrando, 2013). FACTOR is an all-inclusive, free and user-friendly program that was mainly developed for psychometric applications, and particularly for item analysis and individual scoring functionalities (Ferrando & Lorenzo-Seva, 2017; Lorenzo-Seva & Ferrando, 2006). The strengths and limitations of this software are discussed in detail by Ferrando and

Lorenzo-Seva (2017). In a nutshell, FACTOR allows computing robust and accurate estimates, even in small-medium samples (Ferrando & Lorenzo-Seva, 2017).

Chapter 3. Empirical studies

Article 1. Artificial termite-fishing tasks as enrichment for sanctuary-housed chimpanzees: behavioral effects and impact on welfare

Padrell, M., Amici, F., Córdoba, M.P., Giberga, A., Broekman, A., Almagro, S., & Llorente, M. (2021). Artificial termite-fishing tasks as enrichment for sanctuary-housed chimpanzees: behavioral effects and impact on welfare. *Animals*, *11*(10), Article 2941. https://doi.org/10.3390/ani11102941

Photograph by Miquel Llorente

animals

MDPI

Article

Artificial Termite-Fishing Tasks as Enrichment for Sanctuary-Housed Chimpanzees: Behavioral Effects and Impact on Welfare

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Simple Summary: The welfare of captive animals is nowadays a topic of major concern. In order to express their natural behavioral repertoires, however, animals require complex environments and stimuli which are difficult to reproduce in captivity. To overcome this, environmental enrichment is considered one of the most successful tools to increase behavioral opportunities and enhance animal welfare. In this study, we explored whether providing an artificial termite-fishing task, and whether participation in this task, predicted changes in the solitary and social behavior of sanctuary-housed chimpanzees (*Pan troglodytes*). We compared chimpanzee behavior when the enrichment was presented to different periods without enrichment. We found that the presence of the enrichment predicted an increase in tool use and feeding behavior and a decrease in inactivity, especially for those chimpanzees with higher participation. However, we did not detect significant changes in abnormal or self-directed behaviors. Furthermore, we found no variation in affiliation- or aggression-related behaviors, but social proximity increased in chimpanzees that participated more. Our results support previous studies demonstrating that artificial termite-fishing promotes species-typical behaviors in captive chimpanzees with no major effects on social activities.

Abstract: Artificial termite-fishing tasks are a common enrichment for captive great apes, promoting species-typical behaviors. Nonetheless, whether these activities are linked to changes in other behaviors and whether these changes persist over time has seldom been investigated. We assessed whether the use of an artificial termite-fishing task was linked to changes in the solitary behavior and social dynamics in two groups of sanctuary-housed chimpanzees (*Pan troglodytes*). Specifically, we compared chimpanzee behavior during eight enrichment sessions distributed over a two-month period, with similar periods before and after the introduction of the enrichment. Data were collected from combined interval and continuous sampling methods and were analyzed using generalized linear mixed models. We found that participation increased across sessions and that both enrichment and participation predicted an increase in tool use and feeding and a decrease in inactivity, which were all maintained throughout the sessions. Furthermore, participation was positively associated with social proximity, revealing a gathering effect of the task. However, neither enrichment nor participation were linked to changes in abnormal, self-directed, affiliation-related or aggression-related behaviors. Overall, our results support the hypothesis that artificial termite-fishing is a suitable enrichment for captive chimpanzees, maintaining the subjects' interest and promoting species-typical behaviors, with no negative effects on social activities.

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1. Introduction

Concern for the welfare of captive animals has progressively increased over the past few decades. Although early studies mainly focused on farm animals [1,2], the welfare of zoo and sanctuary animals has, more recently, become a topic of major interest, as shown by the increasing number of scientific articles on the topic [3–8], as well as the development of specific guidelines and recommendations on how to assess and improve animal welfare [9]. Similarly, there has been a rise in awareness among zoological institutions, so that welfare is now considered a key factor in animal management [10].

Welfare has been conceptualized as the state of an individual in relation to its attempts to cope with its environment [11]. However, in order to achieve an optimal level of welfare, animals not only need to cope with their environment but also thrive in it [8,12]. In other words, they need to be provided with opportunities to experience positive welfare states to have a "life worth living" [13]. In particular, they must be able to express species-typical behaviors, also known as ethological needs [14,15], or natural behaviors [16] like they exhibit in the wild [17]. Nonetheless, adequate conditions for the expression of a species natural behavioral repertoire demand complex environments and stimuli [18–20]; unfortunately, captive settings often fail to fulfill these requirements. To overcome this, environmental enrichment is generally considered one of the most effective tools to increase behavioral opportunities and enhance welfare; thus, they are a key component of captive animal management [12]. The main goals of environmental enrichment include increasing behavioral diversity, promoting natural behavioral patterns and reducing the occurrence of abnormal behaviors [18]. Furthermore, environmental enrichment may increase positive affective states [21], generate highly motivated behaviors and modify the physiological response of animals [22].

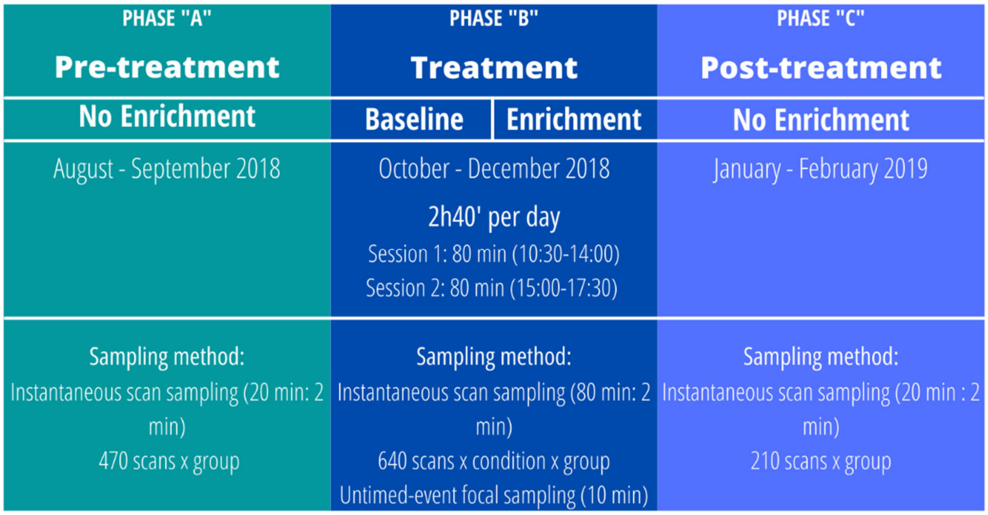
In order to assess the impact of a particular enrichment strategy, researchers usually monitor their subjects' behavior by comparing the frequency of species-typical behaviors and abnormal/stress-related behaviors in the presence (versus in the absence) of the enrichment [16,23]. To date, a wide range of environmental enrichment strategies has been implemented and evaluated in non-human primates, including enclosure design and size, food novelty, foraging devices, computer-based devices, sensory stimulation or exposure to conspecifics or humans (i.e., social enrichment) [24,25]. Because wild non-human primates usually spend more time foraging or feeding than captive primates, it is not surprising that enrichment activities for captive groups have mainly focused on increasing opportunities for foraging or feeding [26–28]. Extractive foraging devices requiring tool use, for instance, are popular enrichments among captive great apes, especially in chimpanzees [28–33]. In great apes, foraging devices often simulate ant- or termite-fishing, as observed in the wild [34,35]. These activities have been mainly used to study cognitive aspects of tool use, such as acquisition and learning [36–38], tool modification [39], flexibility [40] or laterality [41]. However, several authors have also assessed the impact of these enrichment activities on chimpanzee welfare. As expected, these studies found an increase in the frequency of tool use in the presence of the enrichment, as well as changes in other behaviors. For example, Celli and colleagues [29] found that besides predicting an increase in chimpanzee manipulation and tool use, ant-fishing tasks decreased inactivity by 52% and increased foraging time by 31% after 10 days of use. Moreover, foraging devices promoting tool use also decreased stress-related behaviors, such as abnormal and self-directed behaviors [28,32,42]. Self-directed behaviors (e.g., touching, scratching or rubbing one's body or face), in particular, are displacement activities (i.e., species-typical behaviors exhibited out of context or in a higher frequency when animals are anxious [43]) and constitute one of the most commonly used indicators of stress or arousal in non-human primates. In fact, several studies in great apes have reported an increase in these behaviors when animals face challenging situations [44–48].

Foraging devices and other enrichment activities might also affect the social dynamics within the group. If only one device is available, for instance, aggression might increase in the group [28]. In contrast, when foraging devices are designed for more than one animal and/or more devices are provided, aggressive behaviors may decrease because individuals are engaged in non-agonistic activities and do not need to compete for access to the enrichment [42]. Similarly, affiliative interactions may decrease in the presence of enrichment devices if individuals spend more time manipulating the foraging device and less in social activities [42]. However, other studies have found no differences in the frequency of affiliative or aggressive behavior when providing multiple tool-based feeders to chimpanzees [32].

The study of social networks is an interesting and novel approach to measuring the effects of environmental enrichment on social dynamics [49], especially in animals with complex social lives such as non-human primates [50,51]. Nevertheless, this tool has rarely been used for this purpose, except for a few studies which investigated changes in social interactions during cognitive testing [52,53]. In particular, Whitehouse and colleagues [52] found no differences in affiliative and aggressive interactions between conditions in a group of crested macaques (*Macaca nigra*) but did detect an increase in social proximity on testing days. In contrast, Jacobson and colleagues [53] found an increase in aggressive interactions during cognitive testing, although aggression was, overall, low.

Finally, besides monitoring changes in typical behavioral patterns in the presence of enrichment devices, other indicators might be used to assess whether enrichment activities are effective at the individual level. When subjects are free to choose whether to engage in enrichment activities, for example, participation (i.e., whether subjects interact with the device or time spent interacting with it) is usually assumed to be a positive indicator of interest or motivation [24,25,54]. However, when enrichment activities are provided in a social setting, other factors might affect subject participation. For example, higher-ranking individuals or those with more dominant personality traits might have priority to access enrichment devices [29,55]. Furthermore, female chimpanzees have been reported to use tool-based enrichments more often and more efficiently than males [32,42], a pattern which has also been observed in tool-use activities in wild chimpanzees [35,56–58], and which they seem to share with captive bonobos [59,60].

The main aim of this study was to assess whether the presence and use of an artificial termite-fishing task predicted changes in individual behavioral patterns and social dynamics of sanctuary-housed chimpanzees. First, we predicted that participation in enrichment activities would vary across individuals depending on their characteristics (e.g., sex, age) and decrease through time as chimpanzee interest and motivation declined (Prediction 1, Model 1). Second, we predicted that chimpanzee solitary (Models 2–6) and social behaviors (Models 7–9) would generally differ across study phases (Figure 1). That is, if the artificial ant-fishing task had a short-term effect on chimpanzee behavior, the frequency of solitary and social behaviors should differ between the baseline and enrichment conditions during the treatment phase. Furthermore, if enrichment activities had a long-term effect on chimpanzee behavior, the frequency of behaviors in the enrichment condition (treatment phase) and after the enrichment (post-treatment phase) should differ from before the introduction (pre-treatment phase). Third, we predicted that chimpanzee solitary (Models 2b–6b) and social behaviors (Models 7b–9b) would also specifically differ depending on individual participation in enrichment activities during the treatment phase, consistently throughout the study sessions. In Models 2–9/2b–9b, in particular, we expected that the presence of the enrichment/participation would predict changes both in chimpanzee solitary behavior (i.e., increasing species-typical behaviors like tool use and feeding, decreasing undesirable behaviors like inactivity and abnormal and self-directed behaviors; Predictions 2–6/2b–6b), and in their social behavior (i.e., increasing social proximity as more individuals could simultaneously interact with the artificial termite mounds, decreasing affiliation-related behaviors as chimpanzees may spend more time interacting with the enrichment and less time in social activities and increasing aggression-related behaviors due to possible competition over the enrichment; Predictions 7–9/7b–9b). Finally, we used social network analyses to explore possible changes in chimpanzee association patterns in the presence of the enrichment (Model 10).



PHASE "A" **Pre-treatment**	PHASE "B" **Treatment**		PHASE "C" **Post-treatment**
No Enrichment	**Baseline**	**Enrichment**	**No Enrichment**
August - September 2018	October - December 2018 2h40' per day Session 1: 80 min (10:30-14:00) Session 2: 80 min (15:00-17:30)		January - February 2019
Sampling method: Instantaneous scan sampling (20 min: 2 min) 470 scans x group	Sampling method: Instantaneous scan sampling (80 min: 2 min) 640 scans x condition x group Untimed-event focal sampling (10 min)		Sampling method: Instantaneous scan sampling (20 min : 2 min) 210 scans x group

Figure 1. Structure of the experimental design and procedures.

2. Materials and Methods

2.1. Subjects and Study Site

The study sample included 14 chimpanzees belonging to two mixed-sex groups of 7 individuals each (Mutamba and Bilinga groups). The Mutamba group was composed of 2 females and 5 males, with ages between 15 and 35 years (mean = 24.4 years, SD = ± 8.2 years), and the Bilinga group was composed of 3 females and 4 males, with ages between 17 and 36 years (mean = 29.1 years, SD = ± 6.7 years). All chimpanzees were housed at the Fundació Mona, a center dedicated to the rescue, rehabilitation and re-socialization of non-human primates. Supplementary Materials Table S1 contains information on demographic characteristics and background. The study chimpanzees spent their daytime hours in a 5640 m^2 outdoor enclosure, divided into two areas (2420 m^2 and 3220 m^2), both covered with natural vegetation and containing wooden platforms, towers and ropes. Two observation huts (one for each enclosure) around the perimeter allowed behavioral observations of both groups. The animals also had 140 m^2 of indoor facilities where they were housed overnight, but access was usually restricted during the daytime.

2.2. Experimental Procedure

We followed an ABC design (Figure 1), comparing the effects of the treatment phase (B) with a pre-test (A) and a post-test phase (C) (Models 2–9, see below). The treatment phase was structured in two alternated conditions: baseline (control days with no enrichment activity) and enrichment (days where treatment was incorporated). Eight baseline and eight enrichment days were randomly distributed for each group in a two-month period (from 22 October to 21 December 2018), excluding weekends (as visitors are more numerous than on weekdays). That is, the enrichment was available, on average, 1–2 times per week. Moreover, to avoid order effects, we also compared the effects of participation in the enrichment during the treatment phase (including baseline and enrichment days; Models 2b–9b, see below).

We used two artificial termite mounds as enrichment activity during the treatment phase. Both were made of cement and steel, with holes containing removable polyvinyl chloride tubes (length: 15–20 cm, diameter: 2.5 cm), which were attached inside the mound (Figure 2). Each group of chimpanzees had one termite mound in the enclosure. Mounds were installed approximately 10 years ago, and therefore all animals had previous experience with the task. However, they had been mostly out of use for more than 2 years before the study was conducted. That is, they remained in the enclosure, but they were seldom filled with food during this two-year period. The size of the mound and the number of holes (and therefore the tubes to be inserted) were different for each group. The mound in the Mutamba group measured approximately 2 m × 1 m width, 0.8 m height and had 9 holes, whereas the one in the Bilinga group was smaller (1 m × 1 m width and 0.8 m height) and had 5 holes (Figure 3). The tubes were filled with 10 g of honey or peanut butter mixed with 2–3 g of muesli. These quantities were removed from the total amount of food they received during the day in order to maintain a similar daily caloric intake. The use of honey or peanut butter was alternated between sessions, and both groups received the same number of sessions with each type of food. To extract the food, chimpanzees had to use sticks or branches obtained from the vegetation naturally growing in the external enclosures. No additional tools or materials were provided. The mounds were clearly visible from the observation huts around the perimeter, but the distance from the fence prevented visitors from disturbing the chimpanzees interacting with the mounds.

Figure 2. Details of the PVC tubes attached inside of the termite mound (Mutamba group). Credit: M. Llorente.

Figure 3. Termite mounds used during the treatment phase with the Mutamba (right) and Bilinga (left) chimpanzee groups. Credit: M. Llorente.

The termite mounds were filled in the morning, before the chimpanzees went into the outdoor enclosures, and were available throughout the daytime (from 10:30 h to 18:00 h approximately). In the baseline and enrichment days, no additional enrichment devices were provided. However, during the two-month period (i.e., non-baseline and non-enrichment days), other enrichments could be provided approximately once per week following the center's usual routines (e.g., bottles filled with juice, fabrics with different textures, hoses filled with food). These activities have been used for a long time in the center, and they were therefore not novel for the animals. Similarly, during the pre-treatment and post-treatment phases, the termite mounds were not filled, but other enrichments could be provided as part of the center's regular routines.

2.3. Behavioral Observations

2.3.1. Treatment Phase: Baseline and Enrichment Conditions

On both baseline and enrichment days, we collected data for a total of 2 h 40 min per day, divided into two 80-min sessions (one in the morning between 10:30 and 14:00, and one in the afternoon between 15:00 and 17:30). We collected data in the morning because it was when chimpanzees left the indoor facilities and were first exposed to the task. However, given that the chimpanzees did not extract all the food from the termite mound right away, we also observed whether they would use the device later in the day. No observations were conducted around midday, as this was chimpanzee feeding time and usually corresponded with very low activity.

We collected data in two ways: instantaneous scan sampling and untimed-event focal sampling [61]. First, instantaneous scan sampling with 2-minute intervals allowed us to collect data from the entire group at the same time, identifying behaviors of mid to long duration. In particular, we recorded (1) participation in the enrichment, (2) tool use, (3) feeding, (4) abnormal behaviors, (5) self-directed behaviors, (6) social proximity, (7) affiliation-related behaviors and (8) aggression-related behaviors. Details on the ethogram used for this sampling method can be found in Table 1. Some of the behaviors described above (see Table 1) were not mutually exclusive, and therefore, in each scan sampling interval, the chimpanzees could exhibit two or more behaviors at the same time. The total observation time for scan sampling was 85.33 h, equally distributed between conditions and groups, resulting in a total of 640 scans per condition and group. Secondly, we used untimed-event focal sampling [61] to collect additional data on self-directed behaviors. Specifically, we used this methodology to record rubs and scratches, which are behaviors that occur very rarely or last only a short time. Furthermore, rubs and scratches have been repeatedly associated with anxiety or arousal when chimpanzees face novel or challenging tasks [44,46–48], whereas the relationship between other self-directed behaviors (e.g., self-grooming) and stress is more controversial [62]. Each subject was observed for 10 minutes in the morning and 10 minutes in the afternoon. Based on the definitions and classifications provided by other authors [47,48,63], self-directed behaviors registered with untimed-event focal sampling included scratches and rubs directed towards the face and body (see detailed definition in Table 1). Following previous studies [64,65], the incidence of self-directed behaviors was quantified as the number of bouts. A bout ended when (1) the movement of the limb stopped for three or more seconds without losing contact with the body, (2) the contact between the limb and the body ceased or (3) the body target changed. Focal observations were conducted in a pseudo-randomized order to observe each chimpanzee at least once in the morning and once in the afternoon on each day.

Table 1. Ethogram used during behavioral monitoring of chimpanzees.

Behavioral Category	**Definition**
1. Participation *	The Chimpanzee is Actively Interacting or in Contact with The Artificial Termite Mound.
2. Tool use *	To use a Mobile Element, External to the Body, to Perform a Directed Action. Includes Tool Modification and Transportation.
3. Feeding *	Searching, Locating, Handling, and Ingesting or Transporting Food. Includes Fluid Intake.
4. Inactivity	No Action or Activity, Sitting or Lying Down. Includes Self-Observation, Yawning, and Sleeping.
5. Abnormal Behaviors	Maladjusted Stereotypical Behaviors such as Rocking, Pacing, Self–Harm, Coprophagy (Eating Feces), Regurgitation, and Reingestion, Trichotillomania (Hair-Pulling), Trichotillophagia (Hair-Pulling Eating Hair), Ear-Poking, Eye-Poking.
6. Self-Directed Behaviors	**Instantaneous Scan Sampling (All Phases):** Behaviors Directed towards the Subject, such as Body Inspection, Self-Grooming, Masturbation and Scratching or Rubbing One's Body with the Hands or Fingers. **Untimed-Event Focal Sampling (Treatment Phase):** Includes the Following Behaviors: (1) Scratches: Continuous Movement of the Hand over the Skin Involving the Ends of the Digits or Nails; (2) Rubs: Continuous Movement of the Hand over The Skin not Involving the Ends of the Digits Performed Either with the Palmar, Dorsal or Lateral Side of the Hand. This Category also Includes Self-Touches such as Nose-Wiping [48] or Face Stroking [46].
7. Social Proximity *	The Chimpanzee is at Less Than One-Arm Length from One or More Subjects while Performing any Solitary Activity, but with no Social Interaction between Subjects.
8. Affiliation-related Behaviors	Includes the Following Behaviors: (1) Grooming: Body-Cleansing Behavior (Grooming) from one Individual to Another (includes Mutual Grooming), Performed with the Upper Extremities or with the Mouth; (2) Social Play: Playful Behavior between Two or More Individuals Associated with Behavioral Indicators of Play (e.g., Play-Face, Laugh, Friendly Head Bobbing, Soft Knocking on the Ground, and Playful Chasing); (3) Sexual Behavior: Sexual Interaction, or search for Sexual Interaction, between Two Individuals Including Behaviors such as Copulation, Attempted Copulation, Genital Presentation, and Other Behaviors Directed Towards the Genitals of Another Individual; (4) Other Behaviors Identified as Affiliative, but do not fit the Criteria of Grooming, Social Play or Sexual Activity (Embrace, Feed Together and Follow).
9. Aggression-related Behaviors	Includes the Following Behaviors: (1) Agonistic Dominance: Threat-Related Behaviors such as Direct Aggression, Charging Display, Displacement and Resource Appropriation (e.g., Steal Food or Objects). Can be Accompanied by Vocalizations; (2) Agonistic Submission: Avoiding, Bared-Teeth, Displays, Food Submission (e.g., Leave/Drop Food and Move Away when Others try to Steal It), Hand-To-Mouth, Finger-To-Mouth. Can be Accompanied by Vocalizations such as Pant-Grunts. Includes Running Away from Others in Conflict Situations; (3) Other Behaviors Identified as Agonistic, but do not Fit the Criteria of Agonistic Dominance or Agonistic Submission. (Appeasing, Consolation, Reconciliation and Requesting Support).
Not Visible/Not Present	The Chimpanzee or the Behavior cannot be Identified, or the Chimpanzee is not in the Outdoor Enclosure (e.g., he is in the Sleeping Areas or in the Outdoor Cages).

* Participation, feeding and tool use were not mutually exclusive. Social proximity and all solitary behaviors (behaviors 1–6) were also not mutually exclusive (i.e., individuals could be in social proximity while simultaneously engaging in one of the solitary behaviors). Note: All behaviors were collected using 2-minute interval instantaneous scan sampling, except for self-directed behaviors, which were collected using untimed-event focal sampling.

2.3.2. Pre- and Post-Treatment Phases

To further investigate the effects of termite mounds on chimpanzee well-being, we used behavioral data from before and after the introduction of the enrichment (i.e., pre- and post-treatment phases). These data were collected as part of a longitudinal study conducted at Fundació Mona [66,67], using the same ethogram and similar data collection methodology (2-min instantaneous scan sampling, 20-min sessions) that was employed during the baseline and enrichment conditions in the treatment phase. The only difference between the pre- and post-treatment phases and the treatment phase was that self-directed behaviors were only registered using the scan sampling methodology and that no focal sampling was conducted for the detection of rubs and scratches. For both pre- and post-treatment phases, we selected a similar period of time to the treatment phase (2 months) and the same number of data-collection days per group (8 days). Observations were also distributed across all days while chimpanzees were in the outdoor facilities. Nonetheless, observation time per day was variable, as observer availability was uneven during pre- and post-treatment phases. Thus, in the pre-treatment phase (August–September 2018), we were able to use a total of 470 scans per group (15.7 h of observations), whereas, in the post-treatment phase (January–February 2019), only 210 scans per group (7 h of observations) were available.

2.3.3. Rank Calculation

In order to assess the subjects' rank, we used behavioral data from a longitudinal study conducted between January 2017 and December 2019 on the same groups. In this study, instantaneous scan sampling (intervals every 2 min in 20 min sessions) was used to collect dyadic agonistic interactions with a clear winner-loser outcome, including unidirectional dominant behaviors (e.g., aggression, agonistic display, displacement) and unidirectional submissive behaviors (e.g., avoid, bared-teeth, flee). Due to observer availability, observations were not equally distributed throughout the 3-year period. In particular, total observation time for the Mutamba group was 524 h (15720 scans) and 454.57 h (13640 scans) for the Bilinga group.

2.3.4. Inter-Observer Reliability

All behavioral observations were conducted by several observers, who only collected data after completing a training period and successfully passing the inter-observer reliability test (agreement between observers ≥ 85%). All data were collected using ZooMonitor [68], an application that facilitates the recording and analysis of animal behavior [69].

2.4. Data Analyses

Rank was calculated with the "EloRating" package [70] in R (R Core Team, Vienna, Austria, version 3.5.0), taking into account all dyadic agonistic interactions with a clear winner-loser outcome (135 interactions in the Mutamba group, and 23 in the Bilinga group). In each group, we assigned a value between 0 and 1 to every chimpanzee, with 1 corresponding to the highest-ranking subject and 0 to the lowest ranking one. Additionally, to assess rank stability, we calculated the Elo-rating repeatability score using the package "aniDom" [71]. In the Bilinga group, the repeatability score was high (r = 0.820), but given the small number of dyadic interactions in this group, and the fact that the repeatability score in the Mutamba group was very low (r = 0.279), we decided not to include rank in our models.

To investigate chimpanzee enrichment use through time, compare behavior across phases and conditions and assess the effect of participation on chimpanzee behavior, we utilized four sets of generalized linear mixed models (GLMM) [72] using the "glmmTMB" package [73] in R (R Core Team, version 3.5.0). In the first set of models, Model 1 assessed whether participation in the enrichment condition of the testing phase (i.e., the proportion of scans an individual interacted with the enrichment device in an enrichment session) varied across sessions and whether individual characteristics like sex and age predicted participation. In this model, we entered one line per individual and session (only including enrichment sessions), with session number, sex, age and time of the day (morning/afternoon) as test predictors. We further included group as a control variable and subject identity as a random effect, using a beta distribution.

In the second set of models (Models 2–9), we compared chimpanzee behaviors across phases/conditions (pre-treatment, treatment (baseline), treatment (enrichment), and post-treatment) by using phase/condition as the main predictor. In particular, these models assessed whether phase/condition predicted the occurrence of tool use (Model 2), feeding (Model 3), inactivity (Model 4), abnormal behaviors (Model 5), self-directed behaviors, (Model 6), social proximity (Model 7), affiliation-related behaviors (Model 8) and aggression-related behaviors (Model 9). In these models, we entered one line per individual and sampling scan and created binary columns (0/1) for each behavior after excluding the scans in which subjects were not visible. Therefore, the dependent variables (behaviors) were modeled with a binomial distribution. As control predictors, we entered sex, age, group, time of day (morning/afternoon) and scan number, whereas subject identity was included as a random effect.

In the third set of models (Models 2b–9b), we only used a subset of the data (i.e., baseline and enrichment conditions of the treatment phase) to assess the link between participation (i.e., the proportion of scans in each session in which an individual interacted with the enrichment device) and chimpanzee behavior. As in Models 2–9, we modeled each behavior but used participation in interaction with session number (and their main effects) as the main predictor. In particular, Models 2b–9b assessed whether participation predicted the occurrence of tool use (Model 2b), feeding (Model 3b), inactivity (Model 4b), abnormal behaviors (Model 5b), self-directed behaviors (rubs and scratches; Model 6b), social proximity (Model 7b), affiliation-related behaviors (Model 8b), aggression-related behaviors (Model 9b) and whether this effect varied across sessions. In these models, we included one line per subject and session. All the dependent variables collected with the scan sampling method (Models 2b–5b and 7b–9b) were calculated as the number of scans in which the subject performed the behavior (i.e., tool use, feeding, abnormal behaviors, social proximity, affiliation-related behaviors and aggression-related behaviors, respectively), divided by the total number of scans in which the subject was visible. Being proportions, these variables were modeled with a beta distribution. In Model 6b, instead, self-directed behaviors were collected with focal sampling, and the dependent variable was thus calculated as the total number of bouts performed in the time the subject was visible (i.e., rate of self-directed behaviors). Therefore, the dependent variable was modeled as a count (with a negative binomial distribution), adding observation time as an offset in the model. In all models (Models 2b–9b), we modeled sex, age, group and time of day (morning/afternoon) as control predictors and subject identity as a random effect. If we detected overdispersion in any of the models above (i.e., Models 2b, 5b and 9b), we transformed the predictor (participation) into a binomial predictor. If the model was still overdispersed (i.e., Models 5b and 9b), we further transformed the response into a binomial variable. We detected no overdispersion in the models presented below.

In all models, we z-transformed age to facilitate model convergence. To compare full models containing all predictors with null models containing only control predictors, random factors and offset terms, we used a likelihood ratio test (function "anova") [74]. Full models were considered significantly different from null models when $p \le 0.05$. In the second set of models (Models 2–9), when the main categorical predictor phase had a significant effect, we used Tukey's multiple pairwise comparisons ($p < 0.05$) to conduct post-hoc tests with the "emmeans" package [75]. In order to test our predictions, we specifically compared behaviors (i) between the baseline and the enrichment conditions of the treatment phase (i.e., short-term effect of the enrichment), (ii) between the pre-treatment phase and both the enrichment condition of the treatment phase and the post-treatment phase (i.e., long-term effect of the enrichment). In the third set of models (Models 2b–9b), if the 2-way interaction between the main predictors (participation and session number) was not significant, we removed the interaction for subsequent model iterations only, including the main effects. To rule out collinearity, we calculated variance inflation factors (VIF) [76], which were very good in all models (maximum VIF across models = 2.66).

Finally, we used social network analyses (SNA) (package "asnipe") to assess whether the presence of the enrichment could affect the social dynamics in the groups. We focused on social proximity because we expected changes in subject associations for both participants and non-participants, depending on the presence of the enrichment. Thus, for each group and condition of the treatment phase (i.e., baseline and enrichment), we calculated the centrality degree of chimpanzees for social proximity (values between 0 and 1). Then, to assess whether the centrality degree varied in the presence of enrichment, we ran a GLMM (Model 10) using the "glmmTMB" package [73]. In this model, we entered one line per individual and per condition. As test predictors, we included the interaction of condition and group (and their main effects), adding subject identity as a random effect. We detected no converge or collinearity issues in this model (VIF = 2.26).

3. Results

Participation in the enrichment activity varied widely across individuals (mean = 5.65%, SD = 5.97, range = 0.00–18.25%), with 4 out of the 14 chimpanzees in our sample never being observed while interacting with the termite mounds. Supplementary Materials Tables S2 and S3 contain individual and mean values of the incidence of each behavior in the baseline and enrichment conditions of the treatment phase. Results from Models 1–10 and Models 2b–9b are presented in Supplementary Materials Tables S4–S6, respectively. Table 2 contains a summary of predictions and results for all models.

Participation. In Model 1, the full model significantly differed from the null model. Participation in the enrichment increased across sessions (Figure 4) and was higher in the morning than in the afternoon, but sex and age had no significant effect.

Table 2. Summary of predictions and results for all models.

Models & Predictions		**Supported?**			
1. Participation in E…	Decreases Across Sessions	No *			
	is Predicted by:				
	Sex	No			
	Age	No			
	Time (am/pm)	Yes			
E Presence/Participation Predicts a/an…		**E Presence (Models 2–9)**			**Participation (Models 2b–9b)**
		Short–Term	**Long–Term**		
		Baseline ≠ E	**Pre ≠ E**	**Pre ≠ Post**	
2/2b Increase in Tool Use		Yes	Yes	Yes	Yes
3/3b Increase in Feeding		Yes	Yes	Yes	Yes
4/4b Decrease in Inactivity		Yes	Yes	Yes	Yes
5/5b Decrease in Abnormal Behaviors		Yes	No	No **	No
6 Decrease in Self-Directed Behaviors		Yes	No **	No **	–
6b Decrease in Rubs and Scratches		–	–	–	No
7/7b Increase in Social Proximity		No	Yes	Yes	Yes
8/8b Decrease in Affiliation-related Behaviors		No	No **	No **	No
9/9b Increase in Aggression-related Behaviors		No	Yes	No	No
10. E Presence Predicts Changes in Proximity Social Networks		No			

* Model 1 predicted an increase in participation across sessions. ** Significant differences between phases, but in the opposite direction of the one predicted. E stands for Enrichment.

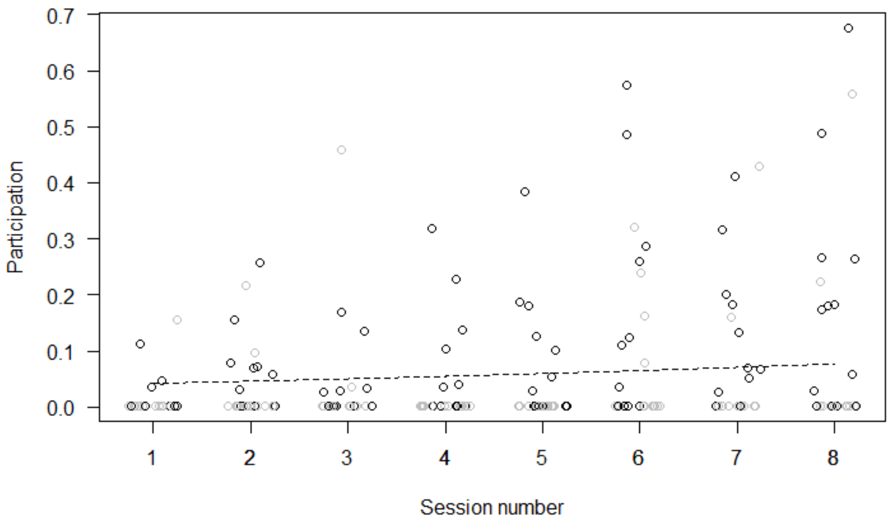


Figure 4. Participation in the enrichment task (i.e., proportion of scans that an individual interacted with the enrichment device in an enrichment session) as a function of time (i.e., enrichment session number) during the treatment phase. Circles represent individual responses in each enrichment session, in the morning (in black) and in the afternoon (in grey). The dashed black line represents the fitted model, which is like Model 1 but unconditional on all the other predictors that were standardized. Data were jittered horizontally to avoid overplotting.

Comparison of behaviors across conditions and phases (Models 2–9). In Model 2 (tool use), the full null model comparison was significant. Post-hoc comparisons indicated that tool use was more likely to occur in the presence of the enrichment (i.e., enrichment condition) than in the baseline condition. No occurrence of tool use was observed during the pre-treatment phase; thus, the frequency of this behavior was higher in the enrichment condition and post-treatment phase. Finally, tool use was more frequent in the enrichment condition than in the post-enrichment phase. In Model 3 (feeding), the full null model comparison was significant, and the post-hoc comparisons indicated that feeding was more likely to occur in the enrichment condition than in the baseline condition, pre-treatment phase and post-treatment phase. Feeding was also more likely in the post-treatment than in the pre-treatment phase. In Model 4 (inactivity), the full null model comparison was significant, and post-hoc comparisons showed that chimpanzees were more likely to be active during the enrichment condition than during the baseline condition, pre-treatment phase and post-treatment phase. Furthermore, they were also more active during the post-treatment phase than during the pre-treatment phase. In Model 5 (abnormal behaviors), the full-null model comparison was significant and post-hoc comparisons indicated that abnormal behaviors were less likely in the enrichment condition than in the baseline condition. No differences were found between the enrichment condition and either the pre- or post-enrichment phases. However, abnormal behaviors were less likely in the pre-treatment than the post-treatment phase. In Model 6 (self-directed behaviors), the full null model comparison was significant, and post-hoc comparisons revealed that self-directed behaviors were less likely in the enrichment condition than in the baseline condition. However, they also increased during the enrichment condition and the post-treatment phase, as compared to the pre-treatment phase, whereas no differences were found between the enrichment condition and the post-treatment phase. In Model 7 (social proximity), the full null model comparison was significant, and post-hoc comparisons showed no differences between the enrichment and baseline conditions. However, social proximity was more likely during the pre-treatment phase than in the enrichment condition or the post-treatment phase and more likely in the post-treatment phase than in the enrichment condition. In Model 8 (affiliation-related behaviors), the full null model comparison was significant, and post-hoc comparisons showed no differences between the enrichment and baseline conditions. Furthermore, affiliation-related behaviors were more frequent during the enrichment condition and post-treatment phase than in the pre-treatment phase, but also more frequent in the post-treatment phase than in the enrichment condition. Finally, in Model 9 (aggression-related behaviors), the full null model comparison was significant and post-hoc comparisons indicated that aggression-related behaviors did not vary between enrichment and baseline conditions nor between the enrichment condition and the post-enrichment phase. However, they increased during the enrichment condition as compared to the pre-treatment phase.

Participation and changes in behaviors within the treatment phase (Models 2b–9b*).* In Model 2b (tool use), the full null model comparison was significant, with participation in the enrichment activities predicting a higher proportion of tool use, which increased across sessions (Figure 5). In Model 3b (feeding), the full null model comparison was significant, revealing that participation in the enrichment predicted a higher proportion of feeding, with no significant changes across sessions (Figure 6). In Model 4b (inactivity), the full null model comparison was significant, showing a link between higher participation and lower inactivity, which did not change across sessions (Figure 7). In Model 5b (abnormal behaviors), the full null model comparison was not significant. In Model 6b (self-directed behaviors (rubs and scratches)), the full model differed significantly from the null model, with the rate of self-directed behaviors decreasing across sessions but no significant effect of participation. In Model 7b (social proximity), the full null model comparison was significant, with higher participation predicting a higher proportion of proximity which did not change across sessions (Figure 8). Finally, the full null model comparison was not significant for either Model 8b (affiliation-related behaviors) or Model 9b (aggression-related behaviors).

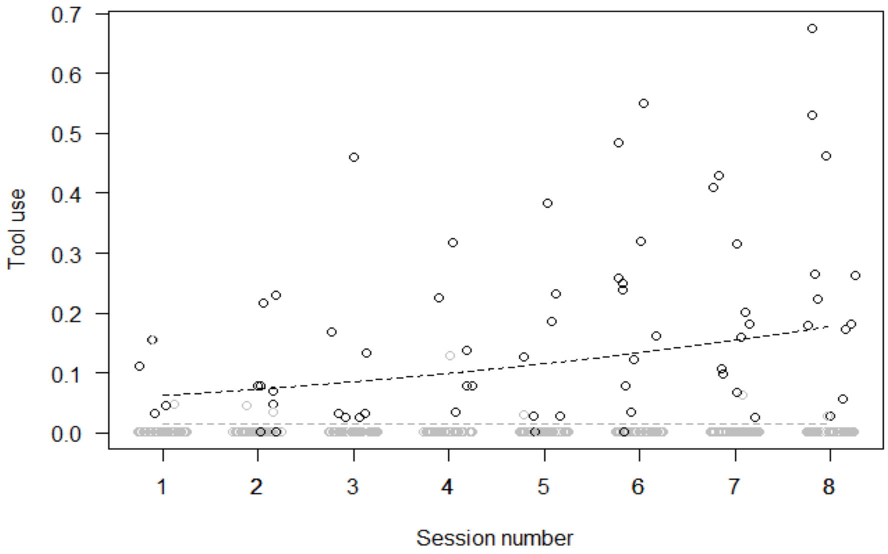


Figure 5. Tool use (i.e., proportion of scans where an individual engaged in tool use out of the total number of scans in which the subject was visible) as a function of time (i.e., enrichment session number) during the treatment phase. Circles represent individual responses in each enrichment session (i.e., in the morning and in the afternoon). Grey circles represent sessions in which the subjects did not participate in the enrichment task, and black circles those in which they participated. The dashed lines represent the fitted model, which is like Model 2b but unconditional on all the other predictors that were standardized. The black line represents the model for subjects participating in the enrichment task, and the grey line represents the model for those who did not participate in the task. Data were jittered horizontally to avoid overplotting.

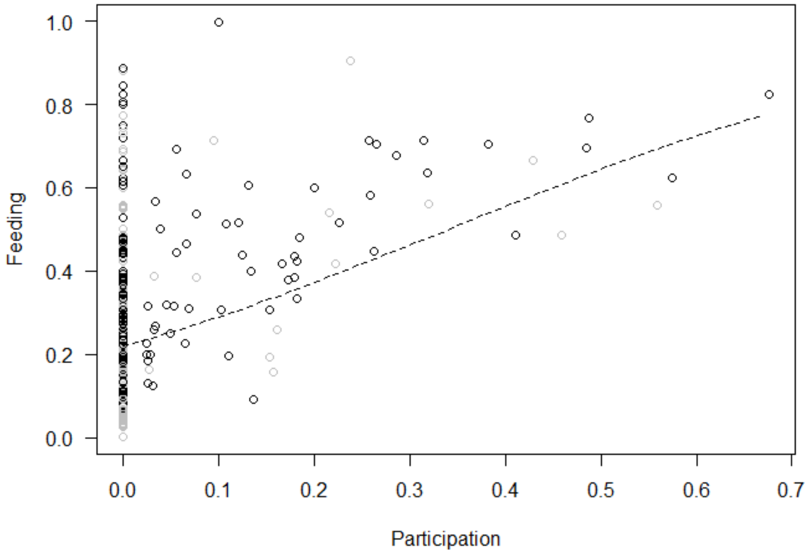


Figure 6. Feeding (i.e., proportion of scans that an individual was feeding, out of the total number of scans in which the subject was visible) as a function of participation (i.e., proportion of scans an individual interacted with the enrichment device in an enrichment session) during the treatment phase. Circles represent individual responses in each enrichment session in the morning (in black) and afternoon (in grey). The dashed line represents the fitted model, which is like Model 3b but unconditional on all the other predictors that were standardized.

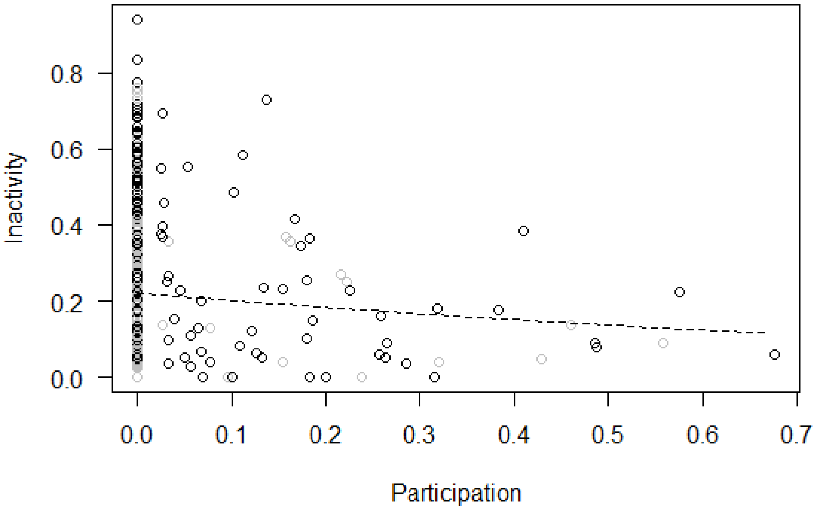


Figure 7. Inactivity (i.e., proportion of scans that an individual was inactive, out of the total number of scans in which the subject was visible) as a function of participation (i.e., proportion of scans an individual interacted with the enrichment device in an enrichment session) during the treatment phase. Circles represent individual responses in each enrichment session in the morning (in black) and afternoon (in grey). The dashed line represents the fitted model, which is like Model 4b but unconditional on all the other predictors that were standardized.

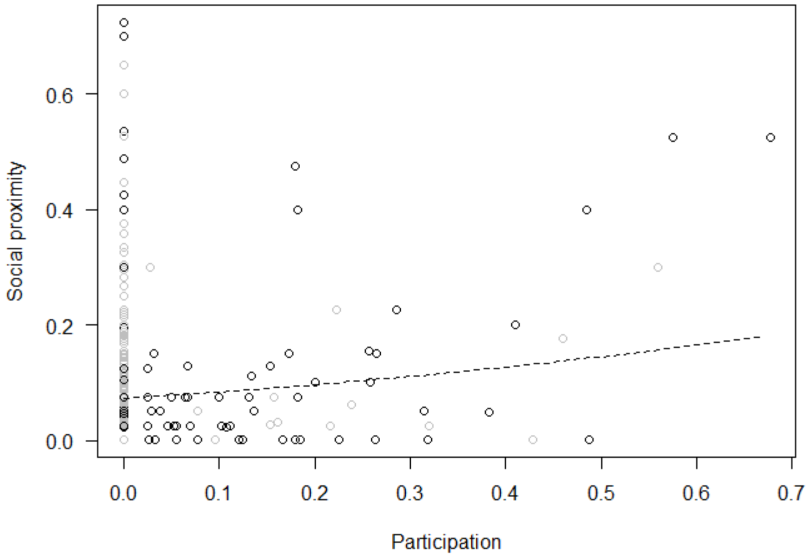


Figure 8. Social proximity (i.e., proportion of scans an individual was in social proximity, out of the total number of scans in which the subject was visible) as a function of participation (i.e., proportion of scans an individual interacted with the enrichment device in an enrichment session) during the treatment phase. Circles represent individual responses in each enrichment session in the morning (in black) and afternoon (in grey). The dashed line represents the fitted model, which is like Model 7b but unconditional on all the other predictors that were standardized.

SNA. In Model 10 (centrality degree for social proximity), the full null model comparison was not significant, revealing no significant differences in proximity patterns between conditions. Sociograms for the baseline and enrichment conditions of the treatment phase are displayed in Supplementary Materials Figure S1.

4. Discussion

This study assessed the impact of an artificial termite-fishing task on the behavioral patterns and social dynamics of two groups of sanctuary-housed chimpanzees. Specifically, we aimed to address: (1) whether participation in the enrichment was linked to individual differences like sex or age, and whether it would decrease across sessions (Model 1, Prediction 1), (2) if chimpanzee behavior changed across phases and conditions (pre-treatment, baseline, enrichment and post-treatment; Models 2–9, Predictions 2–9) and (3) if chimpanzee behavior changed as a function of participation during the treatment phase (Models 2b–9b, Predictions 2b–9b). Additionally, we used social network analyses to explore possible changes in chimpanzee association patterns in the presence of the enrichment (Model 10).

In contrast to our predictions, participation in the enrichment task increased across sessions and strongly varied across subjects, but with no significant effect of sex or age. As expected, the occurrence of solitary and social behaviors partly differed across phases and conditions. Specifically, tool use and feeding increased, and inactivity decreased in the presence of the enrichment, as compared to the baseline condition, the pre- and post-enrichment phases. Additional analyses revealed that changes in these behaviors were directly linked to higher participation in enrichment activities and that they were maintained across sessions. Thus, as expected, chimpanzees that used the termite mounds more often were also more likely to use tools, feed and be active, as compared to chimpanzees who did not participate in the task. We also found that participation, but not enrichment presence, was positively associated with social proximity. In contrast to our predictions, however, neither enrichment presence nor participation had a significant effect on the probability of abnormal, self-directed, affiliation-related or aggression-related behaviors. Finally, social network analyses showed that the enrichment presence did not significantly affect proximity association patterns.

As opposed to similar research conducted in captivity and in the wild, which report a higher probability of tool use activities by female chimpanzees [32,35,42,56–58], we found no sex differences in our termite mound experiments. However, this might depend on the small number of females in our study sample. Furthermore, although young chimpanzees in other studies spent more time in artificial termite-fishing tasks than adults [31], we did not observe age differences in task participation in this study, possibly because all the chimpanzees in our sample were adults and their age range was relatively small (i.e., 15 to 36 years). Regardless of sex or age, individual differences in enrichment use and their effects on animal behavior and welfare have been commonly reported in non-human primates [44,77]. Temperament or personality, for instance, may explain the variance in subjects' interest towards enrichment [78,79]. For example, higher scores in trait openness have been linked to higher participation and performance in foraging puzzles, training activities and computerized activities in chimpanzees and other non-human primates [55,80–83]. Other factors that may influence subject performance include past experiences [84], rearing conditions [85] and genetics [86]. A combination of these variables could explain, for example, why four chimpanzees of our sample never interacted with the termite mounds. Therefore, future studies with larger sample sizes should include these factors when assessing the effect of enrichment on behavior and welfare.

Previous studies show that primates easily lose interest in food-based enrichments and puzzles after relatively short exposure times [87–89]. In our study, however, participation did not decrease over time but actually increased across sessions. Even though animal task engagement does not necessarily provide evidence of a positive effect of the task on their welfare, it surely constitutes a basic indicator of enrichment success [25]. Therefore, the fact that participation increased across sessions indicates that chimpanzees found the termite mounds rewarding, but also that they likely required time to habituate to the task and become efficient at extracting the food. This was an unexpected outcome, considering that all chimpanzees in our sample had been exposed to this enrichment before and had the opportunity to practice the necessary skills to obtain the food from the termite mounds. One possible explanation for the increase in participation through time is that the termite mounds had not been used for a long time and were thus perceived positively as a novel stimulus, so that chimpanzee interest and efficiency would increase through sessions. Furthermore, providing the enrichment only once or twice a week (low doses), in contrast to other studies in which enrichments are continuously available (high doses), might have contributed to maintaining chimpanzee interest during the whole study period. On a side note, the chimpanzees in our study used the termite mounds more frequently in the morning than in the afternoon, likely because the food rewards in the tubes were limited, and their number decreased throughout the day.

Artificial termite-fishing tasks have already been shown to promote species-typical behaviors such as tool use and foraging in chimpanzees [28,29,31] and other great apes [90] while decreasing inactivity [29]. In our study, we observed the same increase in these behaviors when the enrichment was present (compared to the baseline condition) and in individuals who participated more in the enrichment (compared to those participating less). These results suggest a clear positive short-term effect of the enrichment on the occurrence of species-typical behaviors, especially for subjects participating in the enrichment activities. Furthermore, tool use and feeding increased, and inactivity decreased both in the post-enrichment phase and in the enrichment condition (compared to the pre-enrichment phase), suggesting a possible long-term effect of enrichment on these behaviors.

As opposed to other food-based enrichments requiring tools, we did not find a significant reduction in stress-related behaviors (abnormal or self-directed) when the enrichment was provided or if individuals participated in the enrichment [28,32,42]. Abnormal behaviors were less frequent when the enrichment was present as compared to the baseline condition but not to the pre-enrichment phase, suggesting a limited effect of the enrichment on these behaviors. In fact, they actually increased in the post-enrichment phase as compared to the pre-enrichment phase, which might suggest a negative long-term effect of enrichment activities on the occurrence of abnormal behaviors. One possible explanation for these results is that chimpanzees at Fundació Mona have a very low incidence of abnormal behaviors [67]. For example, in the baseline and enrichment conditions, the proportion of abnormal behaviors only represented less than 2.5% of their activity budget (see Supplementary Materials Table S2), which is lower than what has been reported in other captive chimpanzees (2.9 to 7.6%) [91]. It is also worth noting that a lack of change, or even an increase in abnormal and stereotypic behaviors, during or after exposure to enrichment devices is not uncommon in non-human primates [24,92–94]. This raises the question of whether a particular enrichment is truly beneficial if it is not directly linked to a decrease in these undesirable behaviors. In fact, some authors recommend that prior to the onset of an environmental enrichment intervention, a complete evaluation be carried out through a functional behavior assessment (FBA) [95] to identify the events contributing to the origin and maintenance of clinically relevant behavior [96,97]. Despite its potential benefits, FBA is still seldom used in applied animal welfare science with non-human primates. In addition, several authors have questioned the relationship between abnormal behavior and welfare in captive chimpanzees, arguing that the occurrence of abnormal behaviors is endemic to captive populations [91] and depends on historical variables (e.g., rearing conditions) [85]. Chimpanzees that have suffered past traumatic experiences and have spent years in impoverished environments can still engage in stereotypical or abnormal behaviors that are particularly difficult to eradicate, even years after rescue [98]. Thus, eliminating or reducing these deep-rooted behaviors may require a different approach, such as behavioral management [99,100], the application of psychological models of diagnosis and treatment [101,102] and/or pharmacological intervention [103,104].

Similar to abnormal behaviors, self-directed behaviors were less frequent when the enrichment was present than in the baseline condition, but they increased in the enrichment condition and post-enrichment phase as compared to the pre-enrichment phase, thus revealing that the presence of the enrichment had no clear effects on these behaviors. In addition, further analyses showed that higher participation was not linked to changes in the rates of rubs and scratches, which suggests that chimpanzees were not experiencing more anxiety or stress while interacting with the task. Several studies have reported an increase in self-directed behaviors when primates face novel or challenging situations [45,47,48,64]. However, all chimpanzees in our sample had previous experience with the task; despite being non-functional for two years, the termite mounds had been in the outdoor enclosures for a long time. Therefore, the component of novelty was absent in our study. Additionally, and in contrast to most studies assessing cognitive tasks in non-human primates [48,52,53,64,81], the chimpanzees were not isolated in a different location (e.g., an adjacent room) or separated from their group to perform the task. Thus, remaining in the same familiar social context likely decreased their anxiety.

Regarding the effects of enrichment on the social dynamics of the group, our results did not support our predictions. In particular, neither affiliation- nor aggression-related behaviors showed significant differences depending on enrichment presence or individual participation. These findings are consistent with those of Yamanashi and colleagues [32], who provided captive chimpanzees with tool feeders and found no differences in the frequency of affiliative or aggressive interactions when the enrichment was (or was not) available. The absence of change in the incidence of affiliation-related behaviors can be seen as a positive outcome, suggesting that the chimpanzees did not spend more time interacting with the termite mound at the expense of positive social interactions. Furthermore, the fact that several individuals could use the termite mound at the same time may explain why aggression-related behaviors did not increase, as chimpanzees did not have to compete to access the enrichment [28,42]. In fact, in line with our predictions, we did find that participation was positively associated with social proximity, confirming that the enrichment was used simultaneously by several chimpanzees and suggesting that the artificial termite mounds somehow functioned as a “gathering point” in our study groups. Unexpectedly, however, we found no differences in the frequency of social proximity between enrichment and baseline conditions. In addition, the sociograms comparing the centrality degree for social proximity in the baseline and enrichment conditions showed some variation in subject association patterns (see Figure S1), but these differences were not statistically significant. Moreover, social proximity was higher in the pre- and post-enrichment phases than in the enrichment condition. Therefore, overall, the chimpanzees spent less time in close proximity during the treatment phase, regardless of whether the enrichment was provided or not, and only those who participated more spent more time in proximity.

Recent literature claims that caregivers should aim to provide animals with opportunities to express their natural behavioral repertoire so that they experience positive welfare states [8,12,105]. In our study, although the artificial termite mounds did not significantly reduce abnormal or self-directed behaviors, they did allow chimpanzees to express species-typical behaviors such as tool use, which is rare in our groups in the absence of an enrichment that specifically promotes this behavior. Moreover, given that the behavioral effects of enrichment use were maintained across sessions, these results indicate that the artificial termite-fishing task constituted an effective enrichment, at least for the two months of the treatment period. Furthermore, the fact that participation and tool use increased across sessions suggests that, although the termite mounds were not a novel enrichment, the chimpanzees needed time to re-habituate to them and successfully retrieve food after years of not being exposed to the task. This reveals that, contrary to our expectations, the number of sessions may have been too limited to properly evaluate the effectiveness of the enrichment. By monitoring behavioral changes when using the termite mound for longer periods, it may be possible to understand how long this enrichment task may positively impact chimpanzee welfare before they lose interest, and thus optimize frequency and length of enrichment sessions as appropriate. Another limitation of our study was that because of the few agonistic interactions and low-rank stability of our chimpanzee group, we could not explore the effect of rank as we initially intended. Aggression and power conflicts were very rare in our study samples, as the chimpanzees at Fundació Mona have significant chronic social impairment caused by past traumatic experiences [66,67], and also because competition for resources is limited in small captive groups housed in large outdoor enclosures. Nevertheless, although we were unable to explore the role of rank on participation, studies on larger groups with stable hierarchies should consider this variable when studying enrichment activities in a social environment.

5. Conclusions

Our findings are largely in line with previous studies showing that artificial termite-fishing tasks are a successful enrichment for captive chimpanzees, promoting species-typical behaviors such as feeding and tool use and decreasing inactivity, despite not reducing abnormal or self-directed behaviors. The fact that the frequency of rubs and scratches did not increase for those individuals with higher participation suggests that the use of the termite mounds was not a source of stress. Finally, affiliation- and aggression-related behaviors were mostly not affected by the presence of the enrichment, although termite mounds appeared to work as a “gathering point”, with social proximity increasing for those who participated more often. Overall, our results show that artificial termite-fishing tasks can be an effective enrichment for sanctuary-housed chimpanzees, maintaining the subjects’ level of interest and having positive effects on their solitary behaviors without negatively affecting their social interactions.

Supplementary Materials: The following are available online at www.mdpi.com/2076-2615/11/10/2941/s1, Figure S1: Sociograms comparing social proximity (one-arm length) across control and enriched conditions in each chimpanzee group, Table S1: Sociograms comparing social proximity (one-arm length) across control and en-riched conditions in each chimpanzee group, Table S2 and S3: Incidence of behaviors in the base-line (S1) and enrichment (S2) conditions of the treatment phase, Table S4. Estimates, standard er-rors (SE), confidence intervals and p-values for Models 1-10. Reference category for phase/condition is baseline condition, for sex is female, for time is morning and for group is Bilin-ga, Table S5. Estimates, standard errors (SE) and p-values for post-hoc comparisons in Models 2-9. In all models, estimates are in logit-scale Table S6. Estimates, standard errors (SE), confidence in-tervals and p-values for Models 2b-9b. Reference category for sex is female, for time is morning and for group is Bilinga.

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Institutional Review Board Statement: The project was evaluated in 2019 by Universitat de Girona Ethics Committee (Comitè d'Ètica i Bioseguretat de la Recerca de la Universitat de Girona). It was approved by the Committee because the methodology that we used to evaluate animal behavior was purely observational and implied non-invasive procedures. (Ethic Committee Name: Comitè d'Ètica i Bioseguretat de la Recerca de la Universitat de Girona, Approval Code: CEBU 0020-2019, Approval Date: 16 December 2019).

Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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References

1. Committee, E.C.V.S. *The Welfare of Intensively Kept Pigs: Report of the Scientific Veterinary Committee Adopted 30 September 1997*; European Commission: Brussels, Belgium, 1997.
2. Harrison, R. *Animal Machines*; Vincent Stuart Ltd.: London, UK, 1964.
3. Cole, J.; Fraser, D. Zoo Animal Welfare: The Human Dimension. *J. Appl. Anim. Welf. Sci.* **2018**, *21*, 49–58.
4. Kagan, R.; Carter, S.; Allard, S. A Universal Animal Welfare Framework for Zoos. *J. Appl. Anim. Welf. Sci.* **2015**, *18*, S1–S10.
5. Wolfensohn, S.; Shotton, J.; Bowley, H.; Davies, S.; Thompson, S.; Justice, W.S. Assessment of welfare in zoo animals: Towards optimum quality of life. *Animals* **2018**, *8*, 110.
6. Rose, P.; Riley, L. The use of Qualitative Behavioural Assessment to zoo welfare measurement and animal husbandry change. *J. Zoo Aquar. Res.* **2019**, *74*, 150–161.
7. Learmonth, M. J., Dilemmas for natural living concepts of zoo animal welfare. Animals 2019, 9,318.
8. Maple, T.L.; Bloomsmith, M.A. Introduction: The science and practice of optimal animal welfare. *Behav. Process.* **2018**, *156*, 1–2.
9. Mellor, D.; Hunt, S.; Gusset, M. *Caring for Wildlife: The World Zoo and Aquarium Animal Welfare Strategy*; WAZA Executive Office: Gland, Switzerland, 2015.
10. Ward, S.J.; Sherwen, S.; Clark, F.E. Advances in applied zoo animal welfare science. *J. Appl. Anim. Welf. Sci.* **2018**, *21*, 23–33.
11. Broom, D.M. Animal welfare: Concepts and measurement. *J. Anim. Sci.* **1991**, *69*, 4167–4175.
12. Maple, T.L.; Perdue, B.M. Environmental Enrichment. In *Zoo Animal Welfare*; Springer: Berlin/Heidelberg, Germany, 2013; pp. 95–117.
13. Mellor, D.J. Updating Animal Welfare Thinking: Moving beyond the "Five Freedoms" towards "A Life Worth Living". *Animals* **2016**, *6*, 21.
14. Brambell, F.W.R. *Report of the Technical Committee to Enquire into the Welfare of Animals Kept under Intensive Livestock Husbandry Systems*; Her Majesty's Stationery Office: London, UK, 1965.

15. Kiley-Worthington, M. Ecological, ethological, and ethically sound environments for animals: Toward symbiosis. *J. Agric. Environ. Ethics* **1989**, *2*, 323–347.
16. Bracke, M.B.M.; Hopster, H. Assessing the Importance of Natural Behavior for Animal Welfare. *J. Agric. Environ. Ethics* **2006**, *19*, 77–89.
17. Hughes, B.O.; Duncan, I.J.H. The notion of ethological 'need', models of motivation and animal welfare. *Anim. Behav.* **1988**, *36*, 1696–1707.
18. Young, R. *Environmental Enrichment for Captive Animals*; Blackwell Publishing: Oxford, UK, 2003.
19. Mallapur, A. Animal Welfare research and its implications to non-human primate breeding programs: A Case Study of the Lion-tailed macaque conservation breeding program from India. *REDVET* **2008**, *9*, 1–21.
20. Newberry, R.C. Environmental enrichment: Increasing the biological relevance of captive environments. *Appl. Anim. Behav. Sci.* **1995**, *44*, 229–243.
21. Boissy, A.; Manteuffel, G.; Jensen, M. B.; Moe, R. O.; Spruijt, B.; Keeling, L. J.; Winckler, C.; Forkman, B.; Dimitrov, I.; Langbein, J.; Bakken, M.; Veissier, I.; Aubert, A., Assessment of positive emotions in animals to improve their welfare. Physiol. Behav. 2007, 92,375-397
22. Bain, M.; Buffington, C. T., The relationship between mental and physical health. Mental Health and Well-being in Animals 2019,33.

.

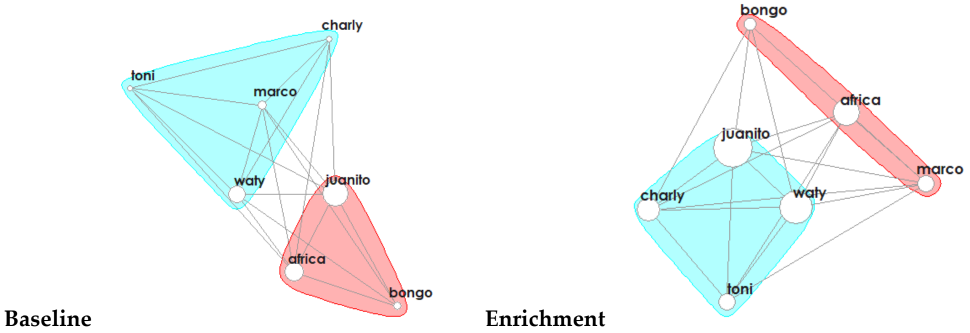
23. Hill, S.P.; Broom, D.M. Measuring zoo animal welfare: Theory and practice. *Zoo Biol.* **2009**, *28*, 531–44.
24. Lutz, C.K.; Novak, M.A. Environmental enrichment for nonhuman primates: Theory and application. *ILAR J.* **2005**, *46*, 178–191.
25. Dutton, M.B.; Pierre, P.J.; Bailoo, J.; Warkins, E.; Michel, G.F.; Bennett, A.J. A Model Quantitative Assessment Tool for Nonhuman Primate Environmental Enrichment Plans. *bioRxiv* **2018**. https://doi.org/10.1101/341206
26. Bloomsmith, M.; Alford, P.; Maple, T. Successful feeding enrichment for captive chimpanzees. *Am. J. Primatol.* **1988**, *16*, 155–164.
27. Baker, K.C. Straw and forage material ameliorate abnormal behaviors in adult chimpanzees. *Zoo Biol.* **1997**, *16*, 225–236.
28. Maki, S.; Alford, P.L.; Bloomsmith, M.A.; Franklin, J. Food puzzle device simulating termite fishing for captive chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* **1989**, *1*, 71–78.
29. Celli, M.L.; Tomonaga, M.; Udono, T.; Teramoto, M.; Nagano, K. Tool use task as environmental enrichment for captive chimpanzees. *Appl. Anim. Behav. Sci.* **2003**, *81*, 171–182.
30. Celli, M.L.; Hirata, S.; Tomonaga, M. Socioecological influences on tool use in captive chimpanzees. *Int. J. Primatol.* **2004**, *25*, 1267–1281.
31. Nash, V.J. Tool use by captive chimpanzees at an artificial termite mound. *Zoo Biol.* **1982**, *1*, 211–221.
32. Yamanashi, Y.; Matsunaga, M.; Shimada, K.; Kado, R.; Tanaka, M. Introducing tool-based feeders to zoo-housed chimpanzees as a cognitive challenge: Spontaneous acquisition of new types of tool use and effects on behaviours and use of space. *J. Zoo Aquar. Res.* **2016**, *4*, 147–155.
33. Llorente, M.; Campi, A. Is "tool use" a welfare tool? Using an artificial ant-fishing task as environmental enrichment in naturalistically housed chimpanzees from the Fundació Mona. *Folia Primatol.* **2014**, *85*, 68–68.
34. Goodall, J. *The Chimpanzees of Gombe: Patterns of Behavior*; Cambridge University Press: Cambridge, MA, USA, 1986.
35. Boesch, C.; Boesch, H. Tool use and tool making in wild chimpanzees. *Folia Primatol.* **1990**, *54*, 86–99.
36. Paquette, D. Discovering and learning tool-use for fishing honey by captive chimpanzees. *Hum. Evol.* **1992**, *7*, 17–30.
37. Hirata, S.; Celli, M.L. Role of mothers in the acquisition of tool-use behaviours by captive infant chimpanzees. *Anim. Cogn.* **2003**, *6*, 235–244.
38. Hirata, S.; Morimura, N. Naive chimpanzees' (*Pan troglodytes*) observation of experienced conspecifics in a tool-using task. *J. Comp. Psychol.* **2000**, *114*, 291–296.
39. Hopper, L.M.; Tennie, C.; Ross, S.R.; Lonsdorf, E.V. Chimpanzees create and modify probe tools functionally: A study with zoo-housed chimpanzees. *Am. J. Primatol.* **2015**, *77*, 162–170.
40. Harrison, R. A.; Whiten, A., Chimpanzees (*Pan troglodytes*) display limited behavioural flexibility when faced with a changing foraging task requiring tool use. *PeerJ* **2018**, 6,e4366.
41. McGrew, W.C.; Marchant, L.F. Chimpanzees, tools, and termites: Hand preference or handedness? *Curr. Anthropol.* **1992**, *33*, 114–119.
42. Brent, L.; Eichberg, J.W. Primate puzzleboard: A simple environmental enrichment device for captive chimpanzees. *Zoo Biol.* **1991**, *10*, 353–360.
43. Maestripieri, D.; Schino, G.; Aureli, F.; Troisi, A. A modest proposal: Displacement activities as an indicator of emotions in primates. *Anim. Behav.* **1992**, *44*, 967–979.
44. Clark, F.E.; Ith, L.J. Effect of a Cognitive Challenge Device Containing Food and Non-Food Rewards on Chimpanzee Well-Being. *Am. J. Primatol.* **2013**, *75*, 807–816.
45. Elder, C.M.; Menzel, C.R. Dissociation of cortisol and behavioral indicators of stress in an orangutan (*Pongo pygmaeus*) during a computerized task. *Primates* **2001**, *42*, 345–357.
46. Itakura, S. Emotional Behavior during the Learning of a Contingency Task in a Chimpanzee. *Percept. Mot. Skills* **1993**, *76*, 563–566.

47. Leavens, D.A.; Aureli, F.; Hopkins, W.D.; Hyatt, C.W. Effects of cognitive challenge on self-directed behaviors by chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* **2001**, *55*, 1–14.
48. Yamanashi, Y.; Matsuzawa, T. Emotional consequences when chimpanzees (Pan troglodytes) face challenges: Individual differences in self-directed behaviours during cognitive tasks. *Anim. Welf.* **2010**, *19*, 25–30.
49. Krause, J.; Croft, D.P.; James, R. Social network theory in the behavioural sciences: Potential applications. *Behav. Ecol. Sociobiol.* **2007**, *62*, 15–27.
50. Jacobs, A.; Petit, O. Social Network Modeling: A Powerful Tool for the Study of Group Scale Phenomena in Primates. *Am. J. Primatol.* **2011**, *73*, 741–7.
51. Kasper, C.; Voelkl, B. A social network analysis of primate groups. *Primates* **2009**, *50*, 343–356.
52. Whitehouse, J.; Micheletta, J.; Powell, L.E.; Bordier, C.; Waller, B.M. The impact of cognitive testing on the welfare of group housed primates. *PLoS ONE* **2013**, *8*, e78308.
53. Jacobson, S.L.; Kwiatt, A.C.; Ross, S.R.; Cronin, K.A. The effects of cognitive testing on the welfare of zoo-housed Japanese macaques (*Macaca fuscata*). *Appl. Anim. Behav. Sci.* **2019**, *212*, 90–97.
54. Schapiro, S.J.; Lambeth, S.P. Control, Choice, and Assessments of the Value of Behavioral Management to Nonhuman Primates in Captivity. *J. Appl. Anim. Welf. Sci.* **2007**, *10*, 39–47.
55. Hopper, L.M.; Price, S.A.; Freeman, H.D.; Lambeth, S.P.; Schapiro, S.J.; Kendal, R.L. Influence of personality, age, sex, and estrous state on chimpanzee problem-solving success. *Anim. Cogn.* **2014**, *17*, 835–847.
56. Pruetz, J.D.; Bertolani, P.; Ontl, K.B.; Lindshield, S.; Shelley, M.; Wessling, E.G. New evidence on the tool-assisted hunting exhibited by chimpanzees (*Pan troglodytes verus*) in a savannah habitat at Fongoli, Sénégal. *R. Soc. Open. Sci.* **2015**, *2*, 140507.
57. Boesch, C.; Boesch, H. Sex differences in the use of natural hammers by wild chimpanzees: A preliminary report. *J. Hum. Evol.* **1981**, *10*, 585–593.
58. McGrew, W., Evolutionary implications of sex differences in chimpanzee predation and tool use. In *The Great Apes*, Benjamin Staples: Menlo Park, CA, USA, 1979; pp 441-463.
59. Boose, K.J.; White, F.J.; Meinelt, A. Sex differences in tool use acquisition in bonobos (*Pan paniscus*). *Am. J. Primatol.* **2013**, *75*, 917–926.
60. Gruber, T.; Clay, Z.; Zuberbühler, K. A comparison of bonobo and chimpanzee tool use: Evidence for a female bias in the Pan lineage. *Anim. Behav.* **2010**, *80*, 1023–1033.
61. Bakeman, R.; Quera, V. *Sequential Analysis and Observational Methods for the Behavioral Sciences*; Cambridge University Press: Cambridge, UK, 2011.
62. Meyer, J.S.; Hamel, A.F. Models of stress in nonhuman primates and their relevance for human psychopathology and endocrine dysfunction. *ILAR J.* **2014**, *55*, 347–360.
63. Schino, G.; Perretta, G.; Taglioni, A.M.; Monaco, V.; Troisi, A. Primate displacement activities as an ethopharmacological model of anxiety. *Anxiety* **1996**, *2*, 186–191.
64. Wagner, K.E.; Hopper, L.M.; Ross, S.R. Asymmetries in the production of self-directed behavior by chimpanzees and gorillas during a computerized cognitive test. *Anim. Cogn.* **2016**, *19*, 343–350.
65. Hopkins, W.D.; Russell, J.L.; Freeman, H.; Reynolds, E.A.; Griffis, C.; Leavens, D.A. Lateralized scratching in chimpanzees (*Pan troglodytes*): Evidence of a functional asymmetry during arousal. *Emotion* **2006**, *6*, 553–559.
66. Crailsheim, D.; Stüger, H.P.; Kalcher-Sommersguter, E.; Llorente, M. Early life experience and alterations of group composition shape the social grooming networks of former pet and entertainment chimpanzees (*Pan troglodytes*). *PLoS ONE* **2020,** *15*, e0226947.
67. Llorente, M.; Riba, D.; Ballesta, S.; Feliu, O.; Rostán, C. Rehabilitation and socialization of chimpanzees (*Pan troglodytes*) used for entertainment and as pets: An 8-year study at Fundació Mona. *Int. J. Primatol.* **2015**, *36*, 605–624.
68. Ross, M.; Niemann, T.; Wark, J.; Heintz, M.; Horrigan, A.; Cronin, K.; Shender, M.; Gillespie, K. Zoomonitor (Version 1) [Mobile Application Software]. 2016. Available online: https://zoomonitor.org (accessed on 10 October 2021).
69. Wark, J.; Cronin, K.; Niemann, T.; Shender, M.; Horrigan, A.; Kao, A.; Ross, M. Monitoring the behavior and habitat use of animals to enhance welfare using the ZooMonitor app. *Anim. Behav. Cogn* **2019**, *6*, 158–167.
70. Neumann, C.; Duboscq, J.; Dubuc, C.; Ginting, A.; Irwan, A.M.; Agil, M.; Widdig, A.; Engelhardt, A. Assessing dominance hierarchies: Validation and advantages of progressive evaluation with Elo-rating. *Anim. Behav.* **2011**, *82*, 911–921.
71. Sánchez-Tójar, A.; Schroeder, J.; Farine, D.R. A practical guide for inferring reliable dominance hierarchies and estimating their uncertainty. *J Anim Ecol.* **2018**; 87, 594– 608.
72. Baayen, R.H. *Analyzing Linguistic Data: A Practical Introduction to Statistics Using R*; Cambridge University Press: Cambridge, UK, 2008.
73. Brooks, M.E.; Kristensen, K.; van Benthem, K.J.; Magnusson, A.; Berg, C.W.; Nielsen, A.; Skaug, H.J.; Machler, M.; Bolker, B.M. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **2017**, *9*, 378–400.
74. Dobson, A.J. *An introduction to generalized linear models*; Chapman & Hall/CRC: Boca Raton, Florida, 2002.
75. Lenth, R. *Emmeans: Estimated Marginal Means, aka Least-Squares Means*, R package version 1.4.7; 2020. https://CRAN.R-project.org/package=emmeans (accessed on 10 October 2021).
76. Field, A. *Discovering Statistics Using SPSS*. SAGE Publications: London, UK, 2009.

77. Izzo, G.N.; Bashaw, M.J.; Campbell, J.B. Enrichment and individual differences affect welfare indicators in squirrel monkeys (*Saimiri sciureus*). *J. Comp. Psychol.* **2011**, *125*, 347.
78. Coleman, K.; Novak, M.A. Environmental enrichment in the 21st century. *ILAR J.* **2017**, *58*, 295–307.
79. Coleman, K. Individual differences in temperament and behavioral management practices for nonhuman primates. *Appl. Anim. Behav. Sci.* **2012**, *137*, 106–113.
80. Altschul, D.; Wallace, E.; Sonnweber, R.; Tomonaga, M.; Weiss, A. Chimpanzee intellect: Personality, performance and motivation with touchscreen tasks. *R. Soc. Open. Sci.* **2017**, *4*, 170169.
81. Herrelko, E.S.; Vick, S.J.; Buchanan-Smith, H.M. Cognitive Research in Zoo-Housed Chimpanzees: Influence of Personality and Impact on Welfare. *Am. J. Phys. Anthropol.* **2012**, *74*, 828–840.
82. Reamer, L.A.; Haller, R.L.; Thiele, E.J.; Freeman, H.D.; Lambeth, S.P.; Schapiro, S.J. Factors affecting initial training success of blood glucose testing in captive chimpanzees (*Pan troglodytes*). *Zoo Biol.* **2014**, *33*, 212–220.
83. Morton, B.F.; Lee, P.C.; Buchanan-Smith, H.M. Taking personality selection bias seriously in animal cognition research: A case study in capuchin monkeys (*Sapajus apella*). *Anim. Cogn.* **2013**, *16*, 677–684.
84. Bard, K.A.; Bakeman, R.; Boysen, S.T.; Leavens, D.A. Emotional engagements predict and enhance social cognition in young chimpanzees. *Dev. Sci.* **2014**, *17*, 682–696.
85. Simpson, E.A.; Sclafani, V.; Paukner, A.; Kaburu, S.S.; Suomi, S.J.; Ferrari, P.F. Handling newborn monkeys alters later exploratory, cognitive, and social behaviors. *Dev. Cogn. Neurosci.* **2019**, *35*, 12–19.
86. Hopkins, W.D.; Keebaugh, A.C.; Reamer, L.A.; Schaeffer, J.; Schapiro, S.J.; Young, L.J. Genetic influences on receptive joint attention in chimpanzees (*Pan troglodytes*). *Sci. Rep.* **2014**, *4*, 1–7.
87. Bloomstrand, M.; Riddle, K.; Alford, P.; Maple, T.L. Objective evaluation of a behavioral enrichment device for captive chimpanzees (*Pan troglodytes*). *Zoo Biol.* **1986**, *5*, 293–300.
88. Csatádi, K.; Leus, K.; Pereboom, J.J. A brief note on the effects of novel enrichment on an unwanted behaviour of captive bonobos. *Appl. Anim. Behav. Sci.* **2008**, *112*, 201–204.
89. Gilloux, I.; Gurnell, J.; Shepherdson, D. An Enrichment Device for Great Apes. *Anim. Welf* **1992**, *1*, 279–289.
90. Nakamichi, M. Tool-use and tool-making by captive, group-living orangutans (*Pongo pygmaeus abelii*) at an artificial termite mound. *Behav. Processes* **2004**, *65*, 87–93.
91. Birkett, L. P.; Newton-Fisher, N. E., How abnormal is the behaviour of captive, zoo-living chimpanzees? *PloS one* **2011,** *6*,e20101-e20101.
92. Gottlieb, D.H.; Ghirardo, S.; Minier, D.E.; Sharpe, N.; Tatum, L.; McCowan, B. Efficacy of 3 types of foraging enrichment for rhesus macaques (*Macaca mulatta*). *J. Am. Assoc. Lab. Anim. Sci.* **2011**, *50*, 888–894.
93. Rooney, M.B.; Sleeman, J. Effects of selected behavioral enrichment devices on behavior of Western Lowland Gorillas (*Gorilla gorilla gorilla*). *J. Appl. Anim. Welf. Sci.* **1998**, *1*, 339–351.
94. Camargo, M.R.; Mendes, F.D.C. Induced Tool Use as Environmental Enrichment for Captive Capuchin Monkeys (*Sapajus libidinosus*)/Inducao do Uso de Ferramentas como Enriquecimento Ambiental para Macacos-prego (*Sapajus libidinosus*) Cativos. *Psicologia: Teoria e Pesquisa* **2016**, *32,* 1–8.
95. Pfaller-Sadovsky, N.; Arnott, G.; Hurtado-Parrado, C. Using Principles from Applied Behaviour Analysis to Address an Undesired Behaviour: Functional Analysis and Treatment of Jumping Up in Companion Dogs. *Animals* **2019**, *9*, 1091.
96. Hanley, G.P.; Iwata, B.A.; McCord, B.E. Functional analysis of problem behavior: A review. *J. Appl. Behav. Anal.* **2003**, *36*, 147–185.
97. Hanley, G.P. Functional assessment of problem behavior: Dispelling myths, overcoming implementation obstacles, and developing new lore. *Behav. Anal. Pract.* **2012**, *5*, 54–72.
98. Lopresti-Goodman, S. M.; Kameka, M.; Dube, A., Stereotypical behaviors in chimpanzees rescued from the african bushmeat and pet trade. *Behav. Sci.* **2013,** *3*,1-20.
99. Bloomsmith, M.A.; Marr, M.J.; Maple, T.L. Addressing nonhuman primate behavioral problems through the application of operant conditioning: Is the human treatment approach a useful model? *Appl. Anim. Behav. Sci.* **2007**, *102*, 205–222.
100. Coleman, K.; Maier, A. The use of positive reinforcement training to reduce stereotypic behavior in rhesus macaques. *Appl. Anim. Behav. Sci.* **2010**, *124*, 142–148.
101. Bradshaw, G.A.; Capaldo, T.; Lindner, L.; Grow, G. Building an inner sanctuary: Complex PTSD in chimpanzees. *J. Trauma Dissociation* **2008**, *9*, 9–34.
102. Kummrow, M. Diagnostic and Therapeutic Guidelines to Abnormal Behavior in Captive Nonhuman Primates. *Vet. Clin. N. Am. Exot. Anim. Pract.* **2021**, *24*, 253–266.
103. Bourgeois, S.R.; Vazquez, M.; Brasky, K. Combination therapy reduces self-injurious behavior in a chimpanzee (Pan Troglodytes Troglodytes): A case report. *J. Appl. Anim. Welf. Sci.* **2007**, *10*, 123–140.
104. Robbertsen, F. *Effect of Intervention on Abnormal Behaviour of Retired Laboratory Chimpanzees*; Utrecht University: Utrecht, The Netherlands, 2014.
105. Miller, L.J.; Vicino, G.A.; Sheftel, J.; Lauderdale, L.K. Behavioral Diversity as a Potential Indicator of Positive Animal Welfare. *Animals* **2020**, *10*, 1211.

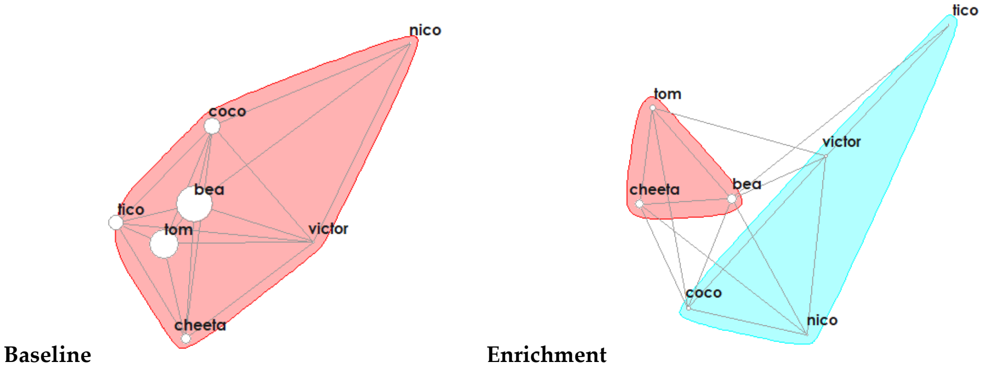
Supplementary Materials

(a) Mutamba group



Baseline **Enrichment**

(b) Bilinga group



Baseline **Enrichment**

Figure S1. Sociograms comparing social proximity (one-arm length) across control and enriched conditions in each chimpanzee group. Nodes are sized according to subjects' centrality degree (strength) and edges represent dyadic associations. Colors indicate different communities in which subjects are more strongly associated (higher incidence of social proximity). N=7 in both groups.

Table S1. Biographical information on the chimpanzees from the study sample.

Subject	Sex	Group	Year of birth	Origin	Former use	Rescue year (at Mona)
Africa	F	Mutamba	1999	wild	Pet	2009
Bea	F	Bilinga	1985	wild	Entertainment	2012
Bongo	M	Mutamba	2000	captive	Entertainment	2002
Charly	M	Mutamba	1989	captive	Entertainment	2001
Cheeta	F	Bilinga	1990	wild	Entertainment	2015
Coco	F	Bilinga	1994	wild	Pet/Entertainment	2012
Juanito	M	Mutamba	2003	captive	Pet/Entertainment	2005
Marco	M	Mutamba	1984	captive	Entertainment	2001
Nico	M	Bilinga	2001	captive	Pet/Entertainment	2004
Tico	M	Bilinga	1987	wild	Entertainment	2005
Tom	M	Bilinga	1985	Wild	Entertainment	2011
Toni	M	Mutamba	1983	wild	Entertainment	2001
Victor	M	Bilinga	1982	captive	Entertainment	2006
Waty	F	Mutamba	1997	captive	Pet/Entertainment	2001

Tables S2 and S3: Incidence of behaviors in the baseline (S1) and enrichment (S2) conditions of the treatment phase. Behaviors collected with scan sampling method (i.e., participation, tool use, feeding, inactivity, abnormal behaviors, social proximity, agonistic behaviors and affiliative behaviors) represent the percentage of scans in which the behavior was observed), whereas behaviors collected with all-occurrence focal sampling (i.e., self-directed behaviors: rubs and scratches) correspond to rates (i.e., number of self-directed behaviors/ observation time in minutes)

Table S2. Baseline condition during Phase «B» Treatment

	Scan sampling							**Focal sampling**
Subject	**Tool use**	**Feeding**	**Inactivity**	**Abnormal behaviors**	**Social proximity**	**Agonistic interactions**	**Affiliative interactions**	**Self-directed behaviors**
Africa	0.21	17.72	46.84	0.00	12.28	0.21	15.40	0.47
Bea	0.00	8.61	52.40	0.25	21.47	0.25	15.95	0.85
Bongo	0.00	18.05	39.00	0.62	4.81	2.08	8.92	0.79
Charly	0.78	26.87	17.57	0.52	2.87	0.78	23.00	0.66
Cheeta	0.00	28.90	36.42	1.93	5.89	0.00	3.28	0.74
Coco	0.00	41.29	16.95	4.30	10.29	0.00	8.35	0.98
Juanito	0.00	23.33	20.84	0.25	16.20	0.25	34.99	0.25
Marco	0.00	39.53	14.35	0.24	4.87	0.00	18.35	0.72
Nico	0.00	30.77	28.00	0.62	0.56	0.62	2.77	0.81
Tico	0.00	10.13	28.86	8.15	8.49	0.00	0.00	1.40
Tom	0.00	13.43	31.71	1.62	14.78	0.93	7.87	0.60
Toni	0.00	10.05	32.54	0.00	3.70	1.44	12.44	1.00
Victor	0.00	28.97	33.41	11.68	3.37	0.47	3.27	1.12
Waty	0.00	19.35	13.10	0.00	9.95	0.00	55.36	1.50
Mean	**0.07**	**22.64**	**29.43**	**2.16**	**8.54**	**0.50**	**15.00**	**0.85**

Table S3. Enrichment condition during Phase «B» Treatment

	Scan sampling								**Focal sampling**
Subject	**Participation**	**Tool use**	**Feeding**	**Inactivity**	**Abnormal behaviors**	**Social proximity**	**Agonistic interactions**	**Affiliative interactions**	**Self-directed behaviors**
Africa	18.25	17.53	29.16	35.60	0.00	14.45	0.00	13.42	0.48
Bea	0.00	0.00	9.78	44.84	0.00	6.26	0.82	12.77	0.95
Bongo	2.10	0.00	20.19	38.48	0.00	5.93	3.24	11.62	0.64
Charly	8.53	8.53	25.59	17.27	2.13	10.76	0.21	30.06	0.38
Cheeta	4.01	4.01	43.69	29.06	0.00	4.58	0.00	5.01	0.80
Coco	9.05	9.05	58.37	7.01	1.36	2.676	0.00	6.56	0.75
Juanito	10.49	10.08	38.27	8.85	0.21	18.94	1.03	37.04	0.17
Marco	13.08	13.08	45.36	10.13	0.00	8.73	0.21	15.40	0.62
Nico	1.59	1.589	36.51	20.11	0.00	1.66	1.85	2.12	1.04
Tico	0.00	0.45	20.98	16.52	6.70	0.48	0.67	0.00	1.01
Tom	0.0	0.00	17.27	20.62	0.00	3.48	1.80	6.96	0.46
Toni	0.00	3.32	4.06	28.04	0.00	8.06	0.00	28.04	0.57
Victor	10.82	9.05	44.81	18.54	2.65	2.35	1.33	2.43	0.73
Waty	1.17	0.24	15.49	15.50	0.00	16.09	0.00	53.99	0.84
Mean	**5.65**	**5.49**	**29.25**	**22.18**	**0.93**	**7.46**	**0.80**	**16.10**	**0.67**

Table S4. Estimates, standard errors (SE), confidence intervals and *p*-values for Models 1-10. Reference category for phase/condition is baseline condition, for sex is female, for time is morning and for group is Bilinga.

Models	Estimate	SE	CI (2.5%)	CI (97.5%)	*p*
Model 1: Participation (GLMM: $\chi^2 = 22.54$, df = 5, $p < 0.001$)					
Intercept	-3.000	0.253			
Session number	0.091	0.031	0.030	0.153	**<0.05**
Sex (male)	-0.162	0.209	-0.570	0.247	0.438
Age	-0.024	0.105	-0.230	0.183	0.823
Time (afternoon)	-0.562	0.138	-0.833	-0.291	**<0.001**
Group (Mutamba)	0.303	0.211	0.110	0.717	0.150
Model 2: Tool use (GLMM: $\chi 2 = 703.42$, df = 3, $p < 0.001$)					
Intercept	-9.883	0.999			
Phase Pre-treatment	-17.06	2884	-5.669	5634.744	0.995
Phase Treatment (Enrichment)	4.612	0.504	3.624	5.600	**<0.001**
Phase Post-treatment	2.491	0.636	1.244	3.738	**<0.001**
Sex (male)	0.272	0.971	-1.632	2.175	0.780
Age	-0.297	0.470	-1.218	0.625	0.528
Time (afternoon)	-1.091	0.122	-1.330	-0.851	**<0.001**
Group (Mutamba)	1.167	0.942	-0.680	3.013	0.216
Scan number	0.004	0.000	0.003	0.004	**<0.001**
Model 3: Feeding (GLMM: $\chi 2 = 579.91$, df = 3, $p < 0.001$)					
Intercept	-0.958	0.310			
Phase Pre-treatment	-0.796	0.055	-0.903	-0.689	**<0.001**
Phase Treatment (Enrichment)	0.418	0.044	0.332	0.504	**<0.001**
Phase Post-treatment	-0.278	0.070	-0.414	-0.141	**<0.001**
Sex (male)	0.053	0.357	-0.649	0.756	0.882
Age	-0.192	0.180	-0.544	0160	0.286
Time (afternoon)	-0.734	0.040	-0.812	-0.656	**<0.001**
Group (Mutamba)	-0.124	0.357	-0.824	0.575	0.728
Scan number	-0.000	0.000	-0.000	0.000	0.129
Model 4: Inactivity (GLMM: $\chi 2 = 1609.8$, df = 3, $p < 0.001$)					
Intercept	-0.254	0.241			
Phase Pre-treatment	1.206	0.043	1.121	1.290	**<0.001**
Phase Treatment (Enrichment)	-0.397	0.043	-0.482	-0.312	**<0.001**
Phase Post-treatment	-0.094	0.060	0.212	0.025	0.121
Sex (male)	-0.195	0.277	-0.738	0.347	0.480
Age	0.053	0.139	-0.220	0.325	0.704
Time (afternoon)	-0.446	0.035	-0.514	-0.378	**<0.001**
Group (Mutamba)	-0.158	0.276	-0.698	0.383	0.568
Scan number	-0.001	0.000	-0.001	-0.001	**<0.001**
Model 5: Abnormal behaviors (GLMM: $\chi 2 = 53.08$, df = 3, $p < 0.001$)					

Intercept	-6.253	0.749			
Phase Pre-treatment	-1.129	0.219	-1.559	-0.700	**<0.001**
Phase Treatment (Enrichment)	-0.950	0.163	-1.269	-0.631	**<0.001**
Phase Post-treatment	-0.209	0.302	-0.801	0.383	0.489
Sex (male)	1.399	0.905	-0.374	3.173	0.122
Age	0.265	0.432	-0.582	1.112	0.540
Time (afternoon)	1.380	0.153	1.080	1.679	**<0.001**
Group (Mutamba)	-2.780	0.914	-4.571	-0.989	**<0.001**
Scan number	0.002	0.000	0.001	0.003	**<0.001**
Model 6: Self-directed behaviors (GLMM: $\chi2 = 266.57$, df = 3, $p < 0.001$)					
Intercept	-2.585	0.426			
Phase Pre-treatment	-1.395	0.095	-1.582	-1.208	**<0.001**
Phase Treatment (Enrichment)	-0.244	0.064	-0.369	-0.119	**<0.001**
Phase Post-treatment	-0.362	0.110	-0.576	-0.147	**<0.001**
Sex (male)	0.227	0.491	-0.736	1.190	0.645
Age	-0.082	0.248	-0.568	0.405	0.743
Time (afternoon)	0.105	0.058	-0.009	0.219	0.072
Group (Mutamba)	-0.833	0.492	-1.798	0.132	0.091
Scan number	0.001	0.058	0.001	0.002	**<0.001**
Model 7: Social proximity (GLMM: $\chi2 = 1127.6$, df = 3, $p < 0.001$)					
Intercept	-2.770	0.330			
Phase Pre-treatment	1.610	0.063	1.486	1.73406	**<0.001**
Phase Treatment (Enrichment)	-0.154	0.070	-0.292	-0.016	**<0.05**
Phase Post-treatment	0.332	0.100	0.137	0.528	**<0.001**
Sex (male)	-0.887	0.377	-1.627	-0.148	**<0.05**
Age	-0.020	0.191	-0.395	0.354	0.915
Time (afternoon)	0.375	0.049	0.280	0.471	**<0.001**
Group (Mutamba)	0.415	0.379	-0.327	1.158	0.273
Scan number	0.001	0.000	0.001	0.001	**<0.001**
Model 8: Affiliative interactions (GLMM: $\chi2 = 100.42$, df = 3, $p < 0.001$)					
Intercept	-3.346	0.489			
Phase Pre-treatment	-0.474	0.074	-0.618	-0.330	**<0.001**
Phase Treatment (Enrichment)	0.071	0.057	-0.040	0.182	0.209
Phase Post-treatment	0.353	0.086	0.186	0.521	**<0.001**
Sex (male)	-1.155	0.570	-2.272	-0.038	**<0.05**
Age	-0.001	0.285	-0.559	0.557	1.000
Time (afternoon)	1.255	0.050	1.157	1.354	**<0.001**
Group (Mutamba)	1.830	0.570	0.712	2.947	**<0.05**
Scan number	0.001	0.000	0.000	0.001	**<0.001**
Model 9: Agonistic interactions (GLMM: $\chi2 = 9.765$, df = 3, $p < 0.05$)					
Intercept	-6.891	0.555			

Phase Pre-treatment	-0.224	0.312	-0.835	0.386	0.471
Phase Treatment (Enrichment)	0.543	0.241	0.071	1.016	**<0.05**
Phase Post-treatment	0.278	0.342	-0.392	0.949	0.416
Sex (male)	1.717	0.526	0.686	2.747	**<0.05**
Age	-0.334	0.231	-0.788	-0.079	0.149
Time (afternoon)	0.983	0.202	0.587	1.379	**<0.001**
Group (Mutamba)	-0.543	0.487	-1.500	0.412	0.265
Scan number	-0.001	0.001	-0.002	0.000	0.051
Model 10: SNA Proximity (GLMM: $\chi2$ = 2.38, df = 3, p = 0.498)					
Intercept	0.492	0.112			
Condition	0.052	0.102	-0.148	0.252	0.608
Group (Mutamba)	0.068	0.159	-0.243	0.379	0.668
Condition: Group (Mutamba)	0.079	0.144	-0.204	0.362	0.582

Table S5. Estimates, standard errors (SE) and *p*-values for post-hoc comparisons in Models 2-9. In all models, estimates are in logit-scale.

Models	**Estimate ± SE**	***P***
Model 2: Tool use		
Enrichment condition > Baseline condition	-4.13 ± 0.48, -8.74 ± 0.69	**< 0.001**
Enrichment condition > Pre-treatment phase	-25.80 ± 2883.63	1.000
Pre-treatment phase < Post-treatment phase		1.000
Model 3: Feeding		
Enrichment condition > Baseline condition	-0.99 ± 0.17, -1.41 ± 0.17	**< 0.001**
Enrichment condition > Pre-treatment phase	-2.20 ± 0.18	**< 0.001**
Pre-treatment phase < Post-treatment phase		**< 0.001**
Model 4: Inactivity		
Enrichment condition < Baseline condition	-1.28 ± 0.14, -0.88 ± 0.14	**< 0.001**
Enrichment condition < Pre-treatment phase	0.32 ± 0.14	**< 0.001**
Pre-treatment phase > Post-treatment phase		**< 0.001**
Model 5: Abnormal behaviors		
Enrichment condition < Baseline condition	-6.69 ± 0.49, -5.74 ± 0.47	**< 0.001**
Enrichment condition = Pre-treatment phase	-6.87 ± 0.50	0.880
Pre-treatment phase < Post-treatment phase		**< 0.05**
Model 6: Self-directed behaviors		
Enrichment condition < Baseline condition	-2.76 ± 0.24, -2.51 ± 0.24	**< 0.001**
Enrichment condition > Pre-treatment phase	-3.91 ± 0.25	**< 0.001**
Pre-treatment phase < Post-treatment phase		**< 0.001**
Model 7: Social proximity		
Enrichment condition = Baseline condition	-2.74 ± 0.19, -2.59 ± 0.19	0.125
Enrichment condition < Pre-treatment phase	-0.98 ± 0.18	**< 0.001**
Pre-treatment phase > Post-treatment phase		**< 0.001**
Model 8: Affiliative interactions		
Enrichment condition = Baseline condition	-2.11 ± 0.28, -2.18±0.28	0.591
Enrichment condition > Pre-treatment phase	-2.65±0.28	**< 0.001**
Pre-treatment phase < Post-treatment phase		**< 0.001**
Model 9: Agonistic interactions		
Enrichment condition = Baseline condition	-5.60± 0.29, -6.14 ± 0.32	0.109
Enrichment condition > Pre-treatment phase	-6.37 ± 0.35	**< 0.05**
Pre-treatment phase = Post-treatment phase		0.501

Table S6. Estimates, standard errors (SE), confidence intervals and *p*-values for Models 2b-9b. Reference category for sex is female, for time is morning and for group is Bilinga.

Models	Estimate	SE	CI (2.5%)	CI (97.5%)	*p*
Model 2b: Tool use (GLMM: $\chi2 = 196.36$, df = 3, $p < 0.001$)					
Intercept	-4.301	0.185			
Participation (binomial)	1.330	0.252	0.836	1.823	**<0.001**
Session number	-0.004	0.023	-0.048	0.041	0.874
Sex (male)	0.030	0.141	-0.246	0.307	0.829
Age	0.003	0.071	-0.142	0.137	0.971
Time (afternoon)	0.075	0.092	-0.107	0.256	0.419
Group (Mutamba)	0.073	0.142	-0.206	0.352	0.607
Participation(binomial)* Session number	0.172	0.042	0.089	0.255	**<0.001**
Model 3b: Feeding (GLMM: $\chi2 = 38.31$, df = 3, $p < 0.001$)					
Intercept	-0.438	0.284			
Participation	3.731	0.609	2.538	4.924	**<0.001**
Session number	-0.048	0.021	-0.089	-0.006	**<0.05**
Sex (male)	0.097	0.309	-0.509	0.703	0.753
Age	-0.180	0.155	-0.483	0.124	0.246
Time (afternoon)	0.989	0.097	-1.180	-0.799	**<0.001**
Group (Mutamba)	-0.367	0.310	-0.975	0.240	0.236
Model 4b: Inactivity (GLMM: $\chi2 = 12.14$, df = 3, $p < 0.05$)					
Intercept	-0.494	0.308			
Participation	-1.154	0.577	-2.285	-0.024	**<0.05**
Session number	-0.047	0.020	-0.086	-0.008	**<0.05**
Sex (male)	-0.329	0.344	-1.002	0.3446	0.339
Age	0.081	0.172	-0.256	0.417	0.639
Time (afternoon)	-0.578	0.091	-0.755	-0.400	**<0.001**
Group (Mutamba)	-0.105	0.344	-0.778	0.568	0.760
Model 5b: Abnormal behaviors (GLMM: $\chi2 = 2.49$, df = 3, $p = 0.477$)					
Intercept	-3.741	0.910			
Participation (binomial)	1.461	1.155	-0.803	3.725	0.206
Session number	-0.013	0.081	-0.172	0.145	0.870
Sex (male)	1.466	0.952	-0.400	3.332	0.124
Age	0.295	0.436	-0.560	1.149	0.499
Time (afternoon)	1.287	0.390	0.521	2.052	**<0.001**
Group (Mutamba)	-1.690	0.916	-3.485	0.106	0.065
Participation(binomial) *Session number	-0.326	0.235	-0.787	0.136	0.167
Model 6b: Self-directed behaviors (rubs and scratches) (GLMM: $\chi2 = 30.74$, df = 3, $p < 0.001$)					
Intercept	0.191	0.193			

Participation	0.318	0.491	-0.644	1.280	0.517
Session number	-0.102	0.019	-0.139	-0.066	**<0.001**
Sex (male)	-0.183	0.201	-0.577	0.212	0.364
Age	0.120	0.101	-0.078	0.317	0.235
Time (afternoon)	0.381	0.084	0.216	0.545	**<0.001**
Group (Mutamba)	0.349	0.201	-0.743	0.046	0.083
Model 7b: Social proximity (GLMM: $\chi2 = 9.96$, df = 3, $p < 0.05$)					
Intercept	-2.736	0.187			
Participation	1.540	0.532	0.497	2.583	**<0.05**
Session number	0.023	0.021	-0.018	0.064	0.271
Sex (male)	-0.375	0.163	-0.694	-0.056	**<0.05**
Age	-0.012	0.082	-0.173	0.148	0.880
Time (afternoon)	0.237	0.095	0.050	0.424	**<0.05**
Group (Mutamba)	0.427	0.163	0.107	0.747	**<0.05**
Model 8b: Affiliative interactions (GLMM: $\chi2 = 0.95$, df = 3, $p = 0.814$)					
Intercept	-2.295	0.223			
Participation	1.007	2.148	-5.216	3.202	0.639
Session number	0.004	0.023	-0.041	0.049	0.853
Sex (male)	-0.429	0.206	-0.832	-0.026	**<0.05**
Age	0.036	0.104	-0.167	0.239	0.730
Time (afternoon)	0.592	0.106	0.385	0.780	**<0.001**
Group (Mutamba)	1.033	0.209	0.624	1.442	**<0.001**
Participation*Session number	0.069	0.326	-0.569	0.707	0.832
Model 9b: Agonistic interactions (GLMM: $\chi2 = 6.37$, df = 3, $p = 0.095$)					
Intercept	-3.729	0.815			
Participation (binomial)	-0.758	1.521	3.739	2.223	0.618
Session number	-0.201	0.084	-0.365	-0.037	**<0.05**
Sex (male)	2.094	0.749	0.627	3.561	**<0.05**
Age	-0.231	0.294	-0.808	0.346	0.433
Time (afternoon)	1.147	0.398	0.367	1.926	**<0.05**
Group (Mutamba)	-0.359	0.639	-1.612	0.894	0.575
Participation(binomial)* Session number	0.134	0.277	-0.409	0.676	0.630

Article 2. Cognitive enrichment in a social setting: assessing the use of a novel food maze in sanctuary-housed chimpanzees

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Photograph by Miquel Llorente

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ORIGINAL ARTICLE

Cognitive enrichment in a social setting: assessing the use of a novel food maze in sanctuary-housed chimpanzees

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Abstract

Foraging devices are effective enrichment tools for non-human primates, as they provide both cognitive and manipulative stimulation that may enhance these animals' welfare. We assessed the behavioral effects of a novel tool-based enrichment on 14 chimpanzees (*Pan troglodytes*) housed at Fundació Mona (Girona, Spain). The device consisted of a vertical maze filled with food rewards, which chimpanzees could extract by using tools. We conducted behavioral observations in two conditions over an approximately 2.5-month period: when the food maze was loaded (12 enrichment days), and when it was empty (12 baseline days). Data were collected using 2-min scan sampling and untimed-event focal sampling during two daily sessions of 80 min each. We expected that the chimpanzees' interest in the enrichment would decrease over time, but that its use would be linked to an increase in the occurrence of species-typical behaviors, a reduction in negative indicators of welfare, and changes in social behaviors. We found that participation widely varied among subjects, being higher in females and decreasing through time. Furthermore, participation was linked to an increase in tool use and a decrease in inactivity, but also to an increase in aggression-related behaviors. In contrast, participation had no effect on the occurrence of abnormal behaviors, social proximity or affiliation-related behaviors. Finally, we detected an increase in self-directed behaviors only when subjects actively interacted with the device. We conclude that, in future studies, these types of devices should be evaluated for longer periods of time and more attention should be paid to individuals' preferences and abilities.

Keywords Behavior · Chimpanzees · Cognitive enrichment · Tool use · Welfare

Introduction

Behavioral diversity and species-typical behaviors, also referred to as "ethological needs," are key concepts related to animal welfare (Browning 2019; Hughes and Duncan 1988; Miller et al. 2020). However, captive settings often lack sufficient complexity to allow the expression of a species-typical behavioral repertoire (Mallapur 2008; Newberry 1995; Young 2003). For this reason, environmental enrichment has become a key component of the management of captive animals (Maple and Perdue 2013), as it is considered an important means of improving animal welfare by providing opportunities for physical, affective and cognitive stimulation (Fernández and Martin 2021; Hoy et al. 2010; Mellor 2015). The extensive variety of enrichment strategies used in non-human primates includes sensory stimulation (Carter et al. 2021; Vaglio et al. 2021), social housing (Chipangura et al. 2020), motor or manipulative engagement (Costa et al. 2018), and more recently, cognitive stimulation (Coleman and Novak 2017; Dutton et al. 2018; Lutz and Novak 2005),

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which also includes the use of digital electronic devices (Clark 2017; Clark et al. 2019; Gray et al. 2018; Grunauer and Walguarnery 2018; Kim-McCormack et al. 2016). In fact, cognitive enrichment has become increasingly popular in zoos, sanctuaries and even farms, where problem-solving opportunities can enhance animal welfare (Clark 2017; Meehan and Mench 2007). Cognitive enrichment can be defined as an enrichment which "(1) engages evolved cognitive skills by providing opportunities to solve problems and control some aspect of the environment, and (2) is correlated to one or more validated measures of well-being" (Clark 2011, p. 6).

Cognitively stimulating environments may be particularly important for captive non-human primates, and more specifically for great apes due to their behavioral, affective and cognitive complexity (Clark 2011). In the wild, great apes continuously face complex ecological and social problems that require complex perception, understanding and decision-making skills (Morimura 2006), so that psychological challenges are likely inherent in their nature. This could explain why chimpanzees, for example, reportedly engage in problem-solving activities even when no reward is involved (Clark and Smith 2013). Furthermore, great apes often explore novel objects (Paquette and Prescott 1988), possess highly developed manipulative skills (Paquette and Prescott 1988; Torigoe 1985), and use and create tools in captive environments (Motes-Rodrigo and Tennie 2021). Therefore, the introduction of novel devices or tasks promoting such behaviors may be a particularly successful enrichment strategy for these species.

Furthermore, non-human primates spend considerable amounts of time foraging for and eating food in the wild, e.g., in chimpanzees, up to 18.8–60% of their time (Boesch and Boesch-Achermann 2000; Doran 1997; Inoue and Shimada 2020; Pruetz and McGrew 2001; Yamanashi and Hayashi 2011). However, captive animals are usually provided with food directly, in ways that require minimal effort. Thus, captive chimpanzees typically spend less time foraging than their wild counterparts (Inoue and Shimada 2020; Yamanashi and Hayashi 2011), and this may be linked to reduced behavioral expression and competence, and heightened negative emotional states (Špinka and Wemelsfelder 2011). For these reasons, enrichment activities were employed in several studies with the focus on increasing opportunities for foraging (Baker 1997; Bloomsmith et al. 1988; Maki et al. 1989; Reinhardt 1993), and included food hidden inside boxes, pipes, tubes or balls (Brooks et al. 2021; Gronqvist et al. 2013; Nash et al. 2021) that could only be extracted by manipulating the objects in a specific manner (e.g., poking, shaking, rotating). The sophistication of a device can be altered to vary the complexity of the problem-solving skills required, but it should provide both manipulative and cognitive stimulation to non-human primates (Dutton et al. 2018), who usually show an interest in food-associated enrichments and motivation to solve puzzles for food rewards (Cheyne 2009; de Rosa et al. 2003; Shohat et al. 2019), even when highly valued foods are not used (Brooks et al. 2021). Furthermore, as foraging devices make food more difficult to obtain, primates spend more time on these activities and less time inactive or engaged in abnormal behaviors (Brent and Eichberg 1991). Similarly, these types of enrichment can increase the general activity of the group over longer periods, even if only a few individuals actively manipulate the devices (Csatádi et al. 2008; Jones and Pillay 2004). Most food-based enrichments for great apes involve toys or objects like boxes, pipes, tubes or balls (Bloomsmith et al. 1990, 1991; Brent and Stone 1998; Lambeth and Bloomsmith 1994; Pruetz and Bloomsmith 1992), i.e., relatively unsophisticated devices, partly because of time constraints (e.g., time to design or manufacture the devices) and limited finances (Hall et al. 2021).

Several studies have employed foraging devices that require tool use in captive great apes, particularly chimpanzees (Celli et al. 2004, 2003; Clark and Smith 2013; Llorente and Campi 2014; Maki et al. 1989; Morimura 2003; Nash 1982; Padrell et al. 2021; Yamanashi et al. 2016; Zaragoza et al. 2011). These devices often simulate behaviors such as termite-fishing, ant-dipping or ant-fishing, which are commonly observed in the wild (Boesch and Boesch 1990; Goodall 1986; Jones and Sabater Pi 1969). In general, these activities enhance chimpanzee welfare by increasing species-typical behaviors and decreasing abnormal behaviors and other negative indicators of welfare. Moreover, these tool-use tasks can provide data on learning (Hirata and Celli 2003; Hirata and Morimura 2000; Paquette 1992), tool modification (Hopper et al. 2015), cognitive flexibility (Hopkins et al. 2014), physical reasoning (Brooks et al. 2021) and problem solving (Seed et al. 2009), or other characteristics such as manual laterality (McGrew and Marchant 1992; Sanz et al. 2016) and dexterity (Bardo et al. 2017; Osuna-Mascaró et al. 2021). It seems likely that enrichment devices that promote tool use will provide more cognitive stimulation than those that do not require tools. In fact, tool use, and more specifically flexible tool use (i.e., the ability to adapt to new situations through innovative solutions), is considered a complex activity that involves motivational, cognitive (i.e., information seeking and recombination) and sensorimotor aspects (i.e., manipulative propensity and specific manipulative skills) (Call 2013; Hunt et al. 2013).

Enrichment activities provided in a social setting might affect social dynamics within the group (Clark 2017), for example, by influencing affiliative or agonistic interactions. However, the few studies that have examined this have reported contradictory results, possibly due to methodological differences. For example, competition for access to the enrichment device may lead to aggression

(Maki et al. 1989; Sha et al. 2012), although this is less likely if various subjects can simultaneously access the device (Brent and Eichberg 1991; Yamanashi et al. 2016). Similarly, affiliative interactions may also be positively or negatively affected by an enrichment (Brent and Eichberg 1991; Clark and Smith 2013; Sha et al. 2012), or not affected at all (Yamanashi et al. 2016).

Other aspects that should be considered when implementing a new enrichment procedure include subjects' participation (i.e., engagement with the device, or proportion of time interacting with it) (Dutton et al. 2018; Lutz and Novak 2005; Schapiro and Lambeth 2007), as particularly in a social setting this might be affected by factors such as rank, personality, sex or age (Celli et al. 2003; Hopper et al. 2014). For instance, dominant chimpanzees may monopolize enrichment devices (Bloomstrand et al. 1986; Celli et al. 2003; Honess and Marin 2006; Paquette and Prescott 1988), which could negatively affect the acquisition of new tool-use behaviors by low-ranking individuals (Paquette 1992). Another important aspect is the level of difficulty of the task, which must be sufficiently stimulating to motivate the animals, yet solvable enough to avoid frustration (Meehan and Mench 2007). Currently there is no consensus on how to evaluate the level of cognitive stimulation and therefore the effectiveness of a particular cognitive enrichment (Clark 2017). Moreover, non-human primates can quickly become habituated to novel devices or tasks (Clark 2011; Vick et al. 2000), leading to the reduced effectiveness of enrichment activities over time (Tarou and Bashaw 2007). However, the effects of the enrichment may widely vary across subjects (Coleman and Novak 2017; Costa et al. 2018; Izzo et al. 2011). For example, Clark and Smith (2013) found that two out of six chimpanzees barely touched an enrichment device, whereas the others frequently interacted with it. Such variation highlights the importance of a more individual approach when evaluating the outcomes of a particular enrichment. This might include assessing subjects' emotional states when interacting with an enrichment device, by measuring the occurrence of self-directed behaviors (e.g., scratching, touching or rubbing their body or face), which are reliable indicators of negative emotional states (i.e., stress or anxiety) in non-human primates (Baker and Aureli 1997; Maestripieri et al. 1992). Several studies have shown increases in self-directed behaviors in great apes faced with novel or more difficult tasks (Elder and Menzel 2001; Itakura 1993; Leavens et al. 2004, 2001; Meyer and Hamel 2014) or in response to errors (Leeds and Lukas 2018; Wagner et al. 2016; Yamanashi and Matsuzawa 2010). Furthermore, reported increases in self-directed behaviors in response to changes in non-human primates' environments (Bonnie et al. 2016; Lukas et al. 2003) suggest that the simple presence of enrichment devices may also lead to such increases.

We evaluated the effects of a novel cognitive enrichment that requires tool use on solitary and social behaviors in two groups of sanctuary-housed chimpanzees. We hypothesized that the enrichment device would overall have a positive effect on the chimpanzees' welfare by promoting species-typical behaviors and reducing negative ones, while also affecting social interactions. In particular, we predicted that the chimpanzees' interest in the device (i.e., participation) would decrease across enrichment sessions (prediction 1), but that greater participation would be linked to an increase in tool use (prediction 2) and a reduction in negative indicators of welfare, such as abnormal behaviors (prediction 3) and inactivity (prediction 4). Moreover, we predicted that participation would increase social proximity (as the device could be used by more than one chimpanzee at a time; prediction 5), decrease affiliative behaviors (as chimpanzees would spend more time interacting with the enrichment and less time in grooming, social play or sexual behavior; prediction 6), and increase aggression-related behaviors (due to possible competition for the enrichment device; prediction 7). Finally, considering that our subjects had no previous experience with the enrichment device and the complexity of the task, we expected an increase in the occurrence of self-directed behaviors during engagement with the device, but not when simply in its presence (prediction 8).

Materials and methods

Subjects and study site

The study subjects were 14 adult chimpanzees (*Pan troglodytes*) living in two mixed-sex groups, each comprising seven individuals (Mutamba and Bilinga). The Mutamba group was composed of two females and five males, aged between 15 and 35 years (mean ± SD = 24.4 ± 8.2 years), and the Bilinga group was composed of three females and four males, aged between 17 and 36 years (mean ± SD = 29.1 ± 6.7 years). Both groups were housed at Fundació Mona, a center in Girona, Spain, dedicated to the rescue and rehabilitation of non-human primates that had been used as pets or in the entertainment industry. The chimpanzees spent their daytime hours in a 5640-m^2 outdoor enclosure, divided into two areas (2420 m^2 and 3220 m^2), both containing natural vegetation and wooden platforms, towers, and ropes. Two observation huts around the perimeter allowed behavioral observation of both groups. The chimpanzees also had 140 m^2 of indoor facilities where they spent the nights, but access to these was usually restricted during the daytime.

Task description and experimental procedure

The enrichment device was a double-sided maze consisting of a rectangular steel structure (approximately 1 × 0.5 m) with frontal transparent plastic panels and wooden shelves with holes at the ends (Fig. 1a). The maze could be filled with preferred food items (dried fruits and nuts), which the chimpanzees had to extract by using sticks or branches obtained from the natural vegetation in the outside enclosures (see Online Resource 1). No additional tools or materials were provided, but to facilitate learning and maintain the chimpanzees' motivation, we randomly distributed food rewards on all the shelves of the device (rather than only on the upper shelf). Before filling the maze, the rewards were weighed and approximately the same quantity of food was removed from the chimpanzees' midday snack to ensure a consistent daily caloric intake. Unlike similar food puzzles described in other studies, the device was double-sided, with two identical, independent mazes within the same structure, separated by an opaque middle panel (see Online Resource 1). Therefore, two chimpanzees could interact with the device at the same time, one on each side of the device (see Fig. 1b).

Each group of chimpanzees had one maze in the enclosure. The mazes were designed for this study, and were unfamiliar to the chimpanzees. Data collection started 1 week after the mazes were first installed in the enclosures, so that the chimpanzees could habituate to them. Then, for each group, we conducted behavioral observations on 24 randomly distributed days over a 2- to 3-month period (Mutamba group, 18 April–19 June 2019; Bilinga group, 17 June–12 September 2019): 12 enrichment days (with the loaded food maze), and 12 baseline days (with the empty maze). The mazes were filled in the morning, before the chimpanzees went into the outdoor enclosures, and were available to the chimpanzees throughout the daytime (approximately from 10.30 a.m to 6.00 p.m). No additional enrichment devices were provided on baseline and enrichment days, but during the rest of the study period other enrichments were sometimes provided in line with the usual routines of the center (e.g., bottles of juice, baited fabrics, hoses filled with food).

Behavioral observations

On baseline and enrichment days we collected behavioral data for a total of 2 h 40 min/day, divided into two 80-min sessions, one in the morning during the period from 10.30 a.m to 2.00 p.m, and one in the afternoon during the period from 3.00 p.m to 6.00 p.m. We expected the chimpanzees to use the maze more frequently in the morning, when it became available. Given the novelty and complexity of the task, however, we also expected that some rewards would not be extracted right away, and so we also collected data in the afternoon. No observations were conducted around midday, as this was the chimpanzees' feeding time and usually corresponded to very low activity levels in the group.

We collected data using instantaneous scan sampling (every 2 min) and untimed-event focal sampling (10 min per subject) (Bakeman and Quera 2011). Scan sampling allowed us to record mid- to long-duration behaviors including (1) engagement with the enrichment, (2) tool use, (3) abnormal behaviors, (4) inactivity, (5) social proximity, (6) affiliation-related behaviors, (7) aggression-related behaviors. Descriptions of the behaviors can be found in Table 1. As some behaviors were not mutually exclusive, in each scan sample interval a chimpanzee could exhibit more than one behavior at the same time (see details in Table 1). Total scan sampling observation time was 128 h, equally distributed between conditions and groups, i.e., 960 scans per condition and group. The untimed-event focal sampling focused on rare or short-duration behaviors (e.g., self-directed behaviors). Based on the definitions in the literature (Leavens et al. 2001; Schino et al. 1996; Yamanashi and Matsuzawa 2010), self-directed behaviors included rubbing and scratching directed towards the face and body (see detailed definition in Table 1), as these have been consistently linked to stress or anxiety, but we excluded self-grooming because it may not always be a good proxy for stress (Meyer and Hamel 2014). Following previous studies (Hopkins et al. 2006;

Fig. 1 Frontal view of the double-sided food maze used in this study (**a**). Chimpanzees using tools to extract the food rewards from the maze (**b**). Photo credits: Miquel Llorente

Table 1 Behavioral catalogue

Behavioral category	Definition
1. Participation	The chimpanzee is actively interacting with or in contact with the food maze while exploring it with the hands, feet or mouth
2. Tool use[a]	The chimpanzee uses a mobile element, external to the body (the tool), to perform a goal-oriented action on another element that modifies its physical properties. It includes tool modification and tool transportation
3. Abnormal behaviors	The chimpanzee displays maladjusted stereotypical behaviors such as rocking, pacing, self–harm, coprophagy (eating feces), regurgitation, re-ingestion, trichotillomania (hair-pulling), trichotillophagia (hair-pulling and eating hair), ear-poking, eye-poking
4. Inactivity	The chimpanzee does not perform any action or activity other than sitting or lying down. It includes self-inspection, yawning, and sleeping
5. Social proximity[b]	The chimpanzee is at less than one-arm's length from one or more subjects while performing a solitary activity, with no social interaction between subjects
6. Affiliation-related behaviors	The chimpanzee exhibits one of the following behaviors: (1) grooming—body-cleansing of one individual by another (includes mutual grooming), performed using the fingers or the mouth; (2) social play—playful behavior between two or more individuals associated with behavioral indicators of play (e.g., play face, laughter, friendly head bobbing, softly knocking on the ground, playful chasing); (3) sexual behavior—sexual interaction, or search for sexual interaction, between two individuals, including behaviors such as copulation, attempted copulation, genital presentation and other behaviors directed towards the genitals of another individual; (4) other behaviors identified as affiliative, but not fitting the criteria of grooming, social play or sexual activity (e.g., embracing, co-feeding, following)
7. Aggression-related behaviors	The chimpanzee exhibits one of the following behaviors: (1) agonistic dominance—threat-related behaviors such as direct aggression, charging display, displacement and resource appropriation (e.g., stealing food or objects) (the behavior may be accompanied by vocalizations); (2) agonistic submission—avoidance, teeth baring, display, food submission (e.g., leaving/dropping food and moving away when others try to steal it), hand-to-mouth, finger-to-mouth (the behavior may be accompanied by vocalizations such as panting/grunting, and includes running away from others in conflict situations); (3) other behaviors occurring in agonistic contexts, but not fitting the criteria of agonistic dominance or agonistic submission (e.g., appeasement, consolation, reconciliation, and requesting support)
8. Self-directed behaviors	The chimpanzee displays one of the following behaviors: (1) scratching—continuous movement of the hand over the skin involving the ends of the digits or nails; (2) rubbing—continuous movement of the hand over the skin not involving the ends of the digits, performed either with the palmar, dorsal or lateral side of the hand [this category also includes self-touching such as nose wiping (Yamanashi and Matsuzawa 2010) or face stroking (Itakura 1993)]
Not visible/not present	The chimpanzee or the behavior cannot be identified, or the chimpanzee is not in the outdoor enclosure (e.g., he/she is in the sleeping area or in an outdoor cage)

Note: data on all behaviors were collected using 2-min instantaneous scan sampling, except for those on self-directed behaviors, which were collected using untimed-event focal sampling

[a] Tool use could occur simultaneously with participation

[b] Social proximity and solitary behaviors (behaviors 1–4) were also not mutually exclusive (i.e., individuals could be in social proximity while simultaneously engaging in one of these behaviors)

Wagner et al. 2016), the incidence of self-directed behaviors was measured as the number of bouts. A bout ended when (1) it stopped for 3 s or more, (2) limb to body contact ceased, or (3) the body target changed. Focal observations were conducted in a pseudo-randomized order, the aim of which was to observe each chimpanzee for at least 10 min in the morning and in the afternoon on each day. If no data were collected because a chimpanzee was not present in the outdoor enclosures during an observation session, we conducted an additional 10-min observation in a later session. Due to observer absence, for one chimpanzee group we conducted focal observations on only 10 of the 12 baseline days; therefore, we randomly selected 10 data collection days for each condition and group for the analysis of self-directed behaviors. Therefore, each chimpanzee was observed for a total of 3.3 h (200 min) in each condition (baseline and enrichment).

To further investigate the effect of the food maze on self-directed behaviors, we videotaped every enrichment session and later coded the data for self-directed behaviors when chimpanzees interacted with the task. For consistency in observation time for baseline and enrichment sessions (with no task interaction), we coded data for approximately 20 min/day per subject when they were interacting with the enrichment (i.e., 10 min in the morning and 10 min in the afternoon). If the duration of subject participation was less than 10 min, we repeated the observation when the chimpanzee resumed participation, and so on until we reached a total observation time of 10 min. To maximize the amount of data on self-directed behaviors while manipulating the enrichment, we videotaped for an additional 30 min per session, and used the video recordings of all 12 enrichment sessions. However, it was not possible to reach 3.3 h of total observation time per subject as in the baseline and enrichment conditions (with no task interaction), as most chimpanzees interacted with the food maze for less time over the whole study period.

Inter-observer reliability

Observations were conducted by several researchers, who had completed a period of training and had to pass an inter-observer reliability test (agreement between observers ≥ 85%) before collecting data. All the data were collected using ZooMonitor (Ross et al. 2016), an application which facilitates the recording and analysis of animal behavior (Wark et al. 2019).

Data analysis

To investigate chimpanzee use of the enrichment device over time and assess the effect of participation on behavior, we ran eight different generalized linear mixed models (GLMM) (Baayen 2008) using the glmmTMB package (Brooks et al. 2017) in R. Model 1 assessed whether participation during enrichment (i.e., the number of scans involving interaction with the device in an enrichment session out of all the scans for that individual) varied across time, and whether individual characteristics—such as sex and age—predicted participation. In this model, we entered one line per individual and session (only including enrichment sessions), with session number, sex, age and time of the day (morning vs. afternoon) as test predictors. We further included group as the control and subject identity as a random effect, using a beta distribution.

We then assessed whether participation (operationalized as in model 1) predicted the occurrence of Tool use (model 2), Abnormal behaviors (model 3), Inactivity (model 4), Social proximity (model 5), Affiliation-related (model 6) and Aggression-related behaviors (model 7), and whether the effects varied across sessions (models 2–7). In all these models we included one line per subject and session. The dependent variables (i.e., the behaviors given above) were operationalized as the number of scans in which the subject performed the behavior divided by the total number of scans in which the subject was visible. Being proportions, these variables were modeled with a beta distribution. Then, we entered as test predictors the two-way interactions between participation and session number, and their main effects. If we detected overdispersion (models 3 and 7), we re-ran the models after transforming response and participation into binomial variables using a binomial distribution. No overdispersion was detected in the models presented below. Finally, model 8 assessed whether Self-directed behaviors were affected by the enrichment. In this model, we also included one line per subject and session, and we operationalized the dependent variable (i.e., self-directed behaviors) as the total number of bouts performed in the time the subject was visible. This variable was a count and, to avoid overdispersion, it was modeled with a negative binomial distribution, adding observation time as an offset in the model. In model 8, the test predictors were the two-way interactions (and their main effects) between session number and the categorical predictor Condition (i.e., whether the observation was conducted during the Baseline, when the enrichment was not present; during the Enrichment No Interaction, when the enrichment was present but the subject was not interacting with it; or during the Enrichment Interaction, when the enrichment was present and the subject was manipulating it). In models 2–8, we entered sex, age, group and time of the day (morning, evening) as control predictors, with subject identity included as a random effect.

In all of the models, age was *z*-transformed to facilitate model convergence. To compare full models containing all predictors with null models containing only controls and random factors, we used a likelihood ratio test (function anova) (Dobson 2002) and a significance level of 0.05. If the full model significantly differed from the null model, we obtained the *p*-values for each test predictor via single-term deletion using the R function drop1 (Barr et al. 2013). If the two-way interactions (which always included their main effects) were not significant, we downgraded them and re-ran the models including only main effects. In the case of significant categorical predictors with more than two levels (model 8), we used Tukey tests in the emmeans package (Lenth 2020) to compare the different levels. To rule out collinearity, we calculated variance inflation factors (Field 2009), which were very low for all of the models (maximum variance inflation factors across all models = 1.34).

Results

Participation in the enrichment varied widely across individuals (mean ± SD = 8.92 ± 15.27% scans, range = 0.22–53.52%), with all the chimpanzees interacting with the device, but some only very briefly (< 1% of scans). One female (Africa; Mutamba group) was particularly interested in the maze, and spent more than 50% of scans engaged with it in the enrichment condition. Two other females (Coco, Bilinga group; Waty, Mutamba group), also spent a high proportion of scans interacting with the device (around 30% and 15%, respectively). Only two of these three females (Africa and Coco) mastered the task, reliably retrieving the rewards from the maze. The other chimpanzees interacted with the maze, usually with tools, but they did not succeed in moving the rewards across the different shelves of the maze. Tables S1 and S2 show individual and mean values of participation and the incidence of other behaviors in the baseline and enrichment conditions. Tables 2 and 3 show a summary of the predictions and results for models 1–8.

Participation (model 1)

For model 1, the full model significantly differed from the null model (GLMM, $\chi^2 = 44.41$, $df = 4$, $p < 0.001$). Participation decreased across sessions ($p < 0.05$) (Fig. 2), and was higher in the morning than in the afternoon ($p < 0.001$). Females participated significantly more than males ($p < 0.05$), but age did not significantly predict participation.

Solitary and social behaviors (models 2–9)

For model 2 (tool use), the full–null model comparison was significant (GLMM, $\chi^2 = 87.05$, $df = 3$, $p < 0.001$), revealing that participation in the enrichment increased tool use ($p < 0.001$), with no differences across sessions (Fig. 3). For model 3 (abnormal behaviors), the full–null model comparison was not significant (GLMM, $\chi^2 = 2.56$, $df = 3$, $p = 0.464$), whereas for model 4 (inactivity), the full model significantly differed from the null model (GLMM, $\chi^2 = 35.93$, $df = 3$, $p < 0.001$), revealing that participation in the enrichment was linked to a decrease in inactivity ($p < 0.001$), with no differences across sessions (Fig. 4). For model 5 (social proximity), the full–null model comparison was significant (GLMM, $\chi^2 = 7.99$, $df = 3$, $p < 0.05$), but participation had no effect on social proximity ($p = 0.278$), which decreased across sessions ($p = 0.010$). For model 6 (affiliation-related behaviors), the full–null model comparison was not significant (GLMM, $\chi^2 = 2.01$, $df = 3$, $p = 0.569$), whereas for model 7 (aggression-related behaviors) the full model significantly differed from the null model (GLMM, $\chi^2 = 11.72$, $df = 3$, $p < 0.05$), showing that only individuals participating in the enrichment increased aggression-related behaviors across sessions ($p < 0.05$) (Fig. 5).

Self-directed behaviors (model 8)

For model 8, the full–null model comparison was significant (GLMM, $\chi^2 = 80.23$, $df = 5$, $p < 0.001$), revealing a significant increase in self-directed behaviors when chimpanzees interacted with the enrichment as compared to when they did not (i.e., in the baseline condition and in the enrichment condition without task interaction, both $p < 0.001$).

Discussion

The aim of this study was to assess the effects of a novel tool-based cognitive feeding enrichment on solitary and social behaviors of sanctuary-housed chimpanzees. We found that engagement with the enrichment decreased across sessions, strongly varied across subjects and was higher in females. As expected, participation was linked to an increase in tool use, a decrease in inactivity, and an increase in agonistic behaviors. However, in contrast to our predictions, participation had no effect on abnormal behaviors, social proximity or affiliative behaviors. Finally, we detected increased self-directed behaviors when subjects interacted

Table 2 Summary of predictions and results for models 1–8

Predictions	Supported?	Model
1. Participation in the enrichment—		1
Remains constant across sessions	No	
Is affected by sex	Yes	
Is affected by age	No	
Is affected by: time (morning/afternoon)	Yes	
Participation in the enrichment predicts a consistent—		
2. Increase in tool use	Yes	2
3. Decrease in abnormal behaviors	No	3
4. Decrease in inactivity	Yes	4
5. Increase in social proximity	No	5
6. Decrease in affiliation-related behaviors	No	6
7. Increase in aggression-related behaviors	Yes[a]	7
8. Interaction with the enrichment predicts an increase in the rate of self-directed behaviors compared to the baseline and enrichment conditions	Yes	8

[a] In model 7, participation predicted an increase in aggression-related behaviors over time (i.e., across sessions)

Table 3 Estimates, SE, confidence intervals (*CI*), likelihood ratio tests (*LRT*), *df* and *p*-values for all variables in models 1–8 (the reference category is given *in parentheses*)

Models	Estimate	SE	CI (2.5%)	CI (97.5%)	LRT	*df*	*p*
Model 1: Participation							
Intercept	− 1.60	0.32	–	–	–	–	–
Session number	− 0.04	0.02	− 0.07	− 0.01	5.395	1	*0.020*
Sex (male)	− 1.05	0.35	− 1.74	− 0.36	6.873	1	*0.006*
Age	− 0.24	0.18	− 0.59	0.10	1.758	1	0.185
Time (afternoon)	− 0.67	0.12	− 0.90	− 0.44	32.251	1	*< 0.001*
Group (Mutamba)[a]	0.50	0.35	− 0.19	1.19	1.898	1	0.168
Model 2: Tool use							
Intercept	− 2.81	0.18	–	–	–	–	–
Participation	1.05	0.10	0.85	1.25	84.129	1	*< 0.001*
Session number	− 0.01	0.01	− 0.03	0.01	1.060	1	0.303
Sex (male)[a]	− 0.41	0.17	− 0.73	− 0.08	4.994	1	*0.025*
Age[a]	− 0.07	0.08	− 0.24	0.09	0.732	1	0.392
Time (afternoon)[a]	− 0.14	0.08	− 0.29	0.02	2.969	1	0.085
Group (Mutamba)[a]	− 0.05	0.17	− 0.38	0.28	0.089	1	0.765
Model 3: Abnormal behaviors							
Intercept	− 2.75	0.87	–	–	–	–	–
Participation	− 0.77	0.78	− 2.31	0.76	–	–	–
Session number	− 0.03	0.04	− 0.12	0.05	–	–	–
Sex (male)[a]	− 0.05	0.95	− 1.92	1.82	0.003	1	0.958
Age[a]	0.15	0.50	− 0.83	1.13	0.090	1	0.764
Time (afternoon)[a]	0.52	0.29	− 0.05	1.08	3.286	1	0.072
Group (Mutamba)[a]	− 0.14	0.97	− 2.05	1.77	0.0215	1	0.883
Participation × session number	0.03	0.11	− 0.19	0.25	0.0697	1	0.792
Model 4: Inactivity							
Intercept	0.13	0.28	–	–	–	–	–
Participation	− 1.98	0.35	− 2.67	− 1.29	34.092	1	*< 0.001*
Session number	0.01	0.01	− 0.01	0.04	1.140	1	0.286
Sex (male)[a]	− 0.21	0.31	− 0.82	0.40	0.439	1	0.508
Age[a]	0.11	0.16	− 0.19	0.42	0.521	1	0.471
Time (afternoon)[a]	− 0.44	0.08	− 0.61	− 0.28	27.179	1	*< 0.001*
Group (Mutamba)[a]	− 0.50	0.31	− 1.11	0.11	2.364	1	0.124
Model 5: Social proximity							
Intercept	− 1.53	0.19	–	–	–	–	–
Participation	− 0.34	0.32	− 0.97	0.28	1.176	1	0.278
Session number	− 0.03	0.01	− 0.05	− 0.01	6.569	1	*0.010*
Sex (male)[a]	− 0.62	0.19	− 1.00	− 0.24	7.780	1	*0.005*
Age[a]	0.01	0.10	− 0.17	0.20	0.024	1	0.878
Time (afternoon)[a]	− 0.48	0.08	− 0.64	− 0.32	33.761	1	*< 0.001*
Group (Mutamba)[a]	− 0.06	0.19	− 0.43	0.32	0.091	1	0.763
Model 6: Affiliation-related behaviors							
Intercept	− 2.31	0.18	–	–	–	–	–
Participation	− 0.47	0.61	− 1.67	0.72	–	–	–
Session number	0.00	0.01	− 0.02	0.03	–	–	–
Sex (male)[a]	− 0.48	0.16	− 0.79	− 0.17	6.967	1	*0.008*
Age[a]	0.04	0.08	− 0.11	0.20	0.319	1	0.572
Time (afternoon)[a]	0.24	0.08	0.08	0.41	8.347	1	*0.004*
Group (Mutamba)[a]	0.39	0.16	0.08	0.70	4.970	1	*0.026*
Participation × session number	0.01	0.08	− 0.15	0.17	0.008	1	0.928
Model 7: Aggression-related behaviors							
Intercept	− 4.33	0.77	–	–	–	–	–

Table 3 (continued)

Models	Estimate	SE	CI (2.5%)	CI (97.5%)	LRT	*df*	*p*
Participation	– 1.93	0.87	– 3.64	– 0.22	–	–	–
Session number	– 0.14	0.05	– 0.24	– 0.05	–	–	–
Sex (male)[a]	2.22	0.67	0.90	3.54	9.534	1	*0.002*
Age[a]	– 0.37	0.25	– 0.87	0.13	1.922	1	0.166
Time (afternoon)[a]	0.69	0.30	0.10	1.28	5.369	1	*0.020*
Group (Mutamba)[a]	1.07	0.56	– 0.03	2.17	3.576	1	0.059
Participation × session number	0.29	0.12	0.06	0.52	5.890	1	*0.015*
Model 8: Self-directed behaviors							
Intercept	0.56	0.17	–	–	–	–	–
Condition (Baseline)	– 0.70	0.10	– 0.89	– 0.51	75.138	1	< *0.001*
Condition (Enrichment no interaction)	– 0.85	0.10	– 1.04	– 0.65			
Session number	– 0.02	0.01	– 0.04	0.00	2.460	1	0.117
Sex (male)[a]	0.20	0.16	– 0.12	0.53	1.462	1	0.227
Age[a]	0.08	0.08	– 0.08	0.24	1.031	1	0.310
Time (afternoon)[a]	– 0.20	0.07	– 0.33	– 0.06	7.678	1	*0.006*
Group (Mutamba)[a]	– 0.42	0.16	– 0.74	– 0.10	5.359	1	*0.021*

[a] Control variables

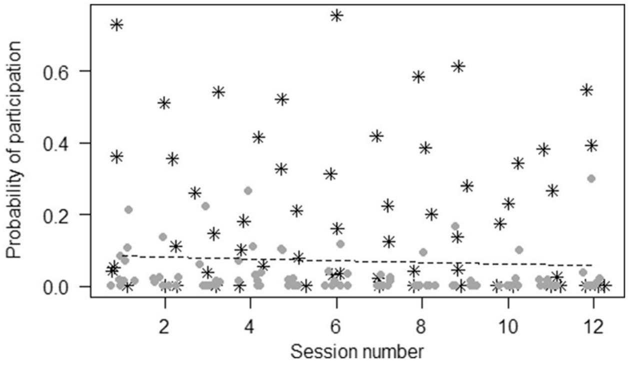

Fig. 2 Jitter plot showing probability of participating in the enrichment activity as a function of session number. *Asterisks* represent female chimpanzees and *circles* male chimpanzees in each session. The *dashed line* represents the fitted model, which is like model 1 but unconditional on all the other predictors that were standardized

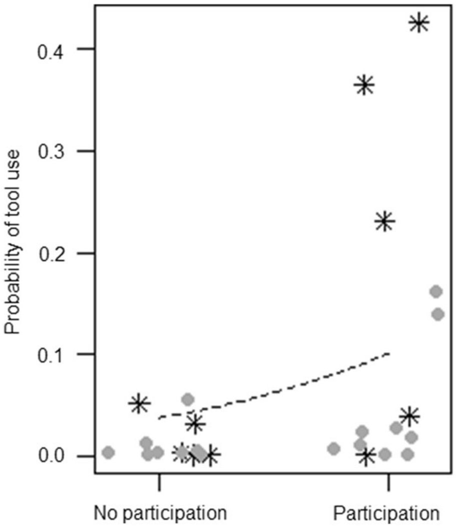

Fig. 3 Jitter plot showing probability of using tools as a function of whether individuals participated in the enrichment activity. *Asterisks* represent female chimpanzees and *circles* male chimpanzees in the two conditions. The *dashed line* represents the fitted model, which is like model 2 but unconditional on all the other predictors that were standardized

with the enrichment device, as compared to when they did not in either baseline or enrichment sessions.

Among our subjects, three females (Africa, Coco and Waty) were the most frequent users of the enrichment, spending between 15 and 50% of the scans interacting with the food maze. The other chimpanzees participated much less, with some hardly interacting with the device at all. Wide inter-individual variation in participation has been reported in other studies that presented cognitive devices to great apes (Clark et al. 2019; Clark and Smith 2013; Tarou et al. 2004) and monkeys (Jacobson et al. 2019; Polgár et al. 2017). It is noteworthy that only Africa and Coco, two of the three more frequent users of the food maze, were able to master the task when the food rewards were in the upper levels of the maze, by moving them across all of the vertical levels. When chimpanzees used a puzzle board containing food rewards in a study by Brent and Eichberg (1991), females also used the device more often than males. Similarly, Yamanishi et al. (2016) found that female chimpanzees mastered new tool-using behaviors faster than males. Therefore, our results are consistent with previous studies supporting sex differences in captive chimpanzees' tool use

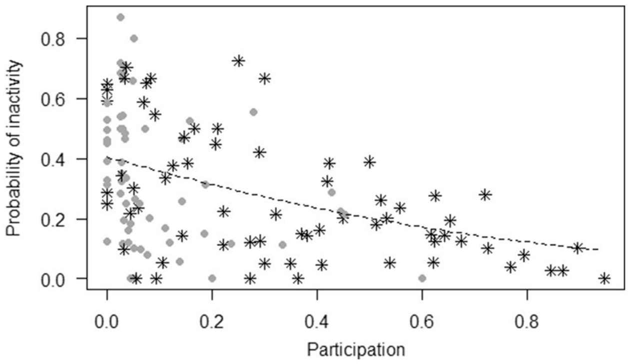

Fig. 4 Jitter plot showing probability of being inactive as a function of participation in the enrichment activity. *Asterisks* represent female chimpanzees and *circles* male chimpanzees in each session. The *dashed line* represents the fitted model, which is like model 4 but unconditional on all the other predictors that were standardized

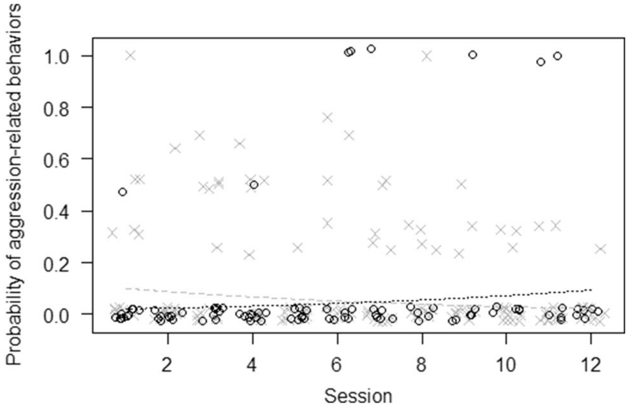

Fig. 5 Jitter plot showing probability of showing aggression-related behaviors as a function of session number and separately for individuals who participated and for those who did not participate in the enrichment activities. *Circles* represent chimpanzees that participated in the enrichment activity in each session and *crosses* those that did not participate. The *dashed line* represents the fitted model, which is like model 7 but unconditional on all the other predictors that were standardized

and proficiency, a pattern that has been repeatedly observed in the wild (Boesch and Boesch 1981, 1990; Lonsdorf 2005; Lonsdorf et al. 2004; McGrew 1979; Pruetz et al. 2015), and in both captive (Boose et al. 2013; Gruber et al. 2010) and wild bonobos (Samuni et al. 2022). Considering our small sample size, however, our findings regarding sex differences should be interpreted with caution.

In line with our predictions, participation decreased across sessions, as observed in other studies in which non-human primates lost interest in puzzle-feeders within several hours of their exposure to them (Bloomstrand et al. 1986; Csatádi et al. 2008). Indeed, non-human primates can quickly become habituated to various novel enrichment devices or tasks (Paquette 1992; Vick et al. 2000). Nonetheless, the level of difficulty should be taken into account when assessing subjects' interest in the enrichment, as complex puzzle feeders might promote subjects' long-term engagement (Clark 2011; Taylor et al. 1994). As only two of our chimpanzees were able to extract the rewards from the maze, the task was clearly not that easy. The decrease in participation over time was likely due to almost all of the chimpanzees approaching and trying to solve the maze at first, but then giving up after several failed attempts (especially for rewards on the upper levels of the maze). Thus, failure to master the task might have led to frustration and loss of motivation (Toates 1986). Our chimpanzees had previous experience with other tool-based enrichments, such as artificial termite mounds, from which they successfully retrieved food rewards (Padrell et al. 2021). These tasks also involved searching for and modifying tools from the environment, but dipping to extract food appears to be less complex than guiding food rewards through a maze, which requires fine motoric skills, precise hand movements, and probably higher cognitive abilities such as planning or an understanding of an object's physical properties (Völter and Call 2014). Furthermore, wild primates can take years to fully master tool-based activities like ant-dipping or nut-cracking (Boesch and Boesch-Achermann 2000; Matsuzawa et al. 2001; Ottoni and Izar 2008). Thus, the chimpanzees in our study, with no prior experience of this type of device, might have needed more time and practice to master the maze.

Overall, our results reveal the importance of considering individual differences when implementing enrichment activities (Coleman and Novak 2017). Variables like sex, age, cognitive skills and personality may strongly affect how subjects respond to a particular cognitive challenge (Altschul et al. 2017; Herrelko et al. 2012; Hopper et al. 2014) and contribute to large differences in participation and success in extracting food from enrichment devices. Additionally, although we used highly preferred food rewards, variability in the subjects' food preferences or food motivation might also have affected participation. Other factors that should be taken into consideration include past experiences and rearing conditions (e.g., Brent et al. 1995; Gluck et al. 1973; Morimura and Mori 2010; Novak and Sackett 2006; Simpson et al. 2019). Unfortunately, however, reliable and precise information about the past life of a rescued chimpanzee is usually unavailable. Finally, it should also be noted that, due to the limited number of agonistic interactions and low rank stability in our chimpanzee groups, we did not include rank in our analyses; future studies on larger groups with stable hierarchies should consider the possible effects of rank on enrichment-related activities.

As expected, and as previously reported in other studies involving puzzle feeders, participation was related to an increase in tool use and a reduction of inactivity, while promoting feeding (Brent and Eichberg 1991; Csatádi et al. 2008; Gilloux et al. 1992; Roberts et al. 1999). However, in contrast to our predictions and the results of some other studies that used puzzle feeders, enrichment was not linked to a reduction in abnormal behaviors in our chimpanzees (see Brent and Eichberg 1991; Maki et al. 1989; Yamanashi et al. 2016). In fact, in our sample, abnormal behaviors were already infrequent (fewer than 1% of the scans in the baseline condition; see Table S1), compared to the 2.9–7.6% of time spent in abnormal behaviors reported for captive chimpanzees in other studies (Bradshaw et al. 2008). Furthermore, abnormal behavior may to some degree be endemic in captive populations (Birkett and Newton-Fisher 2011), and very difficult to eradicate in subjects that have experienced trauma in the past (Lopresti-Goodman et al. 2012), which is the case for some of our chimpanzees.

Considering its novelty, we expected the chimpanzees to gather around the device to explore it and possibly to observe others performing the task. Additionally, the device contained two simultaneously available but independent mazes, usable by two chimpanzees at the same time without mutual interference. However, contrary to our predictions, we found no increase in social proximity for those who participated more, as the maze was usually monopolized by a single chimpanzee in each group (typically one of the females who learned to retrieve the rewards). We further predicted that chimpanzees who participated more would show a decrease in affiliative behaviors due to spending more time at the maze and therefore investing less time in social interactions. In contrast to previous studies (e.g., Brent and Eichberg 1991), however, interacting with the enrichment did not disrupt the occurrence of usual social activities. Thus, our results are in line with those reported by Yamanashi et al. (2016) and Padrell et al. (2021), who also found no changes in the occurrence of affiliative behaviors resulting from tool-based enrichments. Nonetheless, we did find a positive association between participation and agonistic behaviors, which increased across sessions. Although the food maze could be used by more than one chimpanzee at a time, it appeared to promote competition and thus increased aggression (Jacobson et al. 2019; Maki et al. 1989), as expected when tasks are presented in a social setting (Tarou et al. 2004). This may be especially important in our group, considering that all the chimpanzees who failed to master the task were males, who are often aggressive towards females. Furthermore, it has been reported that wild female chimpanzees also tend to be aggressive in the context of feeding competition (Muller and Mitani 2005). One alternative to our method would have been to install single-maze devices (rather than double-sided mazes), in different areas of the enclosure (out of full view of other group members), to decrease direct competition. It should also be noted that, in our behavioral catalogue, agonistic behaviors included both aggressive and submissive behaviors, which are not necessarily indicators of poor welfare. Therefore, although aggression is not desirable in captive primates, the increase in aggression observed in our study may not have been a particularly negative outcome.

Interacting with the enrichment device was linked to an increase in self-rubbing and scratching, as compared to when no enrichment was present (baseline) or when it was present but the subject did not interact with it. These results reflect the complex relationship between enrichment and self-directed behaviors. Although enrichment is supposed to reduce stress-related behaviors, cognitive challenges are expected to trigger them, as a result of emotional arousal (Baker and Aureli 1997; Maestripieri et al. 1992). Thus, in our study, the increase in self-directed behaviors may not be an indicator of stress or anxiety, but rather an expression of arousal in a challenging context. Other studies involving tool-based tasks in social settings have also reported complex results regarding self-directed behaviors. For instance, Yamanashi et al. (2016) found a decrease in self-directed behaviors when tool-based feeders were provided compared to when the enrichment was absent. By contrast, Clark and Smith (2013) found that in the presence of a cognitive device chimpanzees scratched themselves more, whereas using the device was associated with a decrease in scratching. Furthermore, a novel cognitive task presented to zoo-housed chimpanzees by Herrelko et al. (2012) caused no increase in self-directed behaviors (i.e., rubbing and scratching) during training, as compared to a baseline condition. However, in contrast to Herrelko et al. (2012), the chimpanzees in our study were observed in their usual enclosures, with the other group members continuously present. This might have increased competition for food, frustration, and agonistic behaviors (as we found). If the individuals had been observed with exclusive access to the device and no disturbance by other chimpanzees, their anxiety levels might have been lower. Nonetheless, providing these types of activities in a social context better simulates the natural conditions of chimpanzees, including intragroup competition, and thus increases ecological validity (Cronin 2017).

Environmental enrichment usually involves introducing novel stimuli with the ultimate goal of improving captive animal welfare (Azevedo et al. 2007; Sheperdson 2003; Young 2003). In this respect, the food maze in this study had a positive impact on chimpanzees' behavior by (1) promoting tool use, which is a species-typical behavior that rarely occurs in captivity in the absence of specific enrichments; and (2) decreasing inactivity, which is usually considered a positive outcome of environmental enrichment for captive great apes (Baker 1997; Brent 1992; Brent and Eichberg 1991; Celli et al. 2003; Csatádi et al. 2008; Gilloux et al. 1992). Arousal levels, assessed through self-directed behaviors, were not affected by the presence of the enrichment device, but did increase for individuals interacting with it. Finally, one of our aims was to promote activity that stimulated the chimpanzees cognitively by creating learning opportunities that simulate the natural environment (Young et al. 2020), in which animals face challenging situations (e.g., finding food) that often require complex behavioral and cognitive skills such as exploration or problem solving (Shettleworth 2010). The food maze indeed presented a challenge, but as most of the chimpanzees failed to master the task during the study period, longer exposure might lead to better assessment of the impact of this and other similar enrichments on chimpanzee behavior.

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Author contributions Conceptualization, MP, FA and ML; data curation, MP and MPC; formal analysis, MP and FA; funding acquisition, MP and ML; investigation, MP and MPC; methodology, MP and ML; supervision, FA and ML; writing—original draft, MP; writing—review and editing, FA and ML. All the authors read and approved the final version of the manuscript.

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Data availability The data presented in this study are provided as Supplementary files (Supplementary files 2 and 3).

Declarations

Conflict of interest The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of the data; in the writing of the manuscript; or in the decision to publish the results.

Ethical approval This project was evaluated in 2019 by the Universitat de Girona Ethics Committee (Comitè d'Ètica i Bioseguretat de la Recerca de la Universitat de Girona) (CEBU 0020-2019, approval date 16 December 2019).

References

Altschul D, Wallace E, Sonnweber R, Tomonaga M, Weiss A (2017) Chimpanzee intellect: personality, performance and motivation with touchscreen tasks. R Soc Open Sci 4(5):170169. https://doi.org/10.1098/rsos.170169

Azevedo CS, Cipreste CF, Young RJ (2007) Environmental enrichment: a GAP analysis. Appl Anim Behav Sci 102:329–343. https://doi.org/10.1016/j.applanim.2006.05.034

Baayen RH (2008) Analyzing linguistic data: a practical introduction to statistics using R. Cambridge University Press, Cambridge

Bakeman R, Quera V (2011) Sequential analysis and observational methods for the behavioral sciences. Cambridge University Press, Cambridge

Baker KC (1997) Straw and forage material ameliorate abnormal behaviors in adult chimpanzees. Zoo Biol 16(3):225–236

Baker KC, Aureli F (1997) Behavioural indicators of anxiety: an empirical test in chimpanzees. Behaviour 134(13/14):1031–1050

Bardo A, Cornette R, Borel A, Pouydebat E (2017) Manual function and performance in humans, gorillas, and orangutans during the same tool use task. Am J Phys Anthropol 164(4):821–836. https://doi.org/10.1002/ajpa.23323

Barr DJ, Levy R, Scheepers C, Tily HJ (2013) Random effects structure for confirmatory hypothesis testing: keep it maximal. J Mem Lang 68(3):255–278. https://doi.org/10.1016/j.jml.2012.11.001

Birkett LP, Newton-Fisher NE (2011) How abnormal is the behaviour of captive, zoo-living chimpanzees? PLoS ONE 6(6):e20101. https://doi.org/10.1371/journal.pone.0020101

Bloomsmith M, Alford P, Maple T (1988) Successful feeding enrichment for captive chimpanzees. Am J Primatol 16(2):155–164

Bloomsmith MA, Brent LY, Schapiro SJ (1991) Guidelines for developing and managing an environmental enrichment program. Lab Anim Sci 41:372–377

Bloomsmith M, Finlay T, Merhalski J, Maple T (1990) Rigid plastic balls as enrichment devices for captive chimpanzees. Lab Anim Sci 40(3):319–322

Bloomstrand M, Riddle K, Alford P, Maple TL (1986) Objective evaluation of a behavioral enrichment device for captive chimpanzees (*Pan troglodytes*). Zoo Biol 5(3):293–300. https://doi.org/10.1002/zoo.1430050307

Boesch C, Boesch H (1981) Sex differences in the use of natural hammers by wild chimpanzees: a preliminary report. J Hum Evol 10(7):585–593. https://doi.org/10.1016/S0047-2484(81)80049-8

Boesch C, Boesch H (1990) Tool use and tool making in wild chimpanzees. Folia Primatol 54(1–2):86–99. https://doi.org/10.1159/000156428

Boesch C, Boesch-Achermann H (2000) The chimpanzees of the Taï forest: behavioural ecology and evolution. Oxford University Press, USA

Bonnie KE, Ang MY, Ross SR (2016) Effects of crowd size on exhibit use by and behavior of chimpanzees (*Pan troglodytes*) and western lowland gorillas (*Gorilla gorilla*) at a zoo. Appl Anim Behav Sci 178:102–110. https://doi.org/10.1016/j.applanim.2016.03.003

Boose KJ, White FJ, Meinelt A (2013) Sex differences in tool use acquisition in bonobos (*Pan paniscus*). Am J Primatol 75(9):917–926. https://doi.org/10.1002/ajp.22155

Bradshaw GA, Capaldo T, Lindner L, Grow G (2008) Building an inner sanctuary: complex PTSD in chimpanzees. J Trauma Dissociation 9(1):9–34. https://doi.org/10.1080/15299730802073619

Brent L (1992) Woodchip bedding as enrichment for captive chimpanzees in an outdoor enclosure. Anim Welf 1(3):161–170

Brent L, Bloomsmith MA, Fisher SD (1995) Factors determining tool-using ability in two captive chimpanzee (*Pan troglodytes*) colonies. Primates 36(2):265–274. https://doi.org/10.1007/BF02381352

Brent L, Eichberg JW (1991) Primate puzzleboard: a simple environmental enrichment device for captive chimpanzees. Zoo Biol 10(4):353–360. https://doi.org/10.1002/zoo.1430100409

Brent L, Stone A (1998) Destructible toys as enrichment for captive chimpanzees. J Appl Anim Welf Sci 1(1):5–14. https://doi.org/10.1207/s15327604jaws0101_2

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9(2):378–400

Brooks J, Yoshimura H, Taki Y (2021) Knowledge-based enrichment: development of a novel enrichment device for captive chimpanzees. Zoo Biol 40(5):398–406. https://doi.org/10.1002/zoo.21617

Browning H (2019) The natural behavior debate: two conceptions of animal welfare. J Appl Anim Welf Sci 23(3):325–337. https://doi.org/10.1080/10888705.2019.1672552

Call J (2013) Three ingredients for becoming a creative tool user. In: Boesch C, Sanz CM, Call J (eds) Tool use in animals: cognition and ecology. Cambridge University Press, Cambridge, pp 3–20

Carter M, Sherwen S, Webber S (2021) An evaluation of interactive projections as digital enrichment for orangutans. Zoo Biol 40(2):107–114. https://doi.org/10.1002/zoo.21587

Celli ML, Hirata S, Tomonaga M (2004) Socioecological influences on tool use in captive chimpanzees. Int J Primatol 25(6):1267–1281. https://doi.org/10.1023/B:IJOP.0000043962.60837.16

Celli ML, Tomonaga M, Udono T, Teramoto M, Nagano K (2003) Tool use task as environmental enrichment for captive chimpanzees. Appl Anim Behav Sci 81(2):171–182. https://doi.org/10.1016/S0168-1591(02)00257-5

Cheyne S (2009) Studying social development and cognitive abilities in gibbons (*Hylobates* spp.): methods and applications. In: Potocki E, Krasinski J (eds) Primatology: theories, methods and research. Nova Science, New York

Chipangura JK, Ganswindt A, Naidoo V (2020) A report on the housing vervet monkeys adjacent to domestic cats as a means of environmental enrichment. OJVR 87(1):e1–e6. https://doi.org/10.4102/ojvr.v87i1.1870

Clark FE (2011) Great ape cognition and captive care: can cognitive challenges enhance well-being? Appl Anim Behav Sci 135(1–2):1–12. https://doi.org/10.1016/j.applanim.2011.10.010

Clark FE (2017) Cognitive enrichment and welfare: current approaches and future directions. Anim Behav Cogn 4(1):52–71. https://doi.org/10.12966/abc.05.02.2017

Clark FE, Gray SI, Bennett P, Mason LJ, Burgess KV (2019) High-tech and tactile: cognitive enrichment for zoo-housed gorillas. Front Psychol. https://doi.org/10.3389/fpsyg.2019.01574

Clark FE, Smith LJ (2013) Effect of a cognitive challenge device containing food and non-food rewards on chimpanzee well-being. Am J Primatol 75(8):807–816. https://doi.org/10.1002/ajp.22141

Coleman K, Novak MA (2017) Environmental enrichment in the 21st century. ILAR J 58(2):295–307. https://doi.org/10.1093/ilar/ilx008

Costa R, Sousa C, Llorente M (2018) Assessment of environmental enrichment for different primate species under low budget: a case study. J Appl Anim Welf Sci 21:1–15. https://doi.org/10.1080/10888705.2017.1414606

Cronin KA (2017) Studying primate cognition in a social setting to improve validity and welfare: a literature review highlighting successful approaches. PeerJ. https://doi.org/10.7717/peerj.3649

Csatádi K, Leus K, Pereboom JJ (2008) A brief note on the effects of novel enrichment on an unwanted behaviour of captive bonobos. Appl Anim Behav Sci 112(1–2):201–204. https://doi.org/10.1016/j.applanim.2007.09.001

de Rosa C, Vitale A, Puopolo M (2003) The puzzle-feeder as feeding enrichment for common marmosets (*Callithrix jacchus*): a pilot study. Lab Anim 37(2):100–107. https://doi.org/10.1258/00236770360563732

Dobson AJ (2002) An introduction to generalized linear models. Chapman & Hall/CRC, Boca Raton, Florida

Doran D (1997) Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Tai chimpanzees. Int J Primatol 18(2):183–206

Dutton MB, Pierre PJ, Bailoo J, Warkins E, Michel GF, Bennett AJ (2018) A model quantitative assessment tool for nonhuman primate environmental enrichment plans. BioRxiv. https://doi.org/10.1101/341206

Elder CM, Menzel CR (2001) Dissociation of cortisol and behavioral indicators of stress in an orangutan (*Pongo pygmaeus*) during a computerized task. Primates 42(4):345–357. https://doi.org/10.1007/BF02629625

Fernández EJ, Martin AL (2021) Animal training, environmental enrichment, and animal welfare: a history of behavior analysis in zoos. JZBG 2(4):531–543

Field A (2009) Discovering statistics using SPSS, 3rd edn. Sage Publications, London, UK

Gilloux I, Gurnell J, Shepherdson D (1992) An enrichment device for great apes. Anim Welf 1(4):279–289

Gluck JP, Harlow HF, Schiltz KA (1973) Differential effect of early enrichment and deprivation on learning in the rhesus monkey (*Macaca mulatta*). J Comp Physiol Psychol 84(3):598

Goodall J (1986) The chimpanzees of Gombe: patterns of behavior. Cambridge University Press, Cambridge (Massachussets)

Gray S, Clark F, Burgess K, Metcalfe T, Kadijevic A, Cater K, Bennett P (2018) Gorilla game lab: exploring modularity, tangibility and playful engagement in cognitive enrichment design. Proceedings of the Fifth International Conference on Animal-Computer Interaction

Gronqvist G, Kingston-Jones M, May A, Lehmann J (2013) The effects of three types of environmental enrichment on the behaviour of captive Javan gibbons (*Hylobates moloch*). Appl Anim Behav Sci 147(1–2):214–223. https://doi.org/10.1016/j.applanim.2013.04.021

Gruber T, Clay Z, Zuberbühler K (2010) A comparison of bonobo and chimpanzee tool use: evidence for a female bias in the *Pan* lineage. Anim Behav 80:1023–1033. https://doi.org/10.1016/j.anbehav.2010.09.005

Grunauer PP, Walguarnery JW (2018) Relative response to digital tablet devices and painting as sensory enrichment in captive chimpanzees. Zoo Biol 37(4):269–273. https://doi.org/10.1002/zoo.21431

Hall BA, McGill DM, Sherwen SL, Doyle RE (2021) Cognitive enrichment in practice: a survey of factors affecting its implementation in zoos globally. Animals 11(6):1721

Herrelko ES, Vick SJ, Buchanan-Smith HM (2012) Cognitive research in zoo-housed chimpanzees: influence of personality and impact on welfare. Am J Phys Anthropol 74(9):828–840. https://doi.org/10.1002/ajp.22036

Hirata S, Celli ML (2003) Role of mothers in the acquisition of tool-use behaviours by captive infant chimpanzees. Anim Cogn 6(4):235–244. https://doi.org/10.1007/s10071-003-0187-6

Hirata S, Morimura N (2000) Naive chimpanzees' (*Pan troglodytes*) observation of experienced conspecifics in a tool-using task. J Comp Psychol 114(3):291–296. https://doi.org/10.1037/0735-7036.114.3.291

Honess PE, Marin CM (2006) Enrichment and aggression in primates. Neurosci Biobehav Rev 30(3):413–436. https://doi.org/10.1016/j.neubiorev.2005.05.002

Hopkins W, Keebaugh AC, Reamer LA, Schaeffer J, Schapiro SJ, Young LJ (2014) Genetic influences on receptive joint attention in chimpanzees (*Pan troglodytes*). Sci Rep 4(1):1–7. https://doi.org/10.1038/srep03774

Hopkins W, Russell JL, Freeman H, Reynolds EA, Griffis C, Leavens DA (2006) Lateralized scratching in chimpanzees (*Pan troglodytes*): evidence of a functional asymmetry during arousal. Emotion 6(4):553–559. https://doi.org/10.1037/1528-3542.6.4.553

Hopper LM, Price SA, Freeman HD, Lambeth SP, Schapiro SJ, Kendal RL (2014) Influence of personality, age, sex, and estrous state on chimpanzee problem-solving success. Anim Cogn 17(4):835–847. https://doi.org/10.1007/s10071-013-0715-y

Hopper LM, Tennie C, Ross SR, Lonsdorf EV (2015) Chimpanzees create and modify probe tools functionally: a study with zoo-housed chimpanzees. Am J Primatol 77(2):162–170. https://doi.org/10.1002/ajp.22319

Hoy JM, Murray PJ, Tribe A (2010) Thirty years later: enrichment practices for captive mammals. Zoo Biol 29(3):303–316. https://doi.org/10.1002/zoo.20254

Hughes BO, Duncan IJH (1988) The notion of ethological 'need', models of motivation and animal welfare. Anim Behav 36(6):1696–1707. https://doi.org/10.1016/S0003-3472(88)80110-6

Hunt GR, Gray RD, Taylor AH (2013) Why is tool use rare in animals? In: Boesch C, Sanz CM, Call J (eds) Tool use in animals: cognition and ecology. Cambridge University Press, Cambridge, pp 89–118

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

Itakura S (1993) Emotional behavior during the learning of a contingency task in a chimpanzee. Percept Mot Skills 76(2):563–566. https://doi.org/10.2466/pms.1993.76.2.563

Izzo GN, Bashaw MJ, Campbell JB (2011) Enrichment and individual differences affect welfare indicators in squirrel monkeys (*Saimiri sciureus*). J Comp Psychol 125(3):347

Jacobson SL, Kwiatt AC, Ross SR, Cronin KA (2019) The effects of cognitive testing on the welfare of zoo-housed Japanese macaques (*Macaca fuscata*). Appl Anim Behav Sci 212:90–97. https://doi.org/10.1016/j.applanim.2018.12.014

Jones M, Pillay N (2004) Foraging in captive hamadryas baboons: implications for enrichment. Appl Anim Behav Sci 88(1–2):101–110

Jones C, Sabater Pi J (1969) Sticks used by chimpanzees in Rio Muni. West Africa Nature 223(5201):100–101. https://doi.org/10.1038/223100a0

Kim-McCormack NNE, Smith CL, Behie AM (2016) Is interactive technology a relevant and effective enrichment for captive great apes? Appl Anim Behav Sci 185:1–8. https://doi.org/10.1016/j.applanim.2016.09.012

Lambeth S, Bloomsmith M (1994) A grass foraging device for captive chimpanzees (*Pan troglodytes*). Anim Welf 3(1):13–24

Leavens D, Aureli F, Hopkins W (2004) Behavioral evidence for the cutaneous expression of emotion in a chimpanzee (*Pan troglodytes*). Behaviour 141:979–997. https://doi.org/10.1163/1568539042360189

Leavens D, Aureli F, Hopkins WD, Hyatt CW (2001) Effects of cognitive challenge on self-directed behaviors by chimpanzees (*Pan troglodytes*). Am J Primatol 55(1):1–14. https://doi.org/10.1002/ajp.1034

Leeds A, Lukas K (2018) Experimentally evaluating the function of self-directed behaviour in two adult mandrills (*Mandrillus sphinx*). Anim Welf 27:81–86. https://doi.org/10.7120/09627286.27.1.081

Lenth R (2020) Emmeans: estimated marginal means, aka least-squares means. R Package Version 1(4):8

Llorente M, Campi A (2014) Is "tool use" a welfare tool? Using an artificial ant-fishing task as environmental enrichment in naturalistically housed chimpanzees from the Fundació Mona. Folia Primatol 85:68–68

Lonsdorf EV (2005) Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park. Tanzania Anim Behav 70(3):673–683. https://doi.org/10.1016/j.anbehav.2004.12.014

Lonsdorf EV, Eberly LE, Pusey AE (2004) Sex differences in learning in chimpanzees. Nature 428(6984):715–716. https://doi.org/10.1038/428715a

Lopresti-Goodman SM, Kameka M, Dube A (2012) Stereotypical behaviors in chimpanzees rescued from the African bushmeat and pet trade. Behav Sci 3(1):1–20. https://doi.org/10.3390/bs3010001

Lukas KE, Hoff MP, Maple TL (2003) Gorilla behavior in response to systematic alternation between zoo enclosures. Appl Anim Behav Sci 81(4):367–386

Lutz CK, Novak MA (2005) Environmental enrichment for nonhuman primates: theory and application. ILAR J 46(2):178–191

Maestripieri D, Schino G, Aureli F, Troisi A (1992) A modest proposal: displacement activities as an indicator of emotions in primates. Anim Behav 44(5):967–979. https://doi.org/10.1016/S0003-3472(05)80592-5

Maki S, Alford PL, Bloomsmith MA, Franklin J (1989) Food puzzle device simulating termite fishing for captive chimpanzees (*Pan troglodytes*). Am J Primatol Suppl 1:71–78

Mallapur A (2008) Animal welfare research and its implications to non-human primate breeding programs: a case study of the lion-tailed macaque conservation breeding program from India. REDVET 9(10B):1–21

Maple TL, Perdue BM (2013) Environmental´enrichment zoo animal welfare. Springer, Berlin, Heidelberg New York, pp 95–117

Matsuzawa T, Biro D, Humle T, Inoue-Nakamura N, Tonooka R, Yamakoshi G (2001) Emergence of culture in wild chimpanzees: education by master-apprenticeship. In: Matsuzawa T (ed) Primate origins of human cognition and behavior. Springer, Tokyo, pp 557–574

McGrew WC (1979) Evolutionary implications of sex differences in chimpanzee predation and tool use. In: Hamburg DA, McCown ER (eds) The Great Apes. Benjamin Cummings, Menlo Park, California, pp 441–463

McGrew WC, Marchant LF (1992) Chimpanzees, tools, and termites: hand preference or handedness? Curr Anthropol 33(1):114–119. https://doi.org/10.1086/204041

Meehan CL, Mench JA (2007) The challenge of challenge: can problem solving opportunities enhance animal welfare? Appl Anim Behav Sci 102(3–4):246–261. https://doi.org/10.1016/j.applanim.2006.05.031

Mellor DJ (2015) Enhancing animal welfare by creating opportunities for positive affective engagement. N Z Vet J 63(1):3–8. https://doi.org/10.1080/00480169.2014.926799

Meyer JS, Hamel AF (2014) Models of stress in nonhuman primates and their relevance for human psychopathology and endocrine dysfunction. ILAR J 55(2):347–360. https://doi.org/10.1093/ilar/ilu023

Miller LJ, Vicino GA, Sheftel J, Lauderdale LK (2020) Behavioral diversity as a potential indicator of positive animal welfare. Animals 10(7):1211. https://doi.org/10.3390/ani10071211

Morimura N (2003) A note on enrichment for spontaneous tool use by chimpanzees (*Pan troglodytes*). Appl Anim Behav Sci 82(3):241–247

Morimura N (2006) Cognitive enrichment in chimpanzees: an approach of welfare entailing an animal's entire resources. In: Matsuzawa

T, Tomonaga M, Tanaka M (eds) Cognitive development in chimpanzees. Springer, Tokyo, pp 368–391

Morimura N, Mori Y (2010) Effects of early rearing conditions on problem-solving skill in captive male chimpanzees (*Pan troglodytes*). Am J Primatol 72(7):626–633. https://doi.org/10.1002/ajp.20819

Motes-Rodrigo A, Tennie C (2021) Captive great apes tend to innovate simple tool behaviors quickly. Am J Primatol. https://doi.org/10.1002/ajp.23311

Muller MN, Mitani JC (2005) Conflict and cooperation in wild chimpanzees. Advances in the study of behavior, vol 35. Academic Press, Cambridge, pp 275–331

Nash VJ (1982) Tool use by captive chimpanzees at an artificial termite mound. Zoo Biol 1(3):211–221

Nash R, Johnston H, Robbins A, Descovich K (2021) The effect of enrichment filling and engagement time on regurgitation and reingestion behaviour in three zoo-housed orangutans. J Zool Bot Gard 2(1):10–20. https://doi.org/10.3390/jzbg2010002

Newberry RC (1995) Environmental enrichment: increasing the biological relevance of captive environments. Appl Anim Behav Sci 44(2–4):229–243

Novak MA, Sackett GP (2006) The effects of rearing experiences: the early years nursery rearing of nonhuman primates in the 21st century. Springer, Berlin, pp 5–19

Osuna-Mascaró AJ, Ortiz C, Stolz C, Musgrave S, Sanz CM, Morgan DB, Fragaszy DM (2021) Dexterity and technique in termite fishing by chimpanzees (*Pan troglodytes troglodytes*) in the Goualougo triangle. Republic Congo Am J Primatol 83(1):e23215. https://doi.org/10.1002/ajp.23215

Ottoni EB, Izar P (2008) Capuchin monkey tool use: overview and implications. Evol Anthropol Issue News Rev 17(4):171–178. https://doi.org/10.1002/evan.20185

Padrell M, Amici F, Córdoba MP, Giberga A, Broekman A, Almagro S, Llorente M (2021) Artificial termite-fishing tasks as enrichment for sanctuary-housed chimpanzees: behavioral effects and impact on welfare. Animals 11(10):2941. https://doi.org/10.3390/ani11102941

Paquette D (1992) Discovering and learning tool-use for fishing honey by captive chimpanzees. Hum Evol 7(3):17–30. https://doi.org/10.1007/BF02436257

Paquette D, Prescott J (1988) Use of novel objects to enhance environments of captive chimpanzees. Zoo Biol 7(1):15–23. https://doi.org/10.1002/zoo.1430070103

Polgár Z, Wood L, Haskell MJ (2017) Individual differences in zoo-housed squirrel monkeys' (*Saimiri sciureus*) reactions to visitors, research participation, and personality ratings. Am J Primatol. https://doi.org/10.1002/ajp.22639

Pruetz J, Bloomsmith M (1992) Comparing two manipulable objects as enrichment for captive chimpanzees. Anim Welf 1(2):127–137

Pruetz JD, Bertolani P, Ontl KB, Lindshield S, Shelley M, Wessling EG (2015) New evidence on the tool-assisted hunting exhibited by chimpanzees (*Pan troglodytes verus*) in a savannah habitat at Fongoli, Senegal. R Soc Open Sci 2(4):140507. https://doi.org/10.1098/rsos.140507

Pruetz JD, McGrew WC (2001) What does a chimpanzee need? Using natural behavior to guide the care and management of captive populations. In: Brent L (ed) Care and management of captive chimpanzees. American Society of Primatologists, San Antonio, pp 17–37

Roberts RL, Roytburd LA, Newman JD (1999) Puzzle feeders and gum feeders as environmental enrichment for common marmosets. Contemp Top Lab Anim Sci 38(5):27–31

Ross M, Niemann T, Wark J, Heintz M, Horrigan A, Cronin K, Shender M, Gillespie K (2016) Zoomonitor (version 1) (mobile application software). Available from https://zoomonitor.org. Accessed 14 July 2022

Samuni L, Lemieux D, Lamb A, Galdino D, Surbeck M (2022) Tool use behavior in three wild bonobo communities at Kokolopori. Am J Primatol 84(1):e23342. https://doi.org/10.1002/ajp.23342

Sanz CM, Morgan DB, Hopkins WD (2016) Lateralization and performance asymmetries in the termite fishing of wild chimpanzees in the Goualougo triangle, Republic of Congo. Am J Primatol 78(11):1190–1200. https://doi.org/10.1002/ajp.22574

Schapiro SJ, Lambeth SP (2007) Control, choice, and assessments of the value of behavioral management to nonhuman primates in captivity. J Appl Anim Welf Sci 10(1):39–47. https://doi.org/10.1080/10888700701277345

Schino G, Perretta G, Taglioni AM, Monaco V, Troisi A (1996) Primate displacement activities as an ethopharmacological model of anxiety. Anxiety 2(4):186–191. https://doi.org/10.1002/(SICI)1522-7154(1996)2:4%3c186::AID-ANXI5%3e3.0.CO;2-M

Seed AM, Call J, Emery NJ, Clayton NS (2009) Chimpanzees solve the trap problem when the confound of tool-use is removed. J Exp Psychol Anim Behav Process 35(1):23–34. https://doi.org/10.1037/a0012925

Sha J, Han S, Marlena D, Kee J (2012) Effects of single-use and group-use enrichment on stereotypy and intragroup aggressive and affiliative behaviors of a social group of squirrel monkeys (*Saimiri sciureus*) at the Singapore Zoo. J Appl Anim Welf Sci 15(4):358–371. https://doi.org/10.1080/10888705.2012.709148

Sheperdson DJ (2003) Environmental enrichment: past, present and future. Int Zoo Yearbook 38(1):118–124. https://doi.org/10.1111/j.1748-1090.2003.tb02071.x

Shettleworth SJ (2010) Cognition, evolution, and behavior. Oxford University Press, Oxford, New York

Shohat Y, Paz R, Pryluk R, Taub AH (2019) Energy-based and energy-free food-consumption are correlated in captive non-human-primates: a novel dispenser for feeding and behavioral enrichment. BioRxiv. https://doi.org/10.1101/803528

Simpson EA, Sclafani V, Paukner A, Kaburu SS, Suomi SJ, Ferrari PF (2019) Handling newborn monkeys alters later exploratory, cognitive, and social behaviors. Dev Cogn Neurosci 35:12–19. https://doi.org/10.1016/j.dcn.2017.07.010

Špinka M, Wemelsfelder F (2011) Environmental challenge and animal agency. In: Appleby MC, Mench JA, Olsson IAS, Hughes BO (eds) Animal welfare. CABI, Wallingford, pp 27–44

Tarou LR, Bashaw MJ (2007) Maximizing the effectiveness of environmental enrichment: suggestions from the experimental analysis of behavior. Appl Anim Behav Sci 102(3):189–204. https://doi.org/10.1016/j.applanim.2006.05.026

Tarou LR, Kuhar CW, Adcock D, Bloomsmith M, Maple T (2004) Computer-assisted enrichment for zoo-housed orangutans (*Pongo pygmaeus*). Anim Welf 13:445–453

Taylor R, White B, Ferguson S, Binienda Z (1994) The use of foraging devices for environmental enrichment of individually housed rhesus monkeys in a laboratory colony. Contemp Top Lab Anim Sci 33:71–73

Toates FM (1986) Motivational systems. Cambridge University Press, Cambridge

Torigoe T (1985) Comparison of object manipulation among 74 species of non-human primates. Primates 26(2):182–194. https://doi.org/10.1007/BF02382017

Vaglio S, Kaburu SSK, Pearce R, Bryant L, McAuley A, Lott A, Sheppard DJ, Smith S, Tompkins BH, Jelwell E, Fontani S, Young CH, Marliani G, Accorsi PA (2021) Effects of scent enrichment on behavioral and physiological indicators of stress in zoo primates. Am J Primatol 83(5):e23247. https://doi.org/10.1002/ajp.23247

Vick S-J, Anderson JR, Young R (2000) Maracas for *Macaca*? Evaluation of three potential enrichment objects in two species of zoo-housed macaques. Zoo Biol 19(3):181–191. https://doi.org/10.1002/1098-2361(2000)19:3%3c181::aid-zoo2%3e3.0.co;2-w

Völter CJ, Call J (2014) Younger apes and human children plan their moves in a maze task. Cognition 130(2):186–203. https://doi.org/10.1016/j.cognition.2013.10.007

Wagner KE, Hopper LM, Ross SR (2016) Asymmetries in the production of self-directed behavior by chimpanzees and gorillas during a computerized cognitive test. Anim Cogn 19(2):343–350. https://doi.org/10.1007/s10071-015-0937-2

Wark J, Cronin K, Niemann T, Shender M, Horrigan A, Kao A, Ross M (2019) Monitoring the behavior and habitat use of animals to enhance welfare using the ZooMonitor app. Anim Behav Cogn. https://doi.org/10.26451/abc.06.03.01.2019

Yamanashi Y, Hayashi M (2011) Assessing the effects of cognitive experiments on the welfare of captive chimpanzees (*Pan troglodytes*) by direct comparison of activity budget between wild and captive chimpanzees. Am J Primatol 73(12):1231–1238. https://doi.org/10.1002/ajp.20995

Yamanashi Y, Matsuzawa T (2010) Emotional consequences when chimpanzees (*Pan troglodytes*) face challenges: individual differences in self-directed behaviours during cognitive tasks. Anim Welf 19(1):25–30

Yamanashi Y, Matsunaga M, Shimada K, Kado R, Tanaka M (2016) Introducing tool-based feeders to zoo-housed chimpanzees as a cognitive challenge: spontaneous acquisition of new types of tool use and effects on behaviours and use of space. JZAR 4(3):147–155. https://doi.org/10.19227/jzar.v4i3.235

Young R (2003) Environmental enrichment for captive animals. Blackwell Science, Oxford, UK

Young RJ, de Azevedo CS, Cipreste CF (2020) Environmental enrichment. In: Melfi VA, Dorey NR, Ward SJ (eds) Zoo animal learning and training. Wiley-Blackwell, Hoboken, pp 101–118

Zaragoza F, Ibañez M, Mas B, De Laiglesia Gil S, Anzola Delgado B (2011) Influence of environmental enrichment in captive chimpanzees (*Pan troglodytes spp.*) and gorillas (*Gorilla gorilla gorilla*): behavior and faecal cortisol levels. Rev Cientif Fac Cienc Vet Univ Zulia 21(5):447–456

Supplementary Information

Tables S1 and S2: Incidence of behaviors in the baseline (S1) and enrichment (S2) conditions. Behaviors collected with scan sampling method (i.e., participation, tool use, inactivity, abnormal behaviors, social proximity, aggression-related and affiliation-related behaviors) represent the percentage of scans in which the behavior was observed), whereas behaviors collected with all-occurrence focal sampling (i.e., self-directed behaviors: rubs and scratches) correspond to rates (i.e., number of self-directed behaviors/ observation time in minutes).

Table S1. Baseline condition

	Scan sampling						**Focal sampling**
Subject	**Tool use**	**Inactivity**	**Abnormal behaviors**	**Social proximity**	**Aggression-related behaviors**	**Affiliation-related behaviors**	**Self-directed behaviors**
Africa	0.24	64.03	0.72	17.38	0.24	4.92	0.49
Bea	0.00	72.25	0.27	23.44	0.00	9.12	0.61
Bongo	0.00	43.69	0.00	3.63	3.38	2.46	0.57
Charly	0.00	10.09	3.29	2.27	1.88	15.02	0.56
Cheeta	0.00	65.81	0.00	20.16	0.00	4.88	0.73
Coco	5.61	38.14	3.37	9.83	0.00	12.34	0.45
Juanito	0.17	41.01	0.34	19.11	0.84	15.63	0.24
Marco	0.15	33.80	0.00	4.80	1.23	6.02	0.50
Nico	0.85	45.96	0.00	1.80	2.55	7.66	1.46
Tico	1.86	54.97	3.06	3.94	0.00	0.00	0.92
Tom	0.54	55.09	0.27	6.74	0.54	8.85	0.75
Toni	0.23	51.04	0.00	0.16	0.69	6.24	0.43
Victor	3.36	56.32	2.42	9.48	0.13	2.28	0.56
Waty	1.87	26.67	0.00	12.50	0.53	37.07	0.33
Mean±SD	**1.06±1.64**	**47.06±16.62**	**0.98±1.38**	**9.66±7.67**	**0.86±1.06**	**9.46±9.19**	**0.62±0.30**

Table S2. Enrichment condition

Scan sampling								Focal sampling
Subject	**Participation**	**Tool use**	**Inactivity**	**Abnormal behaviors**	**Social proximity**	**Aggression-related behaviors**	**Affiliation-related behaviors**	**Self-directed behaviors**
Africa	53.52	46.35	25.09	0.25	8.81	0.12	4.70	0.70
Bea	1.09	0.00	64.89	0.00	16.23	0.14	11.89	0.49
Bongo	0.79	0.47	34.34	0.16	3.19	2.69	2.53	0.48
Charly	8.04	5.49	17.25	2.75	2.15	0.59	14.31	0.45
Cheeta	1.72	0.92	54.02	0.11	13.41	0.00	6.55	0.65
Coco	31.26	30.96	21.85	1.52	7.16	0.00	7.74	0.89
Juanito	2.95	0.49	33.61	0.33	8.43	0.16	10.16	0.24
Marco	3.25	1.27	28.57	0.14	5.89	0.14	9.34	0.66
Nico	3.71	3.02	54.76	0.00	6.48	0.70	2.32	0.60
Tico	0.22	0.33	65.21	1.09	4.02	0.00	0.22	0.97
Tom	1.44	0.39	58.09	0.26	9.65	0.78	6.53	0.81
Toni	0.95	0.00	36.67	0.00	2.00	0.00	6.90	0.65
Victor	0.52	5.21	55.34	6.25	9.53	0.13	2.86	0.67
Waty	15.44	14.52	21.20	0.46	7.08	0.23	26.04	0.22
Mean±SD	**8.92±15.37**	**7.82±13.96**	**40.78±17.23**	**0.95±1.71**	**7.43±4.08**	**0.41±0.71**	**8.01±6.52**	**0.61±0.22**

Article 3. Personality, cognition and behavior in chimpanzees: a new approach based on Eysenck's model

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Photograph by Miquel Llorente

Personality, cognition and behavior in chimpanzees: a new approach based on Eysenck's model

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ABSTRACT

Personality has been linked to individual variation in interest and performance in cognitive tasks. Nevertheless, this relationship is still poorly understood and has rarely been considered in animal cognition research. Here, we investigated the association between personality and interest, motivation and task performance in 13 sanctuary chimpanzees (*Pan troglodytes*) housed at Fundació Mona (Spain). Personality was assessed with a 12-item questionnaire based on Eysenck's Psychoticism-Extraversion-Neuroticism model completed by familiar keepers and researchers. Additionally, personality ratings were compared to behavioral observations conducted over an 11-year period. Experimental tasks consisted in several puzzle boxes that needed to be manipulated in order to obtain a food reward. Dependent variables included participation (as an indicator of interest), success and latency (as measures of performance), and losing contact with the task (as an indicator of motivation). As predicted, we obtained significant correlations between Eysenck's personality traits and observed behaviors, although some expected associations were absent. We then analyzed data using Generalized Linear Mixed Models, running a model for each dependent variable. In both sexes, lower Extraversion and lower Dominance were linked to a higher probability of success, but this effect was stronger in females. Furthermore, higher Neuropsychoticism predicted higher probability of success in females, but not in males. The probability of losing contact with the task was higher in young chimpanzees, and in those rated lower on Extraversion and higher on Dominance. Additionally, chimpanzees rated higher on Neuropsychoticism were also more likely to stop interacting with the task, but again this was more evident in females. Participation and latency were not linked to any personality trait. Our findings show that the PEN may be a good model to describe chimpanzee personality, and stress the importance of considering personality when interpreting the results of cognitive research in non-human primates.

Subjects Animal Behavior, Zoology
Keywords Chimpanzees, Cognition, Cognitive research, Performance, Personality, Behavior

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INTRODUCTION

Research on animal personality has been defined as behavioral inter-individual differences consistent over time and across contexts (*Réale et al., 2007*), and is a field of growing interest, both from a theoretical and an applied perspective. To date, there is evidence that personality traits in non-human animals are similar to those describing human personality (*Gosling, 2001*; *Sih et al., 2004*), and that these traits share common neurophysiological substrates (*Carere, Caramaschi & Fawcett, 2010*; *Koolhaas et al., 2010*; *Latzman et al., 2015*). From an evolutionary point of view, behavioral variation across individuals can generate differences in terms of fitness, and is therefore subject to natural selection (*Réale et al., 2010*; *Smith & Blumstein, 2008*). The study of animal personality can therefore help us to better understand why subjects may respond differently when they face similar conditions (*Carere & Maestripieri, 2013*), thus becoming an important contribution to the fields of animal behavior and cognition (*Carere & Locurto, 2011*; *Griffin, Guillette & Healy, 2015*; *Guillette, Naguib & Griffin, 2017*). In fact, associations between personality and performance in cognitive contexts have been documented in a wide range of taxa, including fish (*Kareklas, Elwood & Holland, 2017*; *White et al., 2017*), birds (*Amy, Van Oers & Naguib, 2012*; *Medina-García, Jawor & Wright, 2017*), ungulates (*Nawroth, Prentice & McElligott, 2017*) and canids (*Svartberg, 2002*).

Personality has been broadly studied in non-human primates (*Freeman & Gosling, 2010*; *Weiss, King & Murray, 2011*), since our closest living relatives constitute an excellent model for comparative research, thus providing insight on the evolutionary origins of human personality (*Figueredo et al., 2015*; *Michalski & Shackelford, 2010*). Firstly, most non-human primates exhibit complex social structures and behaviors, which likely favored the emergence of individual differences (*Adams et al., 2015*; *Mitani et al., 2012*). Secondly, their phylogenetic closeness to humans allows us to better understand and rate their personality traits using questionnaires (*Weiss & Adams, 2013*). Since one of the most relevant attempts to describe chimpanzee personality using a human model with a hierarchical structure (*King & Figueredo, 1997*), several studies in captivity and in the wild have shown that chimpanzees have specific personality dimensions or traits that are common to their species (*King, Weiss & Farmer, 2005*; *Weiss et al., 2012*; *Weiss et al., 2017*), and that questionnaires adapted from human models are reliable measures of their personality (*Freeman et al., 2013*; *Úbeda & Llorente, 2015*; *Weiss & Adams, 2013*; *Weiss et al., 2009*; *Weiss et al., 2017*). Moreover, several studies have reported correlations between trait rating and observed behavior, both in monkeys (*Ebenau et al., 2019*; *Iwanicki & Lehmann, 2015*) and in great apes (*Eckardt et al., 2015*; *Murray, 2011*; *Schaefer & Steklis, 2014*; *Vazire et al., 2007*; *Pederson, King & Landau, 2005*; *Konečná et al., 2008*), thus confirming that personality ratings can successfully predict individual behavior. Nonetheless, the use of a rating methodology is not without limitations. On the one hand, some authors have identified a bias between personality ratings and behavioral coding (*Uher & Asendorpf, 2008*; *Highfill et al., 2010*; *Uher & Visalberghi, 2016*). On the other hand, most studies finding a correlation between both methods only obtained partial convergent validity, and very limited discriminant validity (see *Šlipogor et al., 2020*). In other words, not all the expected traits associate with specific behaviors; some traits may correlate with several behaviors or some behaviors with more than one trait (*Capitanio, 2004*).

The vast majority of studies assessing personality in non-human primates have used the Hominoid Personality Questionnaire or HPQ (*Weiss et al., 2009*), which is based on the human Five Factor Model (*Goldberg, 1990*). The HPQ constitutes a complex personality model consisting of 54 adjectives to rate, which describes five personality traits homologous to the human traits in the Five Factor Model (FFM): Neuroticism, Extraversion, Agreeableness, Conscientiousness, and Openness (to Experience). In addition, the HPQ further contains the trait Dominance, which was described for the first time in chimpanzees (*King & Figueredo, 1997*). More recently, other authors have applied other top-down human models to study chimpanzee personality, such as Eysenck's Psychoticism-Extraversion-Neuroticism model (*Úbeda & Llorente, 2015*) or Cattell's 16 PF (*Ortín et al., 2019*). The Eysencks' psychobiological theory (*Eysenck & Eysenck, 1964*; *Eysenck & Eysenck, 1975*) is focused on the underlying biological mechanisms of personality dimensions. On this matter, higher-order traits (Psychoticism, Extraversion and Neuroticism; PEN model) are based on genetic (*Eaves et al., 1989*) and neurobiological factors (e.g., extraverts present low arousal levels at the ascending reticular activation system; *Eysenck, 1967*; *Eysenck, 1997*). Both the FFM and the PEN model have been empirically validated and can be easily integrated. In fact, they share two common dimensions or traits (Neuroticism and Extraversion); and the third trait described by Eysenck, Psychoticism, has been negatively related to Agreeableness and Conscientiousness in the FFM (*Goldberg & Rosolack, 1994*; *Zuckerman et al., 1993*). According to *Eysenck (1991)*, however, Conscientiousness, Agreeableness and Openness in the FFM were not major components of personality, but rather represented compounds of what he considered the three higher-order traits. Nonetheless, some authors have found moderate correlations between Openness and Eysenck's Extraversion (*Vorkapić, 2012*). Additionally, *Goldberg & Rosolack (1994)* found a link between Goldberg's clusters and the PEN model. In particular, they showed that in Openness' clusters such us intellectuality, depth and foresight, the presumed PEN factor is E- (lower Extraversion); while for the clusters intelligence, nonconformity, sophistication or curiosity, the presumed PEN factor is E+ (high Extraversion).

In their assessment of the PEN model to describe chimpanzees' personality, *Úbeda & Llorente (2015)* adapted a 12-item questionnaire rated on a 7-point Likert scale. The authors identified three dimensions: Extraversion, Neuropsychoticism and Dominance. The adjectives that loaded onto Extraversion were very similar to those reported for humans in that same dimension, thus facilitating the interpretation of this trait. Conversely, they identified a compound dimension including adjectives that in humans loaded onto both Neuroticism and Psychoticism, and was therefore labeled Neuropsychoticism. Finally, the authors identified a third factor, which was denominated Dominance, because the adjectives that loaded onto this trait were among those reported in previous studies for Dominance in chimpanzees (*King & Figueredo, 1997*). This dimension is not directly comparable with any human trait, but it has been repeatedly described in chimpanzees (*Freeman & Gosling,* 2010; King & Figueredo, 1997) and other non-human primates (Adams et al., 2015; Weiss et al., 2011).

In addition to defining personality traits for each species, studies in non-human primates have allowed researchers to evaluate the influence of personality on critical aspects of animals' life, such as health (Robinson et al., 2018), welfare (Robinson et al., 2017) and longevity (Altschul et al., 2018; Weiss et al., 2013). Moreover, several studies have explored the link between personality and cognitive performance in non-human primates, using a variety of experimental tasks and performance measures. The trait Openness for instance, has been linked to training success in both capuchin monkeys (*Sapajus apella*: Morton, Lee & Buchanan-Smith, 2013) and chimpanzees (*Pan troglodytes*: Reamer et al., 2014). Similarly, Wergård et al. (2016) reported that the personality trait Activity was positively associated with training success in long-tailed macaques (*Macaca fascicularis*). In more cognitively demanding situations, some studies have also reported a positive association between Openness and chimpanzees' participation and performance in computerized activities (Altschul et al., 2017; Herrelko, Vick & Buchanan-Smith, 2012) and foraging puzzles (Hopper et al., 2014). Furthermore, Altschul, Terrace & Weiss (2016) reported that rhesus macaques (*Macaca mulatta*) scoring higher in Openness and Friendliness performed better in serial learning tasks. Additionally, when presented with foraging puzzles, male chimpanzees rated higher on Dominance spent more time interacting with the puzzles (Hopper et al., 2014). Conversely, Altschul et al. (2017) concluded that Dominance did not have a major impact on chimpanzees' participation and performance in the computer-based tasks that they tested. Nevertheless, they found that chimpanzees with high Conscientiousness consistently participated more, performed better and were less likely to drop, although this could depend on their preexisting experience with the task (Altschul et al., 2017).

In humans, Conscientiousness has been repeatedly associated with academic achievement (Noftle & Robins, 2007; Von Stumm, Hell & Chamorro-Premuzic, 2011) and job performance (Hurtz & Donovan, 2000; Mount, Barrick & Strauss, 1999; Rrick & Mount, 1991). Conscientious individuals tend to be more goal-oriented and plan more, and they are better able to delay gratification (Roberts et al., 2009). Furthermore, according to several studies, Conscientiousness in the FFM negatively correlates with Psychoticism in the PEN model (Eysenck, 1992), which would explain the negative impact of Psychoticism on academic performance (Flores-Mendoza et al., 2013; Heaven, Ciarrochi & Vialle, 2007; Poropat, 2011). However, Psychoticism has also been consistently linked to creativity (Abraham et al., 2005; Acar & Runco, 2012; Eysenck, 1995). Regarding other personality dimensions present both in the FFM and in the PEN model, like Extraversion or Neuroticism, studies in human and non-human primates are inconsistent, although there are some exceptions worth noting in humans. For example, several authors have demonstrated a link between higher Neuroticism and poorer performance in cognitive tests, either in academic (Chamorro-Premuzic & Furnham, 2003) or non-academic contexts (Dobson, 2000; Reynolds, McClelland & Furnham, 2014). This has been mainly attributed to the fact that highly neurotic individuals are more likely to experience anxiety when exposed to uncertain or stressful situations. To our knowledge, studies in non-human primates have not detected any significant impact of Neuroticism on cognitive performance. However, *Hopper et al. (2014)* found that while performing cognitive tasks, chimpanzees with higher Neuroticism exhibited more self-directed behaviors, which are a common indicator of anxiety in both catarrhine (*Maestripieri et al., 1992*) and platyrrhine primates (*Manson & Perry, 2000*). Finally, in humans, higher Extraversion has been linked to lower academic achievement, presumably because introverts have a focused, goal-oriented attention, and therefore are less easily distracted (*Entwistle & Entwistle, 1970*), whereas extraverts have selective, stimulus-oriented attention and prefer to focus on social activities (*Sánchez, Rejano & Rodríguez, 2001*; *Fishman, Ng & Bellugi, 2011*). It has also been suggested that extraverts and introverts may show different performance depending on the context (*Cox-Fuenzalida et al., 2006*). That is to say, extraverts naturally possess low levels of cortical arousal and therefore they perform better in stimulating environments, while introverts are characterized by high levels of cortical arousal and tend to be less efficient when facing an exciting stimulus, but are more successful at task of longer duration (*Eysenck, 1983*; *Eysenck & Eysenck, 1985*; *Li et al., 2010*).

In view of the scant literature exploring the relationship between personality and performance in non-human primates, and of the controversial results reported so far, the main aims of this study were to (i) assess the correspondence between the personality traits from the PEN model (previously adapted by *Úbeda & Llorente (2015)*) and chimpanzees' spontaneous behavior, and (ii) evaluate whether individual differences in chimpanzees' personality are linked to their interest, motivation and performance in cognitive tasks. Firstly, we expected to find significant correlations between personality traits and behaviors that match the definitions of the traits (e.g., Extraversion positively correlating with social behaviors and with affiliative interactions, such as grooming and social play; Dominance with agonistic dominance; and Neuropsychoticism with agonistic behaviors and with behaviors related to anxiety, such as self-directed behaviors or abnormal behaviors). Secondly, considering that Eysenck's personality traits have been previously linked to cognitive performance in humans, we expected to detect similar associations in chimpanzees. In particular, we predicted that, chimpanzees with higher scores on Extraversion would be more interested in participating in the experimental sessions, as we would expect extraverted individuals to be more curious towards a novel stimulus. However, introverts' focused attention and lower distractibility are highly desirable attributes to be successful in complex tasks such as the ones presented in this study. Therefore we predicted that higher Extraversion would be related to lower success. Additionally, we expected that chimpanzees rated higher on Neuropsychoticism would also be less successful at solving the tasks, as well as more likely to lose motivation, because they would be less patient and more prone to feel anxious during the experimental sessions. Finally, we predicted that Dominance would not play a determinant role in chimpanzees' performance, as previously shown by *Altschul et al. (2017)* and *Hopper et al. (2014)* when assessing complex cognitive tasks in this species. Moreover, considering that previous studies have shown distinct associations between personality traits and performance in male and female chimpanzees (*Hopper et al., 2014*), we also decided to explore sex differences.

MATERIALS & METHODS

Subjects and study site

The study sample consisted of 14 chimpanzees (*Pan troglodytes*), 9 males and 5 females, that ranged in age from 6 to 27 years (mean age ± SD = 17.71 ± 7.46 years) at the beginning of the study period. They were housed at Fundació Mona (Girona, Spain), a center dedicated to the rescue, rehabilitation and re-socialization of primates that have been previously used as pets or for entertainment. The chimpanzees lived in two separate groups, which have been mostly stable over the years. Under good weather conditions, the chimpanzees spend daytime hours in a 5,640 m^2 outdoor enclosure, divided into two areas (2,420 m^2 and 3,220 m^2), one for each group. The enclosure is covered by natural grasses and other Mediterranean herbaceous vegetation subject to seasonal changes, and contains artificial elements such as wooden platforms, towers and ropes. Besides the exterior enclosures, the chimpanzees also have access to 140 m^2 indoor facilities in which they spend the nights and rainy/cold days. Additionally, there are two 25 m^2 exterior cages containing physical enrichment elements, such as ropes and hammocks, which are used to host newly arrived individuals before their integration in a social group. As explained below, the chimpanzees were isolated in this area during the experimental sessions.

Personality ratings

Personality was assessed using a questionnaire based on the Psychoticism-Extraversion-Neuroticism (PEN) model of personality (*Eysenck, 1967*). This tool was used for the first time in chimpanzees in a previous study at Fundació Mona (*Úbeda & Llorente, 2015*). Therefore, 10 of the 14 individuals of our sample had been previously assessed in 2012 using this questionnaire. As described in *Úbeda & Llorente (2015)*, the PEN questionnaire consisted of 12 adjectives rated on a 7-point Likert scale. A brief definition for each trait was also included at the end of the document. An English translation of the original Spanish version of the questionnaire can be found in Questionnaire S1. To determine personality traits, *Úbeda & Llorente (2015)* conducted two different factorial analyses, the Principal Component Analysis (PCA) and the Regularized Exploratory Factor Analysis (REFA). Both methodologies determined the same personality dimensions or traits: Extraversion, Neuropsychoticism and Dominance. The trait Neuropsychoticism was a compound factor which included aspects of both Neuroticism and Psychoticism as described in PEN model for humans (*Eysenck & Eysenck, 1964*).

The four chimpanzees which were not included in the original study were assessed in March 2018 with the same questionnaire, filled by15 raters (26.67% men and 73.33% women). All raters were highly familiar with the subjects, as they all worked as researchers, volunteers or keepers and knew the animals for a minimum of 4 months. When raters did not answer a question, missing data on the ratings was substituted by a neutral score of 4 (*Costa & McCrae, 2008*; *Weiss et al., 2009*). Following the methodology of previous studies (*Úbeda & Llorente, 2015*; *Weiss et al., 2009*), inter-rater reliability was assessed by calculating two intraclass correlation coefficients (ICC) (*Shrout & Fleiss, 1979*) using IBM® SPSS® Statistics 22: ICC (3,1), which indicates the reliability of the scores for a single rater, and ICC (3, k), which indicates the reliabilities of scores based on the mean

Table 1 Factor loadings obtained for the eysencks PEN model based on a Regularized Exploratory Factor Analysis (REFA) (adapted from *Úbeda & Llorente, 2015*).

	Extraversion	Neuropsychoticism	Dominance
Spontaneous	**.79**	.02	.08
Active	**.80**	.07	.11
Sad	**−.76**	.23	.03
Social	**.71**	−.10	.12
Creative	.37	.06	−.10
Aggressive	.08	**.82**	.12
Anxious	−.06	**.69**	−.08
Impulsive	.43	**.65**	−.03
Cruel	−.22	**.56**	−.04
Bad tempered	−.46	**.61**	.13
Dominant	.23	.07	**.97**
Fearful	−.46	.11	−.38

of the total number of raters. As described by *Weiss et al. (2009)*, individual scores on each personality trait for all the 14 chimpanzees were obtained by summing unit-weighted scores of all the adjectives that had salient loadings (>0.50). We used the factor loadings derived from REFA analysis, as this methodology is specifically designed for small samples (*Jung & Lee, 2011*) (see Table 1).

Correlations between personality ratings and behavior

In line with previous studies (*Pederson, King & Landau, 2005*), to further validate the results obtained with the Eysenck questionnaire, we used Spearman correlations to link the personality ratings with behavioral observations conducted at Fundació Mona for a longitudinal study. We used data collected over a total period of 133 months, from April 2006 to September 2017. Over this 11-year observation period, there were several changes in the group composition to integrate new chimpanzees, transfer animals between groups for welfare reasons or due to the natural death of individuals. While acknowledging the effect of this and other temporal factors (e.g., age, changes in well-being, etc.) on the development of chimpanzees' personality and on their behavior, by definition personality should be stable across time and contexts. Moreover, there is evidence that, despite gradual changes over time, specific personality traits remain fundamentally stable and can therefore be detected at different developmental stages (*Weiss et al., 2017*).

Behavioral data were collected using the scan sampling method with 2-minute intervals. Behaviors observed included solitary activities (i.e., abnormal, locomotion, feeding, manipulation, inactivity, self-directed, and other solitary), social interactions (i.e., grooming, agonistic dominance, agonistic submission, other agonistic, social play, sexual behavior, other affiliative, and social proximity), and interactions with humans (positive and negative). Details on the behavioral catalogue are described in Table S1. Additionally, to facilitate interpretation of the correlations between personality ratings and observational data, we created categories which clustered several behaviors. In particular, we defined total agonistic interactions as the combination of agonistic dominance, agonistic submission and other agonistic behaviors; and total affiliative interactions included grooming, social play, sexual behavior and other affiliative behaviors.

We conducted observation sessions of 20 min from two observation towers in the outdoor enclosures. The sessions were randomly distributed during daytime hours, from 10:00 h to 18:30 h. Observations were conducted by different observers, who were only allowed to collect data after completing a training period and successfully passing the inter-observer reliability test (agreement between observers $\geq$ 85%).We included a total of 274204 scans (mean number of scans per individual ± SD = 19,586 ± 8348.21), resulting in 194,238 recorded behaviors, excluding the categories "not visible" and "not present" (15.55% and 13.59% respectively). We also excluded two additional categories from the analysis ("other social" and "other human interactions") because they had very low frequencies (less than 0.02% of the scans). Due to the fact that not all chimpanzees were present from the beginning of the data collection period, data was normalized by calculating the relative frequencies of behaviors with respect to the total number of observed behaviors per individual.

Experimental tasks and procedure

Cognitive tasks and experimental design are detailed in *Riba (2016)*. In brief, the tasks consisted of 11 puzzle boxes made of methacrylate which included different components such as doors, wooden bars, slides and tubes (see Fig. S1). These elements needed to be manipulated in a particular manner for the chimpanzee to complete the task and obtain the food reward in the box (see details in Table 2). Tasks were classified based on their level of complexity (4 simple, 4 intermediate and 3 complex tasks), measured by means of the number of motor actions necessary to solve them. Thus, simple tasks were described as tasks which could be solved by performing a single motor action, intermediate tasks corresponded to those which required two motor actions, and complex tasks required the chimpanzees to perform three or more motor actions. The chimpanzees were assessed during a total period of 3 years and 7 months, between October 2009 and April 2013. One chimpanzee (Cheetah) had not yet arrived at the sanctuary at that time, and therefore she did not participate in the testing sessions.

The first 5 months corresponded to a pilot phase of the study in which all subjects were exposed to three random tasks in three different sessions. To do so, the chimpanzees were isolated by one familiar keeper in an area called the exterior cages (see description above), where all subsequent experimental sessions were conducted. These habituation sessions lasted 10 min and the chimpanzees could see the puzzle boxes, which were placed within sight outside the cages, but they were not allowed to interact with them. The objectives of the pilot phase were to (1) habituate the subjects to the study area and to the cart which would support the puzzle boxes, (2) train the keepers who were going to participate and/or be present during the experimental sessions, and (3) check for intrinsic aspects of the tasks and the procedure, such as the position of the device on the cart or the type of fixation. After this pilot phase, the animals were presented first with simple tasks (2010–2011), followed by intermediate tasks (2011–2012), and finally complex tasks (2012–2013). Tasks never overlapped in time, and each of them was presented separately within a period of

Table 2 Overview of the experimental tasks classified by the level of complexity and description of the actions required to complete each task.

Complexity level	Task	Actions required
Simple	Open Box	(1) Pull/push the front door of the box
	Moveable Tube	(1) Pull/rotate a vertical moveable tube
	Windows Task	(1) Slide a horizontal wooden bar inserted in a tube
	Tube Cube	(1) Slide/rotate a horizontal tube inserted in the box
Intermediate	Artificial Fruit	(1) Push/pull a wooden bar (2) Slide a lid on the top
	Food Box	(1) Slide the frontal door (2) Insert a tool
	Push Box	(1) Slide a horizontal wooden bar (2) Push/pull the frontal door and insert a tool
	Tower Task	(1) Slide a horizontal wooden bar (2) Rotate/pull a vertical tube.
Complex	Complex Food Box	(1) Slide 2 horizontal wooden bars (right side) (2) Slide 1 vertical wooden bar (3) Slide 2 horizontal wooden bars (left side) (4) Open a door on the top
	Complex Moveable Tube	(1) Slide 3 small wooden bars (2) Slide a large horizontal bar (3) Rotate/pull a tube (4) Slide the front door
	Complex Artificial Fruit	(1) Push/pull a wooden bar (right side) (2) Pull/push a wooden bar (central position) (3) Pull/push a wooden bar (left side) (4) Slide a lid on the top (5) Rotate a plastic tube

two to three months. The experimental sessions were randomly distributed throughout this period, according to the keepers' availability and other management needs.

The original purpose of the study by *Riba (2016)* was to investigate the occurrence of social learning. Therefore, before being tested, subjects received three different types of information on how to solve the puzzle boxes: (1) Control (no information), (2) No social information (the subject only saw the end state of the task, without seeing any of the actions necessary to solve it), and (3) Social information (the subject saw both the actions of the demonstrator and the end state of the task). Each subject received all three conditions in each set of complexity level, but subjects were exposed to a different task within each complexity level. Thus, task, level of complexity and type of information were counterbalanced across subjects, resulting in a total of nine possible combinations This means that not all subjects performed all the tasks, but they all performed 3 simple, 3 intermediate and 3 complex tasks (one Control, one with No social information and one with Social information for each complexity level; see Table S2). Additionally, to evaluate the effect of causal information, every task consisted in two versions of the puzzle box, one transparent and one opaque. Therefore, for each task, subjects were exposed to both the transparent and the opaque version of the apparatus, within the same session. The order in which the two versions were presented was counterbalanced between subjects.

The experimental session began when the subject was called by a keeper to participate in the experiment and entered the exterior cages. After this, the door to the indoor facilities was closed and the subject remained isolated from the group. Before starting the testing phase, there was a 10-minute habituation phase, in which the keeper stayed in close proximity to the cages and the chimpanzees could already see the experimenter and the apparatus from afar (in its initial state). During this phase, the experimenter conducted *ad libitum* observations, particularly looking for behavioral signs of anxiety or discomfort (e.g., abnormal or stereotypical behaviors, agonistic displays). When these behaviors were detected and the chimpanzee did not approach the apparatus in the first 5 min, the session was terminated. Conversely, if no signs of distress were observed during the habituation phase, the experimenter placed the apparatus in front of the subject, specifically in front the barred sliding door of the exterior cages, through which the animals could see it but not touch it (Figs. 1A and 1B). This allowed the subjects to familiarize with the puzzle boxes before starting the testing phase. Exposure time varied according to task complexity (i.e., 1 min for simple tasks, 2 min for intermediate tasks and 3 min for complex tasks). Additionally, in the No social information condition, the apparatus was removed from the individual's view after the first exposure, so that the human experimenter could manipulate it. Then, it was presented once again to the subject in its final state (solved), with the sliding door remaining closed, thus preventing the chimpanzee to reach the apparatus. Exposure time to this final state also varied according to task complexity (6 min for simple tasks, 12 min for intermediate tasks and 20 min for complex tasks). The time elapsed between the two types of exposure (initial state and final state of the apparatus) was between 2 and 5 min, depending on the task complexity. Afterwards, the apparatus was moved out of the chimpanzees' view, so that the experimenter could return it to its initial state (not solved). Immediately after that, it was placed again in front of the animal, before starting the testing phase. Finally, in the Social information condition, the experimenter performed the task in front of the individual for several times (6 demonstrations for simple tasks, 12 demonstrations for intermediate tasks and 20 demonstrations for complex tasks) with the apparatus facing the animal (Fig. 1C).

In all conditions, the testing phase began when the sliding door was displaced (Fig. 1D), thus allowing subjects the first contact with the task. The chimpanzees were presented with one puzzle box per session and they had 8 attempts to solve it (4 for the transparent version and 4 for the opaque version). The time allowed for the solution of the task was 2 min for the simple tasks, 4 min for the intermediate tasks and 6 min for the complex tasks. After this time had elapsed, the trial ended and the apparatus was moved out of the individual's reach, so that the experimenter could return it to its initial state. Immediately after that, it was presented to the subject again, thus initiating a new trial. In total, each subject participated in 9 experimental sessions of 8 trials each, thus making a total of 72 trials: 24 trials for the simple tasks, 24 for the intermediate tasks and 24 for the complex tasks (see details in Table S2). For two chimpanzees (Juanito and Tom) a few trials in the complex tasks (9 and 8, respectively) had to be discarded due to demonstration failures and camera

Figure 1 **Exterior cages in which the experimental sessions were conducted.** (A) Detail of the sliding door. (B) Exposure phase: the door was closed, so that the chimpanzee could see but not touch the apparatus. (C) Social information condition: a keeper performed the task in front of the individual. (D) Testing phase: the sliding door had been displaced and the subject could interact with the task through the bars.

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failure. Besides the experimenter, one familiar keeper was always present throughout the habituation and the testing phases, to provide animals with a safe trusted environment during the tasks. All sessions were videotaped for subsequent analyses with a digital camera placed in a frontal or a semi-lateral position at a distance of 60–80 cm from the subject. Video coding of all sessions was conducted by a single experimenter (David Riba).

Performance measures

We used participation as a measure of interest, success and latency to solve the task as measures of performance, and losing contact with the task as an indicator of lack of motivation. When chimpanzees (1) refused to enter the experimental area, (2) did not approach the apparatus or (3) did not establish contact with it, we assigned them a score of 0 for participation. On the other hand, if they interacted with the apparatus, even if it was for a very short time, we assigned them a score of 1. An attempt was considered successful if the subject completed the task and retrieved the reward from the box within the given time. Latency was described as the time (in seconds) between the first contact with the apparatus and the moment the task was solved. Finally, we considered that a subject lost contact with the task if it stopped manipulating the apparatus or its components for more than 15 s and/or walked away at least 1 meter. We only considered the first-time that subjects lost contact. Thus, for each trial, a subject was assigned a score of 0 if it remained engaged with the task the whole time and a score of 1 if it stopped manipulating it at least once.

Data analysis

To investigate whether interest, motivation and performance were affected by personality, we used Generalized Linear Mixed Models (GLMM) (*Baayen, 2008*). For response variables with binomial distribution (participation, success and losing contact with the task), we used the function "glmer" from the package "lme4" (version 1.1-17; *Bates et al., 2015*) in R (R Core Team, version 3.5.0), whereas for latency, which had a normal distribution, we used the "lmer" function.

We ran 4 different models, one for each response measure as dependent variable: participation (Model 1), success (Model 2), latency (Model 3) and losing contact with the task (Model 4). In all models, age and personality traits (Extraversion, Neuropsychoticism and Dominance) in interaction with sex were included as test predictors, whereas we entered task complexity (simple, intermediate or complex), information provided to the subject (Control, No social information or Social information), trial number (1–4), box color (opaque or transparent) and box order (first opaque or first transparent) as control predictors. We included subject's identity as random effect, fitting random slopes as needed.

In all models, continuous predictors were z-transformed to facilitate model convergence and standardize interpretation of model coefficients. To compare full models containing all predictors with null models containing only control predictors, we used a likelihood ratio test (function "anova") (*Dobson, 2002*). If full models significantly differed from null models ($p \leq 0.05$), we conducted likelihood ratio tests to obtain the p values for each predictor via single-term deletion, using the R function drop1 (*Barr et al., 2013*). If the 2-way interactions were not significant, we downgraded them and re-ran the model including the 2 test predictors as main effects. To rule out collinearity, we calculated variance inflation factors (VIF) (*Field, 2009*), which were very good in all models (maximum VIF across models = 2.39). Finally, we assessed dispersion for the non-gaussian models and we found that, none of them was over-dispersed (dispersion parameters <1), except for Model 4. Therefore, in order to avoid over-dispersion, we ran a simplified version of the model, removing the control predictors "task complexity" and "information type", as well as the random slopes. No convergence issues were detected in the models.

Ethics statement

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures involving animals were in accordance with the ethical standards of the institution at which the studies were conducted (Fundació Mona; Ethical Approval Number: EAFM201801) and with the Spanish Government RD 53/2013. This project also received the ethical approval from the Ethics Committee of the Universitat de Girona (Project Code: CEBRU0020-2019).

Table 3 Intraclass correlation coefficients (ICCs) for the 12 items of the questionnaire. ICC (3, 1) indicates the reliability of the scores for a single rater, and ICC (3, *k*) indicates the reliabilities of scores based on the mean of the total number of raters.

	ICC (3, 1)	**ICC (3, k)**
Social	.42	.81
Active	.49	.85
Dominant	.44	.82
Spontaneous	.38	.79
Anxious	.38	.78
Badtempered	.37	.78
Fearful	.29	.71
Sad	.37	.78
Agresssive	.50	.86
Impulsive	.40	.80
Cruel	.28	.70
Creative	.19	.59
Mean	**.38**	**.77**
SD	**.09**	**.07**

RESULTS

Personality ratings

Considering the 14 chimpanzees whose personality was assessed between 2012 and 2018, the ICCs for the single (3, 1) and average (3, k) ratings were high, indicating that raters tended to agree in their judgments about the personality items (Table 3). ICC (3, 1) ranged from 0.19 (*creative*) to 0.50 (*aggressive*), with a mean reliability of 0.38. On the other hand, ICC (3, k) ranged from 0.59 (*creative*) to 0.86 (*aggressive*), with a mean reliability of 0.77. After being transformed into T-scores (mean ± SD = 50 ± 10), the values of the personality traits ranged from 22.02 to 63.44 (Extraversion), from 35.17 to 64.84 (Neuropsychoticism), and from 37.90 to 63.52 (Dominance).

Correlations between personality ratings and behavior

We obtained significant correlations between personality traits and behaviors which matched their descriptions (Table 4 and Table S3). In particular, Extraversion was positively correlated with social behaviors (i.e., grooming, social play, and the combined category total affiliative interactions); Neuropsychoticism was positively associated with total agonistic interactions (which included both dominant and submissive behaviors); and Dominance positively correlated with agonistic dominance, but also with total agonistic interactions. We also found unexpected correlations, such as higher Extraversion being linked to agonistic dominance and Neuropsychoticism being negatively associated with foraging. Moreover, contrary to our predictions, Neuropsychoticism was not related to behavioral indicators of anxiety, such as self-directed behaviors or abnormal behaviors. Finally, regarding the associations between traits, no significant correlations were found, but the positive correlation between Dominance and Neuropsychoticism was close to significance (Table 5).

Table 4 Behaviors and clusters of behaviors that correlated (Spearman correlation) with Eysencks personality traits.

		Agonistic dominance	Grooming	Social play	Foraging	Agonistic interactions[a]	Affiliative interactions[b]
Extraversion	r	**.614**	**.705**	**.692**	.147	.529	**.730**
	p	**.020**	**.005**	**.006**	.615	.052	**.003**
	95% CI	**[.079, .929]**	**[.147, .957]**	**[.250, .928]**	[−.385, .668]	[−.019, .862]	**[.355, .888]**
Neuropsychoticism	r	.211	.099	−.115	**−.640**	**.562**	.064
	p	.469	.737	0.697	**.014**	**.037**	.828
	95% CI	[−.323, .697]	[−.408, .557]	[−.653, .596]	**[−.945, −.172]**	**[.137, .806]**	[−.493, .554]
Dominance	r	**.557**	.547	−.084	−.055	**.594**	.378
	p	**.039**	.043	.776	.852	**.025**	.182
	95% CI	**[.028, .892]**	[−.014, .900]	[−.623, .454]	[−.563, .476]	**[.118, .871]**	[−.236, .811]

Notes.

$N = 14$. Significant results are marked in bold ($p < 0.05$; 95% CI do not overlap 0).

[a] Agonistic interactions included agonistic dominance, agonistic submission and other agonistic behaviors.

[b] Affiliative interactions included grooming, social play, sexual behavior and other affiliative behaviors.

Table 5 Spearman correlations between chimpanzees' scores on Eysenck's personality dimensions.

		Extraversion	Neuropsychoticism
Extraversion	r		
	p	–	–
	95% CI		
Neuropsychoticism	r	.073	
	p	.805	–
	95% CI	[−.385, .470]	
Dominance	r	.429	.525
	p	.126	.054
	95% CI	[−.220, .886]	[−.115, .865]

Notes.

$N = 14$. Significant results are marked in bold ($p < 0.05$; 95% CI do not overlap 0).

Association between personality traits and interest, motivation and performance

The results obtained in the cognitive tasks are summarized in Table S4. Participation and success were high (mean participation ± SD = 0.81 ± 0.22, range = 0.35–1.00; mean success ± SD = 0.91 ± 0.13, range = 0.57–1.00) and the chimpanzees lost contact with the task very rarely (mean value of losing contact with the task ± SD = 5.21 ± 8.36%, range = 0.00–21.00). Mean latency across all tasks ± SD = 30.55 ± 15.57 s and, as expected, it differed significantly across complexity levels ($\chi^2 = 18.00$, $df = 2$, $p < 0.001$). Results of the 4 models evaluating the relationship between personality and participation, success, latency and losing contact with the task are presented in Table 6.

Participation. In Model 1, the full model significantly differed from the null model (GLMM: $\chi^2 = 26.98$, $df = 8$, $p < 0.001$), but none of the test predictors had a significant effect. After downgrading the non-significant 2-way interactions and including personality traits and sex as main effects, the full-null model comparison was not significant, thus revealing that none of the test predictors predicted participation.

Success. In Model 2, the comparison between full and null models was significant (GLMM: $\chi^2 = 15.84$, $df = 8$, $p = 0.045$). All personality traits in interaction with sex predicted chimpanzees' success (Extraversion*sex: $p = 0.012$; Neuropsychoticism*sex: $p = 0.003$; Dominance*sex: $p < 0.001$), but the test predictor age was not significant. In particular, lower Extraversion slightly increased the probability of being successful in males, while highly increasing it in females (see Table 6; Fig. 2). Similarly, lower Dominance predicted a higher probability of success in both sexes, but this effect was stronger in females (see Table 6; Fig. 3). Finally, higher Neuropsychoticism predicted a higher probability of female success, but a slightly lower probability of success in males (see Table 6; Fig. 4).

Latency. In Model 3, the comparison between the full and null model was not significant (GLMM: $\chi^2 = 2.37$, $df = 8$, $p = 0.967$), even after downgrading the 2-way interactions and re-running the model including the personality traits and sex as main effects. Thus, personality traits, sex and age did not predict individuals' latency to complete the task.

Losing contact with the task. In Model 4, the full-null model comparison was significant (GLMM: $\chi^2 = 27.48$, $df = 8$, $p < 0.001$). Neuropsychoticism in interaction with sex and age were the only significant predictors of the probability of losing motivation and stopping manipulation of the task. After downgrading the non-significant 2-way interactions, we also found a significant effect of Extraversion ($p < 0.001$), Dominance ($p = 0.012$), age ($p = 0.019$), and the 2-way interaction of Neuropsychoticism and sex ($p = 0.002$). In particular, higher Neuropsychoticism highly increased the probability of losing contact with the task in females, and only slightly increased it in males (see Table 6; Fig. 5). In both sexes, higher Extraversion was linked to a lower probability of losing motivation and stopping manipulation of the task (see Table 6; Fig. 6), whereas higher Dominance was associated with a higher probability of losing contact with the task in both sexes (see Table 6; Fig. 7). Finally, younger individuals had a higher probability to lose motivation and stop interacting with the task, as compared to older ones (see Table 6; Fig. 8).

DISCUSSION

In this study, we first compared behavioral observations of 14 captive chimpanzees with ratings from a 12-item personality questionnaire based on Eysenck's PEN model (*Úbeda & Llorente, 2015*); and then we assessed the relationship between personality traits and interest, motivation and performance in cognitive tasks in a subsample of 13 individuals. Firstly, the traits obtained from the ratings significantly correlated with behavioral observations conducted over an 11-year period, but some expected correlations were absent. Secondly, our results showed that participation and latency were not associated with any personality trait from the PEN model. Partially in line with our predictions, the probability of success increased with lower Extraversion and lower Dominance, but this was more evident for females. Unexpectedly, success was also higher in females with higher Neuropsychoticism. The probability of losing motivation and stopping interaction with the task were higher in younger chimpanzees, and in those rated higher on Dominance and lower on Extraversion. Finally, and in agreement with our predictions, individuals scoring higher in Neuropsychoticism were also more likely to lose motivation, especially in females.

Inter-rater reliabilities in the personality questionnaires were similar to those reported in previous studies (*Úbeda & Llorente, 2015*; *King & Figueredo, 1997*; *Weiss et al., 2009*), and indicated substantial agreement among raters. The correlations between personality traits and behaviors confirmed that there was some evidence for convergent validity. In particular, Extraversion positively correlated with total affiliative behaviors and with grooming and social play considered separately; and Dominance correlated with total agonistic interactions and with agonistic dominance independently. These associations were similar to those reported in previous studies on chimpanzees (*Pederson, King & Landau, 2005*; *Vazire et al., 2007*) and other great apes (*Eckardt et al., 2015*; *Kuhar et al., 2006*; *Schaefer & Steklis, 2014*). Moreover, Neuropsychoticism positively correlated with total agonistic interactions, confirming that chimpanzees with higher Neuropsychoticism are in fact more anxious, impulsive and aggressive, which is also consistent with Eysenck's definition of these traits (*Eysenck & Eysenck, 1964*). Neuropsychoticism was also negatively associated with foraging, which we interpreted as neuropsychotic chimpanzees being less prone to explore the enclosures to look for food, or perhaps dedicating more time to vigilance (*Digman, 1990*) or to aggressive interactions. Another possible explanation could be that neuropsychotic individuals have reduced levels of activity, as it has been found in bonobos that show more anxious behavior (i.e., higher rates of self-scratching) (*Staes et al., 2016*). Hence, a decrease in foraging would simply be a consequence of lower levels of general activity. Contrary to our predictions, however, Neuropsychoticism was not related to behavioral indicators of anxiety, such as self-directed behaviors or abnormal behaviors. However, it should be noted that our definition of self-directed behaviors included some behaviors, such as body inspection and self-grooming, which may not necessarily be indicators of anxiety or stress (*Meyer & Hamel, 2014*). Finally, we found some unexpected correlations, such as higher Extraversion being linked to agonistic dominance. Surprisingly, previous studies have reported an association between aggression and Extraversion in chimpanzees (*Freeman et al., 2013*) and in gorillas (*Kuhar et al., 2006*). Nonetheless, an important limitation of our study is that the category agonistic dominance encompassed a wide range of behaviors, from directed displays to resource displacement, but also aggression. Therefore, to further investigate the association between personality and aggression, a more detailed behavioral catalogue should be employed in the future, to better distinguish between aggressive and non-aggressive dominant behaviors.

It should also be noted that some behaviors or clusters of behaviors correlated with more than one trait (e.g., agonistic dominance correlating with both Dominance and Extraversion; and total agonistic interactions correlating with both Dominance and Neuropsychoticism), thus revealing limited discriminant validity for the PEN model.

Nevertheless, this was not entirely unexpected. Firstly, the positive correlation between the traits Dominance and Neuropsychoticism, which was close to significance, suggested that, at least in our study sample, these two traits were partially associated. Therefore, it was no surprise that, some behaviors were common for both traits. Furthermore, finding

Table 6 **Results of Models 1–4.** For each model and predictor, estimates, standard errors (SE), likelihood ratio tests (LRT), degrees of freedom (df), and *p*-values (*p*).

Models	Estimate	SE	LRT	df	*P*
Model 1: Participation					
Intercept	1.151	1.794	–	–	–
Dominance	−1.320	1.578	0.84	1	0.360
Extraversion	2.383	1.240	3.51	1	0.061
Neuropsychoticism	−1.025	1.582	0.55	1	0.458
Sex (male)	4.486	2.179	3.81	1	0.051
Age	1.477	1.486	1.18	1	0.278
Task complexity	−0.256	0.564	0.21	1	0.648
Information type	0.747	0.654	1.43	1	0.232
Trial number	−0.297	0.138	4.53	1	**0.033**
Box color	0.328	0.285	1.28	1	0.258
Box order	−0.470	0.396	1.36	1	0.244
Model 2: Success					
Intercept	6.934	2.282	–	–	–
Dominance	−13.120	2.906	–	–	–
Extraversion	−23.638	7.868	–	–	–
Neuropsychoticism	12.106	3.374	–	–	–
Sex (male)	−3.328	2.191	–	–	–
Dominance*Sex(male)	12.676	3.042	11.03	1	**<0.001**
Extraversion*Sex(male)	22.811	7.642	6.28	1	**0.012**
Neuropsychoticism*Sex(male)	−12.563	3.462	8.78	1	**0.003**
Age	−1.226	0.819	1.95	1	0.162
Task complexity	−0.290	0.606	0.19	1	0.660
Information type	0.977	0.252	12.17	1	**<0.001**
Trial number	0.805	0.191	20.51	1	**<0.001**
Box color	0.130	0.358	0.13	1	0.719
Box order	−0.205	0.412	0.24	1	0.623
Model 3: Latency					
Intercept	46.724	9.043	–	–	–
Dominance	−1.123	3.697	0.19	1	0.667
Extraversion	4.230	4.150	1.70	1	0.193
Neuropsychoticism	0.671	3.375	0.06	1	0.800
Sex (male)	7.176	5.838	2.36	1	0.125
Age	0.677	3.364	0.11	1	0.742
Task complexity	41.209	1.983	339.59	1	**<0.001**
Information type	−2.465	1.872	1.72	1	0.190
Trial number	−5.545	1.533	13.16	1	**<0.001**
Box color	0.819	3.134	0.08	1	0.781
Box order	1.682	3.298	0.18	1	0.669
Model 4: Lose contact with task					
Intercept	−11.514	1.867	–	–	–

(*continued on next page*)

Table 6 (*continued*)

Models	Estimate	SE	LRT	df	*P*
Dominance	1.033	0.451	6.35	1	**0.012**
Extraversion	−1.466	0.340	12.50	1	**<0.001**
Neuropsychoticism	7.433	1.337	–	–	–
Sex (male)	7.572	1.687	–	–	–
Dominance*Sex(male)	–	–	–	–	–
Extraversion*Sex(male)	–	–	–	–	–
Neuropsychoticism*Sex (male)	−6.901	1.434	10.02	1	**0.002**
Age	−0.930	0.337	5.52	1	**0.019**
Task complexity	–	–	–	–	–
Information type	–	–	–	–	–
Trial number	−0.451	0.176	6.91	1	**0.009**
Box color	0.168	0.345	0.24	1	0.626
Box order	0.123	0.354	0.12	1	0.727

Notes.

$N = 13$. Reference categories for categorical predictors are included in parentheses. Significant results are marked in bold. Personality traits, age and trial number were z-transformed prior to analyses. In all models, subject identity was included as random effect. In Model 4 complexity and information type were removed from the model to avoid overdispersion.

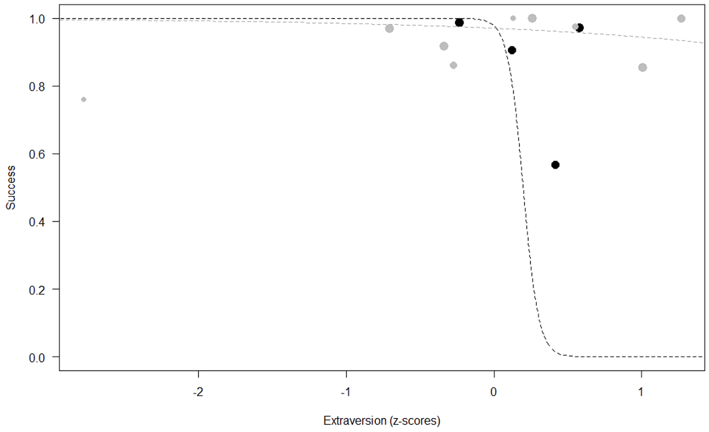

Figure 2 **Probability of success as a function of Extraversion.** The dots represent the individuals tested (females in black, males in grey), with their size being proportional to the number of trials in which they participated. The dashed lines depict the models, which have been back-transformed from the log-odds ratio scale (black for females, grey for males).

Full-size DOI: 10.7717/peerj.9707/fig-2

a straightforward correspondence between personality traits and behaviors is a challenging endeavor (*Pederson, King & Landau, 2005*; *Konečná et al., 2008*), as several traits likely play a role in defining how a subject behaves (*Capitanio, 2004*). In particular, given that the questionnaire used in this study was fairly short, and only three dimensions were considered, the convergence of several behaviors in one trait was expected. Hierarchical personality models, like Eysenck's or the FFM, describe higher order traits which include several specific traits; and these lower traits are characterized by several behavioral responses (*Eysenck, 1990*; *DeYoung, 2006*; *DeYoung, 2010*). Finally, it should be noted than we only had a small sample of chimpanzees, all coming from the same site (a primate rescue centre),

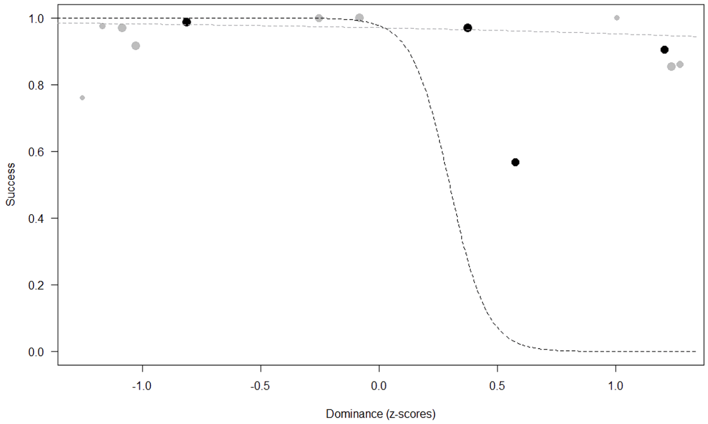

Figure 3 **Probability of success as a function of Dominance.** The dots represent the individuals tested (females in black, males in grey), with their size being proportional to the number of trials in which they participated. The dashed lines depict the models, which have been back-transformed from the log-odds ratio scale (black for females, grey for males).

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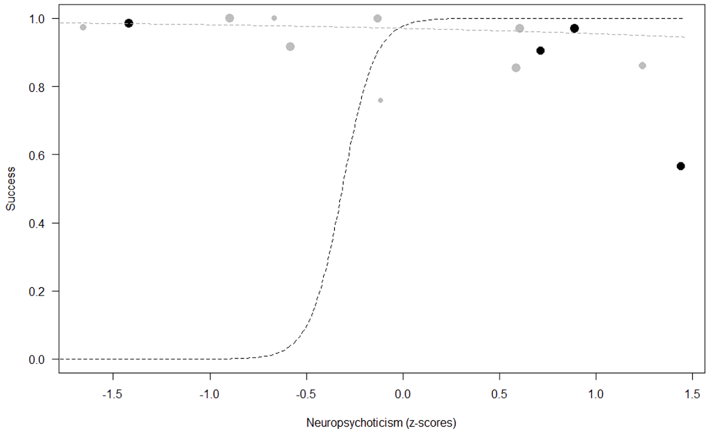

Figure 4 **Probability of success as a function of Neuropsychoticism.** The dots represent the individuals tested (females in black, males in grey), with their size being proportional to the number of trials in which they participated. The dashed lines depict the models, which have been back-transformed from the log-odds ratio scale (black for females, grey for males).

Full-size 🖼 DOI: 10.7717/peerj.9707/fig-4

with some of them having been exposed to traumatic past experiences which most likely shaped their personality (*Ortín et al., 2019*) and their behavior (*Crailsheim et al., 2020*).

Regarding our predictions for personality and performance in the puzzle boxes, only the models for success and losing contact with the task were significant. In view of the association between Extraversion in the PEN model and Openness in the FFM (*Vorkapić, 2012*); and taking into account that, by definition, extraverts are more explorative and curious, we expected individuals higher in Extraversion to be more interested in the tasks (i.e., to participate more). Additionally, considering the male-dominated hierarchy of chimpanzees both in the wild (*Kaburu & Newton-Fisher, 2015*; *Newton-Fisher, 2004*) and in

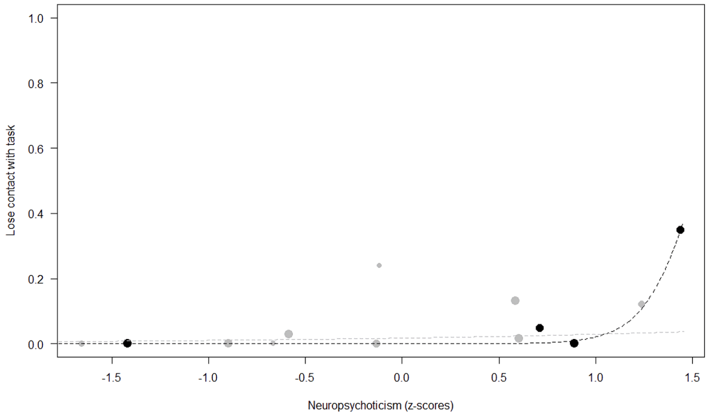

Figure 5 **Probability of losing contact with the task as a function of Neuropsychoticism.** The dots represent the individuals tested (females in black, males in grey), with their size being proportional to the number of trials in which they participated. The dashed lines depict the models, which have been back-transformed from the log-odds ratio scale (black for females, grey for males).

Full-size DOI: 10.7717/peerj.9707/fig-5

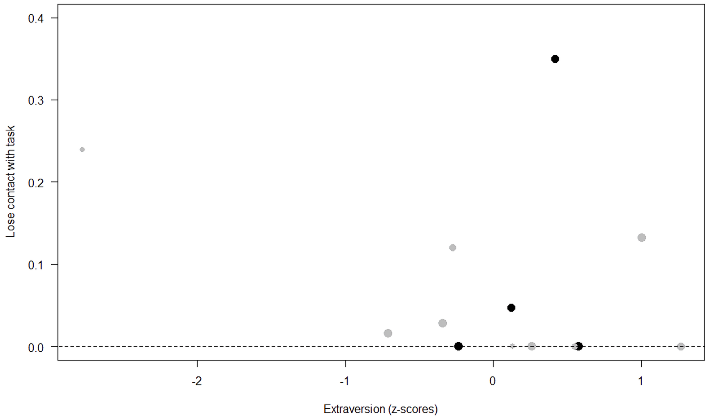

Figure 6 **Probability of losing contact with the task as a function of Extraversion.** The dots represent the individuals tested (females in black, males in grey), with their size being proportional to the number of trials in which they participated. The dashed lines depict the model, which has been back-transformed from the log-odds ratio scale.

Full-size DOI: 10.7717/peerj.9707/fig-6

captivity (*De Waal, 1986*; *Noë, De Waal & Van Hooff, 1980*), it would not be surprising that dominant males would feel more confident in front of a novel stimulus. Previous studies in chimpanzees reported a positive association between Dominance and participation in cognitive testing, but with inconsistencies across tasks (*Altschul et al., 2017*). *Hopper et al. (2014)* found that males scoring higher in Dominance spent more time interacting with a foraging puzzle, which can also be considered an indicator of interest. However, neither Extraversion nor Dominance was related to participation in the puzzle boxes. A possible explanation might be that, in our questionnaire, none of the adjectives directly assessed curiosity or exploration. Among the adjectives that loaded onto Extraversion, we

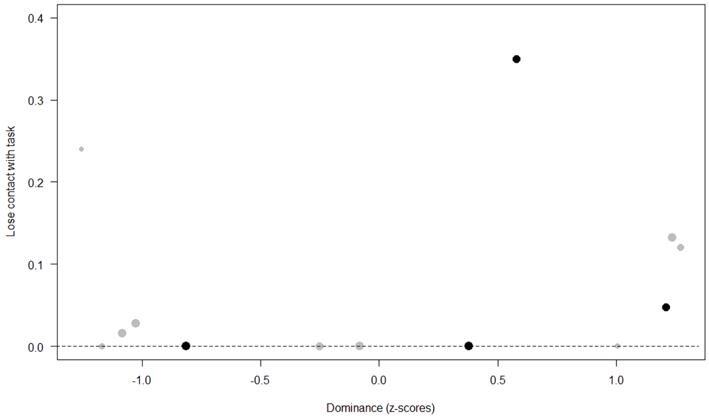

Figure 7 **Probability of losing contact with the task as a function of Dominance.** The dots represent the individuals tested (females in black, males in grey), with their size being proportional to the number of trials in which they participated. The dashed lines depict the model, which has been back-transformed from the log-odds ratio scale.

Full-size DOI: 10.7717/peerj.9707/fig-7

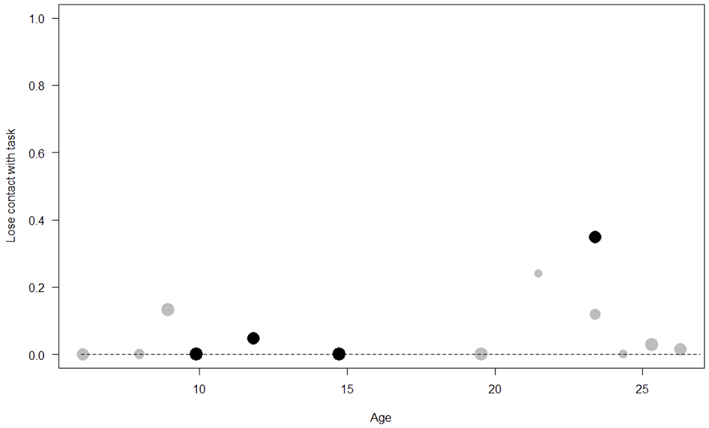

Figure 8 **Probability of losing contact with the task as a function of age.** The dots represent the individuals tested (females in black, males in grey), with their size being proportional to the number of trials in which they participated. The dashed lines depict the model, which has been back-transformed from the log-odds ratio scale.

Full-size DOI: 10.7717/peerj.9707/fig-8

find "spontaneous" and "active", which could somehow be related to exploration, but we also have "not sad" and "social", which may not be particularly relevant in a testing context. Therefore, Extraversion in our model may be more descriptive of the social aspect of the trait. Finally, it should be pointed out that, in this study, chimpanzees were actively encouraged to participate in the experimental sessions by the keepers. Therefore, we could assume that extraverts would show a greater response to this social stimulus, or rather that the role of the keeper might have affected the results by greatly increasing overall participation, regardless of personality. In the future, it would be recommended to set up an experimental design in which subjects can actively decide whether to engage in the task or not.

The probability to be successful was positively associated with lower Dominance and lower Extraversion in both sexes, although for both traits this relationship was more evident in females. This would contradict previous findings in chimpanzees indicating that dominant males were more successful in a foraging puzzle (*Hopper et al., 2014*). However, our results are in line with an experiment using a touchscreen testing system (*Leighty et al., 2011*), in which dominant mandrills (*Mandrillus sphinx*) required more sessions to be successful than subordinates. The authors suggested that dominant monkeys were more likely to focus their attention on social interactions than engaging in solitary activities, and were thus less successful. Similarly, *Morton, Lee & Buchanan-Smith (2013)* found a negative relationship between Assertiveness and performance in capuchin monkeys, which they also attributed to highly assertive individuals prioritizing social interactions over task engagement. In line with this, it has been stated that male chimpanzees would be primarily interested in social relationships and dominance hierarchy, as compared to females (*Lonsdorf, 2005*). However, in this study, we found no evidence that the link between Dominance and success was stronger in males. Nonetheless, sex differences in the effect of personality traits in success should be taken with caution, given that our sample only included a small number of females and that one female showed a particularly poor performance.

Our results on Extraversion confirmed our predictions, showing a negative effect of this trait on the probability of success. According to Eysenck's theory, introverts are more patient and have more goal-oriented attention. Furthermore, introverts' higher levels of cortical arousal allow them to sustain their attention even under less stimulating conditions (*Eysenck, 1981*). In our study, puzzle boxes required animals to persist in assembling the different components without getting any reward until they completely solved the task. Therefore, more introverted individuals might have been advantaged when solving these tasks. These results are in line with previous research on humans, showing a negative relationship between Extraversion and academic performance, possibly because extraverts are more social, easily distracted and impulsive (*Chamorro-Premuzic & Furnham, 2003*; *Sánchez, Rejano & Rodríguez, 2001*), but also more reward sensitive (*Depue & Collins, 1999*; *Smillie, 2013*). However, the effect of Extraversion in non-human primates is, to date, more controversial. *Altschul et al. (2017)*, for instance, found that chimpanzees scoring higher in Extraversion were more accurate in a touchscreen cognitive task. Furthermore, studies on macaques (*Macaca mulatta* and *Macaca fascicularis*) showed a link between success in cognitive tasks and being "active" or "friendly" (*Altschul, Terrace & Weiss, 2016*; *Wergård et al., 2016*), which are adjectives that load onto the trait Extraversion. In our study, however, subjects had to be isolated from the social group during the test, and this might have also contributed to the negative association we found between higher Extraversion and success. In particular, more introverted individuals might have been less disturbed by isolation, and might have been more likely to focus on solitary activities. Also, this may be especially true for the chimpanzees in our study, as they are rarely isolated from their group and, with the exception of the experiments described in this study, they hardly ever participate in testing sessions.

In contrast with our predictions, Neuropsychoticism was linked to higher probability of success in females. Nonetheless, as expected, higher scores on this trait slightly increased the probability of success in males. Studies in non-human primates have failed to report any relationship between Neuroticism and cognitive performance (*Altschul et al., 2017*; *Morton, Lee & Buchanan-Smith, 2013*). However, in an experiment on social learning in wild baboons (*Papio ursinus*), *Carter et al. (2014)* reported that more anxious individuals were more likely to improve their performance in a hidden-object task after watching a demonstrator. In contrast, *Schubiger et al. (2015)* found that male marmosets (*Callithrix jacchus*) showing higher emotional reactivity towards the experimenter (i.e., highly neurotic individuals) were less likely to participate in cognitive tasks, but this did not affect their performance. In humans, higher Neuroticism and higher Psychoticism have been repeatedly linked to poorer performance, both in academic (*Chamorro-Premuzic & Furnham, 2003*; *Flores-Mendoza et al., 2013*; *Poropat, 2011*) and non-academic contexts (*Dobson, 2000*; *Reynolds, McClelland & Furnham, 2014*), and especially under stressful conditions (*Byrne, Silasi-Mansat & Worthy, 2015*). Nonetheless, *Eysenck (1981)* suggested that the relationship between Neuroticism and performance depends on the intelligence of the subject: higher Neuroticism is related to higher academic achievement in more intelligent individuals, who are better able to cope with anxiety, while the opposite pattern is observed for less intelligent subjects. Other researchers have suggested that neurotics are more creative problem-solvers, because they tend to think about different possibilities and scenarios when they face a new situation (*Perkins et al., 2015*). Similarly, the dimension Psychoticism in humans includes adjectives such as "imaginative" (*Goldberg & Rosolack, 1994*), and it has been linked to creativity (*Abraham et al., 2005*; *Acar & Runco, 2012*; *Eysenck, 1995*).

Unsurprisingly, Neuropsychoticism was positively associated with the probability of losing motivation in both sexes, but again this effect was stronger in females. In our study, the puzzle boxes required individuals to be persistent and constant, attributes that are quite opposite to the adjectives that load onto this factor, such as "anxious" and "impulsive" (*Úbeda & Llorente, 2015*). Therefore, individuals higher in Neuropsychoticism might have been more likely to become anxious and frustrated during the task, ultimately resulting in loss of motivation. Earlier research in chimpanzees has linked higher Neuroticism with the production of self-directed behaviors (a common indicator of anxiety) during cognitive tasks (*Herrelko, Vick & Buchanan-Smith, 2012*). These findings appear consistent with research in humans, in which Neuroticism has been associated with high levels of tension (*Zajenkowska, Zajenkowski & Jankowski, 2015*) and test anxiety (*Zeidner & Matthews, 2000*). On the other hand, Psychoticism in humans is not only related to impulsivity (*Chico et al., 2003*; *Eysenck et al., 1985*), but also to low persistence and lack of cooperation (*Howarth, 1986*). Although the puzzle boxes did not require cooperative behavior, they did require collaboration with the experimenter and the keeper, who were always present during the experimental sessions and interacted with the puzzle boxes in some conditions. Therefore, being more collaborative might have favored motivation in our study. Likewise, this could also explain why, for both sexes, Extraversion was negatively linked to the probability of losing contact with the task. Initially, more extraverted individuals might have been less predisposed to leave their group to participate in the testing sessions. However, once the chimpanzee was in the experimental area, he received the attention of the experimenter, and more importantly, of a familiar keeper. In contrast, Dominance was found to be positively associated with the probability of losing contact with the task, suggesting that dominant chimpanzees might have been less interested in the testing sessions and more eager to return to their group. Finally, our results showed that younger individuals were more likely to lose motivation and stop manipulating the tasks, perhaps because they were more active and attentive to their surroundings, and thus more susceptible to distraction (*Riopelle & Rogers, 1965*). Studies with larger samples of non-human primates have indeed reported controversial results regarding the effect of age on interest and motivation towards new stimuli (*Almeling et al., 2016*; *Bliss-Moreau & Baxter, 2019*; *Massen et al., 2013*). Our results may be also explained by the characteristics of our study sample, which included 4 juveniles and otherwise relatively young adults (all <28 years), but no older individuals. Therefore, a negative effect of aging described by some authors (*Almeling et al., 2016*) would have been, by all means, impossible to detect.

Overall, regardless of personality, participation and success were considerably high (above 80% and 90% respectively), and chimpanzees lost contact with the task in only 5% of the trials in which they participated. This suggests that our study subjects were highly interested in the puzzle boxes: they made considerable efforts to solve them, and were often successful. Besides participation, latency was also not related to any personality trait. These results, however, were not entirely unexpected. Firstly, in one of the few studies assessing this measure, *Hopper et al. (2014)* also failed to report any link between personality traits and latency to success. Moreover, in our study, latency was highly influenced by the fact that a limited time was given to the chimpanzees to solve the tasks, and this time increased with complexity. Thus, as we anticipated, subjects spent more time solving complex than intermediate tasks, and more time solving intermediate than simple tasks. In other words, task complexity was the most important factor predicting latency. In this study, the time given to subjects to solve the puzzle boxes was deemed to be sufficient and in accordance with their level of difficulty. Nonetheless, it is impossible to tell whether, given the opportunity, subjects would continue trying to solve the boxes and if so, for how long.

To our knowledge, this study is the first to link Eysenck's personality dimensions with cognition in non-human primates, providing some theoretical and practical advantages. Firstly, the PEN model (*Eysenck, 1967*) associates personality traits with the functioning and structure of cortical and limbic brain regions (*Mitchell & Kumari, 2016*), which facilitates the understanding of non-human primates personality from an evolutionary and neurobiological perspective. On the other hand, and in contrast with other rating models, the questionnaire we used is less time consuming for the raters, as it includes only 12 adjectives to evaluate. This is particularly useful, considering that most raters are animal keepers who usually lack the time to dedicate to research activities. Therefore, shorter questionnaires can be especially advantageous to evaluate personality in zoos and sanctuaries (*Hopper & Cronin, 2018*). Nonetheless, we are aware of the limits of the PEN model, which lacks traits like Openness or Conscientiousness (which are described in the FFM), that might importantly affect performance in experimental contexts. In the future, more studies should use different personality questionnaires to better assess the link between personality and cognitive performance. Also, rather than comparing personality ratings with spontaneous behavior, as we did in the present study, assessing behavioral patterns in a testing context could provide a complementary approach to the study of personality (*Massen et al., 2013*).

We would also like to highlight that the purpose of this study was not to establish a link between personality and a specific cognitive ability (*Griffin, Guillette & Healy, 2015*), as the tasks here described were not designed for this purpose. Furthermore, comparisons with other species need to be taken with caution, as cognitive tasks are done with different procedures and personality is often assessed with different tools across species (see *Morton et al., 2013*). Finally, our results warn against generalizing cognitive abilities at the species level, particularly if testing a small sample of subjects, as they could substantially differ in their performance due to personality variation. Moreover, other sources of individual differences may also modulate subjects' performance, such as past experiences (*Bard et al., 2014*), rearing conditions (*Simpson et al., 2019*), affective state (*Bethell et al., 2012*), and genetic variables (*Hopkins et al., 2014*). Additionally, future studies may also consider assessing rank when studying primate cognition particularly if tasks are presented in a social context (*Wergård et al., 2016*). This was unfortunately not possible in the present study, due to changes in group composition and dominance hierarchies that occurred throughout the data collection period. Finally, one of the main limitations of this study was the low statistical power due to the small sample, as well as the fact that males and females were unevenly represented, with males greatly outnumbering females. Therefore, we need to be especially cautious when interpreting sex differences in our models. For example, the fact that personality traits more strongly affected performance in females could depend on the small number of females tested, with inter-individual differences having been magnified.

Last but not least, studying the relationship between personality and measures like interest or motivation can have important implications for animal welfare. Given that individuals with different personality profiles may benefit from different types of cognitive enrichment (*Carere & Locurto, 2011*), understanding individual differences in personality may be transferred to improving management and quality of life in animals under human control, thus having a positive impact on welfare and conservation (*Gartner & Weiss, 2018*). In line with this, besides personality, future cognitive research involving captive animals should also consider including welfare indicators that can be monitored during experimental testing. Furthermore, cognitive experiments in a social setting should be considered as an alternative to subjects' isolation, which would increase validity of findings and improve animal welfare (*Cronin, 2017*).

CONCLUSIONS

In line with our predictions, chimpanzees' behavior correlated with some of the personality dimensions described by Eysenck's PEN model, although construct validity was relatively low. Nonetheless, the PEN model offers some practical advantages compared to other questionnaires, being simpler and less time consuming. Moreover, as predicted, personality traits were related to subjects' performance in an experimental context. In particular, success was negatively related to Extraversion and Dominance, with these associations being more evident in females. Furthermore, Neuropsychoticism was positively associated with success in females, but not in males. As expected, higher Neuropsychoticism was associated with loss of motivation and therefore higher probability of the chimpanzees stopping manipulating the puzzle boxes, especially in females. Additionally, younger chimpanzees, and those rated lower on Extraversion and higher on Dominance were also more likely to stop interacting with the task. Participation and latency were not related to any personality trait. These findings stress the importance of considering personality when assessing cognitive performance in non-human primates, as the outcomes of a particular test may not necessarily reflect the subject's ability to perform the task, but rather individual differences in personality.

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Maria Padrell and Yulán Úbeda analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, collection of personality data, and approved the final draft.
- David Riba conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Federica Amici analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Miquel Llorente analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

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Data Availability

The following information was supplied regarding data availability:

Raw data for performance measures, personality and behaviour are available in the Supplemental Files.

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REFERENCES

Abraham A, Windmann S, Daum I, Güntürkün O. 2005. Conceptual expansion and creative imagery as a function of psychoticism. *Consciousness and Cognition* **14**:520–534 DOI 10.1016/j.concog.2004.12.003.

Acar S, Runco MA. 2012. Psychoticism and creativity: a meta-analytic review. *Psychology of Aesthetics, Creativity, and the Arts* **6(4)**:341–350 DOI 10.1037/a0027497.

Adams M, Majolo B, Ostner J, Schülke O, Marco A, Thierry B, Engelhardt A, Widdig A, Gerald MS, Weiss A. 2015. Personality structure and social style in macaques. *Journal of Personality and Social Psychology* **109**:338–353 DOI 10.1037/pspp0000041.

Almeling L, Hammerschmidt K, Sennhenn-Reulen H, Freund AM, Fischer J. 2016. Motivational shifts in aging monkeys and the origins of social selectivity. *Current Biology* **26**:1744–1749 DOI 10.1016/j.cub.2016.04.066.

Altschul DM, Hopkins WD, Herrelko ES, Inoue-Murayama M, Matsuzawa T, King JE, Ross SR, Weiss A. 2018. Personality links with lifespan in chimpanzees. *eLife* **7**:e33781 DOI 10.7554/eLife.33781.

Altschul DM, Terrace HS, Weiss A. 2016. Serial cognition and personality in macaques. *Animal Behavior and Cognition* **3**:46–64 DOI 10.12966/abc.02.04.2016.

Altschul DM, Wallace E, Sonnweber R, Tomonaga M, Weiss A. 2017. Chimpanzee intellect: personality, performance and motivation with touchscreen tasks. *Royal Society Open Science* **4(5)**:170169 DOI 10.1098/rsos.170169.

Amy M, Van Oers K, Naguib M. 2012. Worms under cover: relationships between performance in learning tasks and personality in great tits (*Parus major*). *Animal Cognition* **15**:763–770 DOI 10.1007/s10071-012-0500-3.

Baayen RH. 2008. *Analyzing linguistic data: a practical introduction to statistics using R*. Cambridge: Cambridge University Press.

Bard KA, Bakeman R, Boysen ST, Leavens DA. 2014. Emotional engagements predict and enhance social cognition in young chimpanzees. *Developmental Science* **17**:682–696 DOI 10.1111/desc.12145.

Barr DJ, Levy R, Scheepers C, Tily HJ. 2013. Random effects structure for confirmatory hypothesis testing: keep it maximal. *Journal of Memory and Language* **68**:255–278 DOI 10.1016/j.jml.2012.11.001.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv* **67**:48 DOI 10.18637/jss.v067.i01.

Bethell EJ, Holmes A, Maclarnon A, Semple S. 2012. Cognitive bias in a non-human primate: husbandry procedures influence cognitive indicators of psychological well-being in captive rhesus macaques. *Animal Welfare* **21**:185–195 DOI 10.7120/09627286.21.2.185.

Bliss-Moreau E, Baxter MG. 2019. Interest in non-social novel stimuli as a function of age in rhesus monkeys. *Royal Society Open Science* **6(9)**:182237 DOI 10.1098/rsos.182237.

Byrne KA, Silasi-Mansat CD, Worthy DA. 2015. Who chokes under pressure? The big five personality traits and decision-making under pressure. *Personality and Individual Differences* **74**:22–28 DOI 10.1016/j.paid.2014.10.009.

Capitanio J. 2004. Personality factors between and within species. In: Thierry B, Singh M, Kaumanns W, eds. *Macaque societies: a model for the study of social organization*. Cambridge: Cambridge University Press, 13–33.

Carere C, Caramaschi D, Fawcett TW. 2010. Covariation between personalities and individual differences in coping with stress: converging evidence and hypotheses. *Current Zoology* **56**:728–740 DOI 10.1093/czoolo/56.6.728.

Carere C, Locurto C. 2011. Interaction between animal personality and animal cognition. *Current Zoology* **57**:491–498 DOI 10.1093/czoolo/57.4.491.

Carere C, Maestripieri D. 2013. *Animal personalities: behavior, physiology, and evolution*. Chicago: University of Chicago Press.

Carter AJ, Marshall HH, Heinsohn R, Cowlishaw G. 2014. Personality predicts the propensity for social learning in a wild primate. *PeerJ* **2**:e283 DOI 10.7717/peerj.283.

Chamorro-Premuzic T, Furnham A. 2003. Personality traits and academic examination performance. *European Journal of Personality* **17**:237–250 DOI 10.1002/per.473.

Chico E, Tous J, Lorenzo-Seva U, Vigil-Colet A. 2003. Spanish adaptation of Dickman's impulsivity inventory: its relationship to Eysenck's personality questionnaire. *Personality and Individual Differences* **35**:1883–1892 DOI 10.1016/S0191-8869(03)00037-0.

Costa PT, McCrae RR. 2008. The Revised NEO Personality Inventory (NEO-PI-R). In: Boyle GJ, Matthews G, Saklofske DH, eds. *The sage handbook of personality theory and assessment: Volume 2—personality measurement and testing*. London: SAGE Publications, 179–198 DOI 10.4135/9781849200479.n9.

Cox-Fuenzalida L-E, Angie A, Holloway S, Sohl L. 2006. Extraversion and task performance: a fresh look through the workload history lens. *Journal of Research in Personality* **40**:432–439 DOI 10.1016/j.jrp.2005.02.003.

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

Cronin KA. 2017. Studying primate cognition in a social setting to improve validity and welfare: a literature review highlighting successful approaches. *PeerJ* **5**:e3649 DOI 10.7717/peerj.3649.

De Waal FBM. 1986. The brutal elimination of a rival among captive male chimpanzees. *Ethology and Sociobiology* **7**:237–251 DOI 10.1016/0162-3095(86)90051-8.

Depue RA, Collins PF. 1999. Neurobiology of the structure of personality: dopamine, facilitation of incentive motivation, and extraversion. *Behavioral and Brain Sciences* **22**:491–517 DOI 10.1017/s0140525x99002046.

DeYoung CG. 2006. Higher-order factors of the Big Five in a multi-informant sample. *Journal of Personality and Social Psychology* **91**:1138–1151 DOI 10.1037/0022-3514.91.6.1138.

DeYoung CG. 2010. Personality neuroscience and the biology of traits. *Social and Personality Psychology Compass* **4**:1165–1180 DOI 10.1111/j.1751-9004.2010.00327.x.

Digman JM. 1990. Personality structure: emergence of the five-factor model. *Annual Review of Psychology* **41**:417–440 DOI 10.1146/annurev.ps.41.020190.002221.

Dobson AJ. 2002. *An introduction to generalized linear models*. Boca Raton: Chapman & Hall/CRC.

Dobson P. 2000. An investigation into the relationship between neuroticism, extraversion and cognitive test performance in selection. *International Journal of Selection and Assessment* **8**:99–109 DOI 10.1111/1468-2389.00140.

Eaves LJ, Eysenck HJ, Martin NG, Jardine R, Heath AC, Feingold L, Young PA, Kendler KS. 1989. *Genes, culture, and personality*. London: Academic Press.

Ebenau A, Von Borell C, Penke L, Ostner J, Schülke O. 2019. Integrative personality assessment in wild Assamese macaques (*Macaca assamensis*). *Journal of Comparative Psychology* **134**:27–41 DOI 10.1037/com0000190.

Eckardt W, Steklis DH, Steklis NG, Fletcher AW, Stoinski TS, Weiss A. 2015. Personality dimensions and their behavioral correlates in wild Virunga mountain gorillas (*Gorilla beringei beringei*). *Journal of Comparative Psychology* **129**:26–41 DOI 10.1037/a0038370.

Entwistle NJ, Entwistle D. 1970. The relationships between personality, study methods and academic performance. *British Journal of Educational Psychology* **40**:132–143 DOI 10.1111/j.2044-8279.1970.tb02113.x.

Eysenck HJ. 1967. *The biological basis of personality*. Springfield: Charles C. Thomas.

Eysenck HJ. 1981. General features of the model. In: Eysenck HJ, ed. *A model for personality*. Berlin, Heidelberg: Springer, 1–37.

Eysenck HJ. 1983. Psychophysiology and personality: extraversion, neuroticism and psychoticism. In: Gale A, Edwards JA, eds. *Individual differences and psychopathology*. London: Academic Press, 13–30.

Eysenck HJ. 1990. Biological dimensions of personality. In: Pervin LA, ed. *Handbook of personality: theory and research*. New York: The Guilford Press, 244–276.

Eysenck HJ. 1991. Dimensions of personality: 16, 5 or 3? Criteria for a taxonomic paradigm. *Personality and Individual Differences* **12**:773–790 DOI 10.1016/0191-8869(91)90144-Z.

Eysenck HJ. 1992. Four ways five factors are not basic. *Personality and Individual Differences* **13**:667–673 DOI 10.1016/0191-8869(92)90237-J.

Eysenck HJ. 1995. Creativity as a product of intelligence and personality. In: Saklofske DH, Zeidner M, eds. *International handbook of personality and intelligence*. Boston: Springer, 231–247.

Eysenck HJ. 1997. Personality and experimental psychology: the unification of psychology and the possibility of a paradigm. *Journal of Personality and Social Psychology* **73**:1224–1237 DOI 10.1037/0022-3514.73.6.1224.

Eysenck HJ, Eysenck MW. 1985. *Personality and individual differences: a natural science approach*. New York: Plenum.

Eysenck HJ, Eysenck SBG. 1975. *Manual of the Eysenck personality questionnaire*. London: Hodder and Stoughton.

Eysenck SBG, Eysenck HJ. 1964. An improved short questionnaire for the measurement of extraversion and neuroticism. *Life Sciences* **3**:1103–1109 DOI 10.1016/0024-3205(64)90125-0.

Eysenck SBG, Pearson PR, Easting G, Allsopp JF. 1985. Age norms for impulsiveness, venturesomeness and empathy in adults. *Personality and Individual Differences* **6**:613–619 DOI 10.1016/0191-8869(85)90011-X.

Field A. 2009. *Discovering statistics using SPSS*. London: SAGE Publications.

Figueredo AJ, Sefcek JA, Vasquez G, Brumbach BH, King JE, Jacobs WJ. 2015. Evolutionary personality psychology. In: Buss DM, ed. *The handbook of evolutionary psychology*. Hoboken: John Wiley & Sons, 851–877 DOI 10.1002/9780470939376.ch30.

Fishman I, Ng R, Bellugi U. 2011. Do extraverts process social stimuli differently from introverts? *Cognitive Neuroscience* **2**:67–73.

Flores-Mendoza C, Widaman K, Mansur-Alves M, Bacelar TD, Saldanha R. 2013. Psychoticism and disruptive behavior can be also good predictors of school achievement. *The Spanish Journal of Psychology* **16**:E13 DOI 10.1017/sjp.2013.3.

Freeman HD, Brosnan SF, Hopper LM, Lambeth SP, Schapiro SJ, Gosling SD. 2013. Developing a comprehensive and comparative questionnaire for measuring personality in chimpanzees using a simultaneous top-down/bottom-up design. *American Journal of Primatology* **75**:1042–1053 DOI 10.1002/ajp.22168.

Freeman HD, Gosling SD. 2010. Personality in nonhuman primates: a review and evaluation of past research. *American Journal of Primatology* **72**:653–671 DOI 10.1002/ajp.20833.

Gartner M, Weiss A. 2018. Studying primate personality in zoos: implications for the management, welfare and conservation of great apes. *International Zoo Yearbook* **52**:79–91 DOI 10.1111/izy.12187.

Goldberg LR. 1990. An alternative "description of personality": the big-five factor structure. *Journal of Personality and Social Psychology* **59**:1216–1229 DOI 10.1037/0022-3514.59.6.1216.

Goldberg LR, Rosolack TK. 1994. The Big Five factor structure as an integrative framework: an empirical comparison with Eysenck's P-E-N model. In: Halverson CF, Kohnstamm GA, Martin RP, eds. *The developing structure of temperament and personality from infancy to adulthood*. Hillsdale: Lawrence Erlbaum Associates, Inc., 7–35.

Gosling SD. 2001. From mice to men: what can we learn about personality from animal research? *Psychological Bulletin* **127**:45–86 DOI 10.1037/0033-2909.127.1.45.

Griffin AS, Guillette LM, Healy SD. 2015. Cognition and personality: an analysis of an emerging field. *Trends in Ecology & Evolution* **30**:207–214 DOI 10.1016/j.tree.2015.01.012.

Guillette LM, Naguib M, Griffin AS. 2017. Individual differences in cognition and personality. *Behavioural Processes* **134**:1–3 DOI 10.1016/j.beproc.2016.12.001.

Heaven PCL, Ciarrochi J, Vialle W. 2007. Conscientiousness and Eysenckian psychoticism as predictors of school grades: a one-year longitudinal study. *Personality and Individual Differences* **42**:535–546 DOI 10.1016/j.paid.2006.07.028.

Herrelko ES, Vick SJ, Buchanan-Smith HM. 2012. Cognitive research in zoo-housed chimpanzees: influence of personality and impact on welfare. *American Journal of Physical Anthropology* **74**:828–840 DOI 10.1002/ajp.22036.

Highfill L, Hanbury D, Kristiansen R, Kuczaj S, Watson S. 2010. Rating vs. coding in animal personality research. *Zoo Biology* **29**:509–516 DOI 10.1002/zoo.20279.

Hopkins WD, Keebaugh AC, Reamer LA, Schaeffer J, Schapiro SJ, Young LJ. 2014. Genetic influences on receptive joint attention in chimpanzees (*Pan troglodytes*). *Scientific Reports* **4**:3774 DOI 10.1038/srep03774.

Hopper LM, Cronin KA. 2018. A multi-institutional assessment of a short-form personality questionnaire for use with macaques. *Zoo Biology* **37**:281–289 DOI 10.1002/zoo.21439.

Hopper LM, Price SA, Freeman HD, Lambeth SP, Schapiro SJ, Kendal RL. 2014. Influence of personality, age, sex, and estrous state on chimpanzee problem-solving success. *Animal Cognition* **17**:835–847 DOI 10.1007/s10071-013-0715-y.

Howarth E. 1986. What does Eysenck's psychoticism scale really measure? *British Journal of Psychology* **77**:223–227 DOI 10.1111/j.2044-8295.1986.tb01996.x.

Hurtz GM, Donovan JJ. 2000. Personality and job performance: the big five revisited. *Journal of Applied Psychology* **85**:869–879 DOI 10.1037/0021-9010.85.6.869.

Iwanicki S, Lehmann J. 2015. Behavioral and trait rating assessments of personality in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology* **129**:205–217 DOI 10.1037/a0039318.

Jung S, Lee S. 2011. Exploratory factor analysis for small samples. *Behavioral Research Methods* **43**:701–709 DOI 10.3758/s13428-011-0077-9.

Kaburu SSK, Newton-Fisher NE. 2015. Egalitarian despots: hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, *Pan troglodytes*. *Animal Behaviour* **99**:61–71 DOI 10.1016/j.anbehav.2014.10.018.

Kareklas K, Elwood RW, Holland RA. 2017. Personality effects on spatial learning: comparisons between visual conditions in a weakly electric fish. *Ethology* **123**:551–559 DOI 10.1111/eth.12629.

King JE, Figueredo AJ. 1997. The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality* **31**:257–271 DOI 10.1006/jrpe.1997.2179.

King JE, Weiss A, Farmer KH. 2005. A chimpanzee (*Pan troglodytes*) analogue of cross-national generalization of personality structure: zoological parks and an African sanctuary. *Journal of Personality* **73**:389–410 DOI 10.1111/j.1467-6494.2005.00313.x.

Konečná M, Lhota S, Weiss A, Urbánek T, Adamová T, Pluháček J. 2008. Personality in free-ranging Hanuman langur (*Semnopithecus entellus*) males: subjective ratings and recorded behavior. *Journal of Comparative Psychology* **122**:379–389 DOI 10.1037/a0012625.

Koolhaas JM, De Boer SF, Coppens CM, Buwalda B. 2010. Neuroendocrinology of coping styles: towards understanding the biology of individual variation. *Frontiers in Neuroendocrinology* **31**:307–321 DOI 10.1016/j.yfrne.2010.04.001.

Kuhar CW, Stoinski TS, Lukas KE, Maple TL. 2006. Gorilla behavior index revisited: age, housing and behavior. *Applied Animal Behaviour Science* **96**:315–326 DOI 10.1016/j.applanim.2005.06.004.

Latzman RD, Hecht LK, Freeman HD, Schapiro SJ, Hopkins WD. 2015. Neuroanatomical correlates of personality in chimpanzees (*Pan troglodytes*): associations between personality and frontal cortex. *NeuroImage* **123**:63–71 DOI 10.1016/j.neuroimage.2015.08.041.

Leighty KA, Maloney MA, Kuhar CW, Phillips RS, Wild JM, Chaplin MS, Bettinger TL. 2011. Use of a touchscreen-mediated testing system with mandrill monkeys. *International Journal of Comparative Psychology* **24**:60–75.

Li J, Tian M, Fang H, Xu M, Li H, Liu J. 2010. Extraversion predicts individual differences in face recognition. *Communicative & Integrative Biology* **3**:295–298 DOI 10.4161/cib.3.4.12093.

Llorente M, Riba D, Ballesta S, Feliu O, Rostán C. 2015. Rehabilitation and socialization of chimpanzees (*Pan troglodytes*) used for entertainment and as pets: an 8-year study at Fundació Mona. *International Journal of Primatology* **36**:605–624 DOI 10.1007/s10764-015-9842-4.

Lonsdorf EV. 2005. Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes* schweinfurthii, of Gombe National Park, Tanzania. *Animal Behaviour* **70**:673–683 DOI 10.1016/j.anbehav.2004.12.014.

Maestripieri D, Schino G, Aureli F, Troisi A. 1992. A modest proposal: displacement activities as an indicator of emotions in primates. *Animal Behaviour* **44**:967–979 DOI 10.1016/S0003-3472(05)80592-5,.

Manson JH, Perry S. 2000. Correlates of self-directed behaviour in wild white-faced capuchins. *Ethology* **106**:301–317 DOI 10.1046/j.1439-0310.2000.00527.x.

Massen JJ, Antonides A, Arnold AM, Bionda T, Koski SE. 2013. A behavioral view on chimpanzee personality: exploration tendency, persistence, boldness, and tool-orientation measured with group experiments. *American Journal of Primatology* **75**:947–958 DOI 10.1002/ajp.22159.

Medina-García A, Jawor JM, Wright TF. 2017. Cognition, personality, and stress in budgerigars, Melopsittacus undulatus. *Behavioral Ecology* **28**:1504–1516 DOI 10.1093/beheco/arx116.

Meyer JS, Hamel AF. 2014. Models of stress in nonhuman primates and their relevance for human psychopathology and endocrine dysfunction. *ILAR Journal* **55(2)**:347–360 DOI 10.1093/ilar/ilu023.

Michalski RL, Shackelford TK. 2010. Evolutionary personality psychology: reconciling human nature and individual differences. *Personality and Individual Differences* **48**:509–516 DOI 10.1016/j.paid.2009.10.027.

Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB. 2012. *The evolution of primate societies.* Chicago: University of Chicago Press.

Mitchell RLC, Kumari V. 2016. Hans Eysenck's interface between the brain and personality: modern evidence on the cognitive neuroscience of personality. *Personality and Individual Differences* **103**:74–81 DOI 10.1016/j.paid.2016.04.009.

Morton BF, Lee PC, Buchanan-Smith HM. 2013. Taking personality selection bias seriously in animal cognition research: a case study in capuchin monkeys (*Sapajus apella*). *Animal Cognition* **16**:677–684 DOI 10.1007/s10071-013-0603-5.

Morton BF, Lee PC, Buchanan-Smith HM, Brosnan SF, Thierry B, Paukner A, De Waal FBM, Widness J, Essler JL, Weiss A. 2013. Personality structure in brown capuchin monkeys (*Sapajus apella*): Comparisons with chimpanzees (*Pan troglodytes*), orangutans (*Pongo spp.*), and rhesus macaques (*Macaca mulatta*). *Journal of Comparative Psychology* **127**(**3**):282–290 DOI 10.1037/a0031723.

Mount MK, Barrick MR, Strauss JP. 1999. The joint relationship of conscientiousness and ability with performance: test of the interaction hypothesis. *Journal of Management* **25**:707–721 DOI 10.1016/S0149-2063(99)00022-7.

Murray L. 2011. Predicting primate behavior from personality ratings. In: Weiss A, King JE, Murray L, eds. *Personality and temperament in nonhuman primates.* New York: Springer, 129–167.

Nawroth C, Prentice PM, McElligott AG. 2017. Individual personality differences in goats predict their performance in visual learning and non-associative cognitive tasks. *Behavioural Processes* **134**:43–53 DOI 10.1016/j.beproc.2016.08.001.

Newton-Fisher NE. 2004. Hierarchy and social status in Budongo chimpanzees. *Primates* **45**:81–87 DOI 10.1007/s10329-003-0064-6.

Noë R, De Waal FBM, Van Hooff JARAM. 1980. Types of dominance in a chimpanzee colony. *Folia Primatologica* **34**:90–110 DOI 10.1159/000155949.

Noftle EE, Robins RW. 2007. Personality predictors of academic outcomes: big five correlates of GPA and SAT scores. *Journal of Personality and Social Psychology* **93**(**1**):116–130 DOI 10.1037/0022-3514.93.1.116.

Ortín S, Ubeda Y, Garriga RM, Llorente M. 2019. Bushmeat trade consequences predict higher anxiety, restraint, and dominance in chimpanzees. *Developmental Psychobiology* **61**(**2**):874–887 DOI 10.1002/dev.21853.

Pederson AK, King JE, Landau VI. 2005. Chimpanzee (*Pan troglodytes*) personality predicts behavior. *Journal of Research in Personality* **39**:534–549 DOI 10.1016/j.jrp.2004.07.002.

Perkins AM, Arnone D, Smallwood J, Mobbs D. 2015. Thinking too much: self-generated thought as the engine of neuroticism. *Trends in Cognitive Sciences* **19**:492–498 DOI 10.1016/j.tics.2015.07.003.

Poropat AE. 2011. The Eysenckian personality factors and their correlations with academic performance. *British Journal of Educational Psychology* **81**:41–58 DOI 10.1348/000709910x497671.

Réale D, Dingemanse NJ, Kazem AJN, Wright J. 2010. Evolutionary and ecological approaches to the study of personality. *Philosophical Transactions of the Royal Society of London B* **365**:3937–3946 DOI 10.1098/rstb.2010.0222.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* **82**:291–318 DOI 10.1111/j.1469-185x.2007.00010.x.

Reamer LA, Haller RL, Thiele EJ, Freeman HD, Lambeth SP, Schapiro SJ. 2014. Factors affecting initial training success of blood glucose testing in captive chimpanzees (*Pan troglodytes*). *Zoo Biology* **33**:212–220 DOI 10.1002/zoo.21123.

Reynolds J, McClelland A, Furnham A. 2014. An investigation of cognitive test performance across conditions of silence, background noise and music as a function of neuroticism. *Anxiety, Stress, & Coping* **27**:410–421.

Riba D. 2016. *Mecanismos cognitivos de aprendizaje social en chimpancés (Pan troglodytes): evaluación experimental a través de múltiples tareas. D. Phil. Thesis*, Universitat Rovira i Virgili DOI 10.1002/dev.21853.

Riopelle AJ, Rogers CM. 1965. Age changes in chimpanzees. In: Schrier AM, Harlow HF, Stolnitz F, eds. *Behavior of nonhuman primates: modern research trends.* New York: Academic Press, 449–462.

Roberts BW, Jackson JJ, Fayard JV, Edmonds G, Meints J. 2009. Conscientiousness. In: Leary MR, Hoyle RH, eds. *Handbook of individual differences in social behavior.* New York: The Guilford Press, 369–381.

Robinson LM, Altschul DM, Wallace EK, Úbeda Y, Llorente M, Machanda Z, Slocombe KE, Leach MC, Waran NK, Weiss A. 2017. Chimpanzees with positive welfare are happier, extraverted, and emotionally stable. *Applied Animal Behaviour Science* **191**:90–97 DOI 10.1016/j.applanim.2017.02.008.

Robinson LM, Coleman K, Capitanio JP, Gottlieb DH, Handel IG, Adams MJ, Leach MC, Waran NK, Weiss A. 2018. Rhesus macaque personality, dominance, behavior, and health. *American Journal of Primatology* **80**:e22739 DOI 10.1002/ajp.22739.

Rrick MR, Mount MK. 1991. The Big Five personality dimensions and job performance: a meta-analysis. *Personnel Psychology* **44**:1–26 DOI 10.1111/j.1744-6570.1991.tb00688.x.

Sánchez MM, Rejano EI, Rodríguez YT. 2001. Personality and academic productivity in the university student. *Social Behavior and Personality: an International Journal* **29**:299–305 DOI 10.2224/sbp.2001.29.3.299.

Schaefer SA, Steklis HD. 2014. Personality and subjective well-being in captive male western lowland gorillas living in bachelor groups. *American Journal of Primatology* **76**:879–889 DOI 10.1002/ajp.22275.

Shrout PE, Fleiss JL. 1979. Intraclass correlations: uses in assessing rater reliability. *Psychological Bulletin* **86**:420–428.

Schubiger MN, Wüstholz FL, Wunder A, Burkart JM. 2015. High emotional reactivity toward an experimenter affects participation, but not performance, in cognitive tests with common marmosets (Callithrix jacchus). *Animal cognition* **18(3)**:701–712 DOI 10.1007/s10071-015-0837-5.

Sih A, Bell AM, Johnson JC, Ziemba RE. 2004. Behavioral syndromes: an integrative overview. *The Quarterly Review of Biology* **79**:241–277 DOI 10.1086/422893.

Simpson EA, Sclafani V, Paukner A, Kaburu SSK, Suomi SJ, Ferrari PF. 2019. Handling newborn monkeys alters later exploratory, cognitive, and social behaviors. *Developmental Cognitive Neuroscience* **35**:12–19 DOI 10.1016/j.dcn.2017.07.010.

Šlipogor V, Burkart JM, Martin JS, Bugnyar T, Koski SE. 2020. Personality method validation in common marmosets (*Callithrix jacchus*): getting the best of both worlds. *Journal of Comparative Psychology* **134**:52–70 DOI 10.1037/com0000188.

Smillie LD. 2013. Extraversion and reward processing. *Current Directions in Psychological Science* **22**:167–172 DOI 10.1177/0963721412470133.

Smith BR, Blumstein DT. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* **19**:448–455 DOI 10.1093/beheco/arm144.

Staes N, Weiss A, Helsen P, Korody M, Eens M, Stevens JMG. 2016. Bonobo personality traits are heritable and associated with vasopressin receptor gene 1a variation. *Scientific Reports* **6**:38193 DOI 10.1038/srep38193.

Svartberg K. 2002. Shyness–boldness predicts performance in working dogs. *Applied Animal Behaviour Science* **79**:157–174 DOI 10.1016/S0168-1591(02)00120-X.

Úbeda Y, Llorente M. 2015. Personality in sanctuary-housed chimpanzees: a comparative approach of psychobiological and penta-factorial human models. *Evolutionary Psychology* **13(1)**:182–196 DOI 10.1177/147470491501300111.

Uher J, Asendorpf JB. 2008. Personality assessment in the great apes: comparing ecologically valid behavior measures, behavior ratings, and adjective ratings. *Journal of Research in Personality* **42**:821–838 DOI 10.1016/j.jrp.2007.10.004.

Uher J, Visalberghi E. 2016. Observations versus assessments of personality: a five-method multi-species study reveals numerous biases in ratings and methodological limitations of standardised assessments. *Journal of Research in Personality* **61**:61–79 DOI 10.1016/j.jrp.2016.02.003.

Vazire S, Gosling SD, Dickey AS, Schapiro SJ. 2007. Measuring personality in non-human animals. In: Robins RW, Fraley RC, Krueger RF, eds. *Handbook of research methods in personality psychology*. New York: Guilford Press, 190–206.

Von Stumm S, Hell B, Chamorro-Premuzic T. 2011. The hungry mind. *Perspectives on Psychological Science* **6**:574–588 DOI 10.1177/1745691611421204.

Vorkapić ST. 2012. The significance of preschool teacher's personality in early childhood education: analysis of Eysenck's and big five dimensions of personality. *International Journal of Psychologyd Behavioral Sciences* **2**:28–37 DOI 10.5923/j.ijpbs.20120202.05.

Weiss A, Adams M. 2013. Differential behavioral ecology. In: Carere C, Maestripieri D, eds. *The structure, life history, and evolution of primate personality*. Chicago: University of Chicago Press, 96–123.

Weiss A, Adams MJ, Widdig A, Gerald MS. 2011. Rhesus macaques (*Macaca mulatta*) as living fossils of hominoid personality and subjective well-being. *Journal of Comparative Psychology* **125**:72–83 DOI 10.1037/a0021187.

Weiss A, Gartner MC, Gold KC, Stoinski TS. 2013. Extraversion predicts longer survival in gorillas: an 18-year longitudinal study. *Proceedings of the Royal Society B:Biological Sciences* **280(1752)**:20122231 DOI 10.1098/rspb.2012.2231.

Weiss A, Inoue-Murayama M, Hong KW, Inoue E, Udono T, Ochiai T, Matsuzawa T, Hirata S, King JE. 2009. Assessing chimpanzee personality and subjective well-being in Japan. *American Journal of Primatology* **71**:283–292 DOI 10.1002/ajp.20649.

Weiss A, Inoue-Murayama M, King JE, Adams M, Matsuzawa T. 2012. All too human? Chimpanzee and orang-utan personalities are not anthropomorphic projections. *Animal Behaviour* **83**:1355–1365 DOI 10.1016/j.anbehav.2012.02.024.

Weiss A, King JE, Murray L. 2011. *Personality and temperament in nonhuman primates.* New York: Springer.

Weiss A, Wilson ML, Collins AD, Mjungu D, Kamenya S, Foerster S, Pusey AE. 2017. Personality in the chimpanzees of Gombe National Park. *Scientific Data* **4**:170146 DOI 10.1038/sdata.2017.146.

Wergård E-M, Westlund K, Spångberg M, Fredlund H, Forkman B. 2016. Training success in group-housed long-tailed macaques (*Macaca fascicularis*) is better explained by personality than by social rank. *Applied Animal Behaviour Science* **177**:52–58 DOI 10.1016/j.applanim.2016.01.017.

White SL, Wagner T, Gowan C, Braithwaite VA. 2017. Can personality predict individual differences in brook trout spatial learning ability? *Behavioural Processes* **141**:220–228 DOI 10.1016/j.beproc.2016.08.009.

Zajenkowska A, Zajenkowski M, Jankowski KS. 2015. The relationship between mood experienced during an exam, proneness to frustration and neuroticism. *Learning and Individual Differences* **37**:237–240 DOI 10.1016/j.lindif.2014.11.014.

Zeidner M, Matthews G. 2000. Intelligence and personality. In: Sternberg R, ed. *Handbook of intelligence.* New York: Cambridge University Press, 581–610 DOI 10.1017/CBO9780511807947.027.

Zuckerman M, Kuhlman DM, Joireman J, Teta P, Kraft M. 1993. A comparison of three structural models for personality: the big three, the big five, and the alternative five. *Journal of Personality and Social Psychology* **65(4)**:757–768 DOI 10.1037/0022-3514.65.4.757.

Supplemental Information

Figure S1. Cognitive tasks used in this study categorized by complexity levels (simple, intermediate and complex) according to the number of elements that needed to be solved

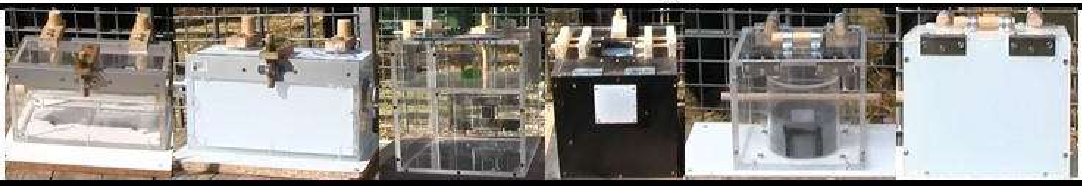
SIMPLE TASKS

Open Box Moveable Tube Windows Task Tube Cube

INTERMEDIATE TASKS

Tower Task Artificial Fruit Food Box Push Box

COMPLEX TASKS



Complex Food Box Complex Fixed Tube Complex Artificial Fruit

Table S1. Behavioral catalogue used to monitor chimpanzees' behvavior at Fundació Mona from 2006 to 2017 (adapted from Llorente et al., 2015)

Behavioral category	Name of behavior	Definition
Solitary	Abnormal behavior	Maladjusted stereotypical behaviors such as rocking, pacing, self–harm, coprophagy (eating feces), regurgitation, and reingestion, trichotillomania (hair-pulling), trichotillophagia (hair-pulling eating hair), ear-poking, eye-poking.
	Locomotion	
	Feeding	
	Manipulation	Inspecting elements of the environment or enrichment that are not food with the upper or lower extremities.
	Inactivity	
	Self-directed behavior	
	Other solitary	Individual behaviors that are not better defined by any other solitary behaviors (e.g. excretion).
Social	Grooming	Body-cleansing behavior from one individual to another (includes mutual grooming), performed with the upper extremities or with the mouth.
	Agonistic dominance	Threat-related behaviors such as direct aggression, charging display, displacement and resource appropriation (e.g. steal food or objects). Can be accompanied by vocalizations.
	Agonistic submission	Avoiding, food submission (e.g. leave/drop food and move away when others try to steal it), hand-to-mouth, finger-to-mouth. Can be accompanied by vocalizations such as pant-grunts. Includes running away from others in conflict situations.
	Other agonistic	Other behaviors identified as agonistic, but do not fit the criteria of Agonistic dominance or Agonistic submission (e.g. appeasing, consolation, reconciliation, and requesting support).
	Social play	Playful behavior between two or more individuals associated with behavioral indicators of play (e.g. play-face, laugh, friendly head bobbing, soft knocking on the ground, and playful chasing).
	Sexual behavior	Sexual interaction, or search for sexual interaction, between two individuals including behaviors such as: copulation, attempted copulation, genital presentation, and other behaviors directed towards the genitals of another individual.
	Other affiliative	Other behaviors identified as affiliative, but do not fit the criteria of Grooming, Social play or Sexual behavior (e.g. embrace, greetings).
	Social proximity	The chimpanzee is at less than one-arm length from one or more subjects, but there is no social interaction between them.
Other	Not Visible	The chimpanzee or the behavior cannot be identified.
	Not Present	The chimpanzee is not in the outdoor enclosure (e.g. he is in the sleeping areas or in the outdoor cages).
	Human Positive	Affiliative or neutral interaction between chimpanzees and humans (without physical contact). Includes staring at humans from a close distance (1.5m meters from the fence), following humans around the enclosure.
	Human Negative	Agonistic-type interaction or looking for agonistic-type interaction, with humans.

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

Table S2. Possible combinations of experimental conditions (task complexity, social information and causal information), number of tasks, and trials performed by each subject in each condition

Task complexity	**Social information**	**Tasks per subject**	**Causal information (apparatus version)**	**Trials per subject**
SIMPLE	Control	1	Transparent	4
			Opaque	4
	No social information	1	Transparent	4
			Opaque	4
	Social information	1	Transparent	4
			Opaque	4
TOTAL SIMPLE		**3**		**24**
INTERMEDIATE	Control	1	Transparent	4
			Opaque	4
	No social information	1	Transparent	4
			Opaque	4
	Social information	1	Transparent	4
			Opaque	4
TOTAL INTERMEDIATE		**3**		**24**
COMPLEX	Control	1	Transparent	4
			Opaque	4
	No social information	1	Transparent	4
			Opaque	4
	Social information	1	Transparent	4
			Opaque	4
TOTAL COMPLEX		**3**		**24**

Table S3. Spearman correlations between Eysenck's personality traits and observed behaviors

		Abnormal behavior	Locomotion	Foraging	Manipulation	Inactivity	Self-directed behavior	Other solitary	Grooming	Agonistic dominance	Agonistic submission	Other agonistic	Social play	Sexual behavior	Other affiliative	Social proximity	Human positive	Human negative
Extraversion	**r**	-.275	.284	.147	-.132	-.433	-.477	-.152	**.705**	**.614**	-.076	-.179	**.692**	.449	0.310	-.077	.367	.499
	p	.342	.326	.615	.653	.122	.085	.605	**.005**	**.020**	.797	.541	**.006**	.108	281	.794	.197	.069
	95% CI	[-.786, .325]	[-.261, .761]	[-.385, .668]	[-.626, .429	[-.881, .375]	[-.837, .163]	[-.649, .436]	**[.147, .957]**	**[.079, .929]**	[-.539, .425]	[-.730, .510]	**[.250, .928]**	[-.053, .830]	[-.268, .796]	[-.607, .468]	[-.182, .732]	[-.086, .900]
Neuropsychoticism	**r**	.007	-.336	**-.640**	-.271	-.015	.020	.152	.099	0.211	0.327	0.400	-.115	.449	0.143	0.508	-.165	.232
	p	.982	.240	**.014**	.349	.958	.946	.605	.737	0.469	0.254	0.157	.697	.108	0.626	0.064	.573	.425
	95% CI	[-.555, .654]	[-.675, .196]	**[-.945, -.172]**	[-.802, .521]	[-.549, .538]	[-.573, .626]	[-.501, .705]	[-.408, .557]	[-.323, .697]	[-.332, .765]	[-.193, .814]	[-.653, .596]	[-.123, .845]	[-.493, .787]	[-.181, .919]	[-.625, .381]	[-.303, .711]
Dominance	**r**	-.442	.218	-.055	-.469	-.393	-.429	-.011	.547	**.557**	.205	-.246	-.084	.486	-.160	.341	.042	.404
	p	.114	.455	.852	.091	.164	.126	.970	.043	**.039**	.483	.397	.776	.078	.584	.233	.887	.151
	95% CI	[-.770, .234]	[-.344, .729]	[-.563, .476]	[-.887, .170]	[-.791, .307]	[-.833.145]	[-.527, .447]	[-.014, .900]	**[.028, .892]**	[-.366, .688]	[-.693, .334]	[-.623, .454]	[-.096, .873]	[-.642, .460]	[-.389, .791]	[-.674, .647]	[-.144, .831]

N=14. Significant results are marked in bold (p<0.05; 95% CI do not overlap 0).

Table S4. Individual results in the cognitive tasks

4A. Overall results (all tasks). For each subject, sex, age (in 2009), mean and standard deviation (x̄ ± SD) of participation (0=subject refused to participate, 1=the subject engaged in the task), success (0=failed attempt, 1=successful attempt), latency (in seconds), and percentage of trials in which the subject lost contact with the task.

Subject	Sex	Age	Participation	Success	Latency	Lose contact with task
África	Female	10	0.94± 0.23	0.97± 0.17	43.06 ± 67.61	0.00
Bea	Female	24	0.83 ± 0.38	0.57 ± 0.50	13.15 ± 12.84	29.17
Bongo	Male	9	0.94± 0.23	0.85± 0.36	26.70 ± 42.08	12.50
Charly	Male	20	0.97 ± 0.17	1.00± 0.00	47.54 ± 61.63	0.00
Coco	Female	15	0.97± 0.17	0.99± 0.12	29.07 ± 40.97	0.00
Juanito	Male	6	1.00± 0.00	1.00± 0.00	46.46 ± 49.38	0.00
Marco	Male	25	0.44± 0.50	1.00± 0.00	10.56 ± 9.23	0.00
Nico	Male	8	0.56± 0.50	0.98± 016	11.28 ± 15.24	0.00
Tico	Mal	22	0.35± 0.48	0.76 ± 0.44	6.68 ± 4.18	8.33
Tom	Male	24	0.78± 0.42	0.86 ± 0.35	40.02 ± 46.12	9.38
Toni	Male	26	1.00± 0.00	0.92± 0.28	48.58 ± 68.53	2.78
Victor	Male	27	0.89± 0.32	0.97 ± 0.18	31.80 ± 48.07	1.39
Waty	Female	12	0.88 ± 0.33	0.90 ± 0.30	42.42 ± 61.31	4.17
x̄ ± SD			**0.81 ± 0.22**	**0.91± 0.13**	**30.55± 15.57**	**5.21± 8.36**

4B. Results for simple tasks. For each subject, sex, age (in 2009), mean and standard deviation (x̄ ± SD) of participation (0=subject refused to participate, 1=the subject engaged in the task), success (0=failed attempt, 1=successful attempt), latency (in seconds), and percentage of trials in which the subject lost contact with the task.

Subject	Sex	Age	Participation	Success	Latency	Lose contact with task
África	Female	10	1.00± 0.00	0.92± 0.28	7.45± 14.47	0.00
Bea	Female	24	0.67± 0.48	0.88± 0.34	7.14± 6.25	4.17
Bongo	Male	9	1.00± 0.00	0.96± 0.20	5.70± 5.41	0.00
Charly	Male	20	1.00± 0.00	1.00± 0.00	4.13± 2.66	0.00
Coco	Female	15	0.92± 0.28	1.00± 0.00	4.64± 3.20	0.00
Juanito	Male	6	1.00± 0.00	1.00± 0.00	15.08± 18.29	0.00
Marco	Male	25	1.00± 0.00	1.00± 0.00	7.13± 3.35	0.00
Nico	Male	8	1.00± 0.00	0.96± 0.20	8.09± 6.91	0.00
Tico	Mal	22	0.50± 0.51	1.00± 0.00	4.92± 2.15	0.00
Tom	Male	24	0.83± 0.38	0.90± 0.31	15.24± 26.70	4.17
Toni	Male	26	1.00± 0.00	0.92± 0.28	8.82± 8.06	4.17
Victor	Male	27	1.00± 0.00	1.00± 0.00	6.58± 6.95	0.00
Waty	Female	12	0.67± 0.48	0.75± 0.45	4.58± 4.44	4.17
x̄ ± SD			**0.89± 0.17**	**0.94± 0.07**	**7.65± 3.63**	**1.28± 2.00**

4C. Results for intermediate tasks. For each subject, sex, age (in 2009), mean and standard deviation (x̄ ± SD) of participation (0=subject refused to participate, 1=the subject engaged in the task), success (0=failed attempt, 1=successful attempt), latency (in seconds) and percentage of trials in which the subject lost contact with the task.

Subject	Sex	Age	Participation	Success	Latency	Lose contact with task
África	Female	10	1.00± 0.00	1.00 ± 0.00	15.54 ± 16.95	0.00
Bea	Female	24	1.00± 0.00	0.83± 0.38	17.35 ± 14.64	16.67
Bongo	Male	9	1.00± 0.00	0.92± 0.28	15.18 ± 14.57	8.33
Charly	Male	20	1.00± 0.00	1.00± 0.00	21.17 ± 15.04	0.00
Coco	Female	15	1.00± 0.00	1.00± 0.00	15.63 ± 12.35	0.00
Juanito	Male	6	1.00± 0.00	1.00± 0.00	49.46 ± 56.62	0.00
Marco	Male	25	0.33 ± 0.48	1.00± 0.00	20.88 ± 13.36	0.00
Nico	Male	8	0.67 ± 0.48	1.00± 0.00	15.88 ± 21.92	0.00
Tico	Mal	22	0.33 ± 0.00	0.88± 0.35	9.71 ± 5.19	4.17
Tom	Male	24	0.67 ± 0.48	0.69± 0.48	22.09 ± 42.80	20.83
Toni	Male	26	1.00 ± 0.00	1.00± 0.00	18.79 ± 15.40	0.00
Victor	Male	27	0.67 ± 0.48	1.00± 0.00	10.25 ± 5.14	0.00
Waty	Female	12	1.00 ± 0.00	0.92± 0.28	22.50 ± 42.21	8.33
x̄ ± SD			**0.82± 0.26**	**0.94± 0.10**	**19.57 ± 9.86**	**4.49 ± 7.11**

4D. Results for complex tasks. For each subject, sex, age (in 2009), mean and standard deviation (x̄ ± SD) of participation (0=subject refused to participate, 1=the subject engaged in the task), success (0=failed attempt, 1=successful attempt), latency (in seconds) and percentage of trials in which the subject lost contact with the task.

Subject	Sex	Age	Participation	Success	Latency	Lose contact with task
África	Female	10	0.83± 0.38	1.00± 0.00	115.25± 84.56	0.00
Bea	Female	24	0.83± 0.38	0.00± 0.00	-	66.67
Bongo	Male	9	0.83± 0.38	0.65± 0.49	83.23± 58.52	29.17
Charly	Male	20	0.92± 0.28	1.00± 0.00	123.00± 57.53	0.00
Coco	Female	15	1.00± 0.00	0.96± 0.20	66.48± 52.55	0.00
Juanito	Male	6	1.00± 0.00	1.00± 0.00	91.87± 32.68	0.00
Marco	Male	25	0.00± 0.00	-	-	0.00
Nico	Male	8	0.00± 0.00	-	-	0.00
Tico	Mal	22	0.21± 0.41	0.00± 0.00	-	20.83
Tom	Male	24	0.88± 0.34	1.00± 0.00	84.21± 35.24	0.00
Toni	Male	26	1.00± 0.00	0.83± 0.38	128.05± 78.17	4.17
Victor	Male	27	1.00± 0.00	0.92± 0.28	75.00± 60.03	4.17
Waty	Female	12	0.96± 0.20	1.00± 0.00	81.22± 71.45	0.00
x̄ ± SD			**0.73 ± 0.38**	**0.76 ± 0.39**	**94.26 ± 22.22**	**9.62 ± 19.50**

Questionnaire S1. English version of the personality questionnaire completed by the raters

PERSONALITY QUESTIONNAIRE FOR CHIMPANZEES

INSTRUCTIONS:

- Please answer the questionnaire individually, without discussing it with other keepers, volunteers or researchers.

- Evaluate each personality trait by assigning a numerical value on a scale of 1 to 7, depending on whether the subject is better identified with one end of the scale or the other. Example for a subject considered “social”:

Antisocial 1 2 3 4 5 [✓ 6] 7 Social

1: Very antisocial 2: Antisocial 3: Slightly antisocial 4: Neutral 5: Slightly social
6: Social 7: Very social

- It is important to evaluate all the adjectives for all the subjects. Some traits might be difficult to assess, and some may be very similar. However, in order to obtain a complete personality profile of each individual, it is highly desirable that you evaluate all adjectives. Nevertheless, if you experience a great difficulty assessing a certain adjective, you can leave it blank.

-Each item should be evaluated by focusing on the two opposite adjectives. If necessary, at the end of the document you will find explanatory definitions for all the adjectives used (with their antonyms in brackets), in order to facilitate the assessment.

- Traits involving social aspects can refer to how subjects behave with humans or with their conspecifics (other chimpanzees), and assessment of these traits should include both. Nevertheless, if the subject behaves differently with humans than with other chimpanzees, the evaluation should focus on its relationships with conspecifics.

NAME OF THE CHIMPANZEE:

Social	1 2 3 4 5 6 7	Antisocial
Active	1 2 3 4 5 6 7	Passive
Dominant	1 2 3 4 5 6 7	Submissive
Spontaneous	1 2 3 4 5 6 7	Not spontaneous
Calm	1 2 3 4 5 6 7	Anxious
Good-tempered	1 2 3 4 5 6 7	Bad-tempered
Brave	1 2 3 4 5 6 7	Fearful
Cheerful	1 2 3 4 5 6 7	Sad
Pacific	1 2 3 4 5 6 7	Aggressive
Cautious	1 2 3 4 5 6 7	Impulsive
Empathic	1 2 3 4 5 6 7	Cruel
Not creative	1 2 3 4 5 6 7	Creative

ADJECTIVES' DEFINITIONS:

Social: The subject enjoys interacting with others (≠Antisocial)
Active: Energetic, engaging in physical activity (≠Passive)
Dominant: The subject exercises power over the other individuals (≠Submissive)
Spontaneous: The subject has an open, natural and uninhibited behaviour (≠Not spontaneous)
Calm: The subject does not show tension or anger (≠Anxious)
Good-tempered: Naturally friendly and pleasant (≠Bad-tempered)
Brave: Determined, daring (≠Fearful)
Cheerful: The subject expresses joy and happiness (≠Sad)
Pacific: The subject does not start conflicts, nor participates in them (≠Aggressive)
Cautious: Forehanded, thoughtful (≠Impulsive)
Empathic: The subject shows concern for the states and needs of others (≠Cruel)
Creative: The subject is able to produce new ideas, solve and find answers to new problems (≠Not creative).

Questionnaire S2. Original Spanish version of the personality questionnaire completed by the raters

CUESTIONARIO PARA EVALUAR LA PERSONALIDAD EN PRIMATES NO HUMANOS

INSTRUCCIONES:

- Responda al cuestionario de manera individual, sin comentarlo con sus compañeros.

- Evalúe los rasgos de personalidad marcando el valor que crea más adecuado en la puntuación de la escala de intensidad, dependiendo de si identifica más a un individuo en un extremo del eje o en el otro. Ejemplo para un individuo social:

Antisocial 1 2 3 4 5 [✓ 6] 7 Social

1: Muy antisocial 2: Antisocial 3: Poco antisocial 4: Neutro 5: Poco social 6: Social 7: Muy social

- Es importante evaluar todos los adjetivos para todos los sujetos de estudio. Entendemos que ciertos adjetivos pueden ser difíciles de valorar, además de muy parecidos. Sin embargo, es muy importante para obtener un buen perfil de personalidad de los sujetos intentar evaluar todos los adjetivos. Aun así, si encuentra demasiada dificultad para evaluar algún adjetivo, puede dejar el espacio en blanco.

- Los cuestionarios están diseñados para poder ser evaluados únicamente con los adjetivos bipolares propuestos. No obstante, en caso necesario, al final de este documento podrá encontrar unas definiciones aclaratorias de los adjetivos utilizados (con sus respectivos antónimos entre paréntesis) para que le faciliten la evaluación.

- Ciertos adjetivos de carácter social pueden hacer referencia a cómo se comportan los sujetos en su relación con los humanos o en relación con los conespecíficos (otros chimpancés). La evaluación de estos adjetivos de carácter social deberá incluir ambos ámbitos. No obstante, ante determinados contextos un sujeto puede comportarse de manera opuesta (Ej. un sujeto se muestra de manera social con humanos y en un modo asocial con conespecíficos), en dichas ocasiones aunque se persiga una valoración global, prevalecerá su relación con sus congéneres, frente a su relación con los humanos.

NOMBRE DEL CHIMPANCÉ:

Social *(Social)*	1 2 3 4 5 6 7	Antisocial *(Unsocial)*
Activo *(Active)*	1 2 3 4 5 6 7	Pasivo *(Passive)*
Dominante *(Dominant)*	1 2 3 4 5 6 7	Sumiso *(Submissive)*
Espontaneo *(Spontaneous)*	1 2 3 4 5 6 7	No espontaneo *(Not spontaneous)*
Tranquilo *(Calm)*	1 2 3 4 5 6 7	Ansioso *(Anxious)*
Con buen humor *(Good-tempered)*	1 2 3 4 5 6 7	Mal humorado *(Bad-tempered)*
Valiente (Brave)	1 2 3 4 5 6 7	Temeroso *(Fearful)*
Alegre *(Happy, cheerful)*	1 2 3 4 5 6 7	Triste *(Sad)*
Pacífico *(Not aggressive)*	1 2 3 4 5 6 7	Agresivo *(Aggressive)*
Cauto *(Not impulsive)*	1 2 3 4 5 6 7	Impulsivo *(Impulsive)*
Empático *(Empathic)*	1 2 3 4 5 6 7	Cruel *(Cruel)*
No creativo *(Not creative)*	1 2 3 4 5 6 7	Creativo *(Creative)*

DEFINICIONES ADJETIVOS:

Social: Le gusta relacionarse con otros (≠Antisocial)
Activo: Enérgico, que actúa con energía o desarrolla gran actividad (≠Pasivo)
Dominante: Que ejerce poder sobre el resto de individuos (≠Sumiso)
Espontáneo: Que manifiesta comportamientos voluntarios, de forma natural (≠No espontáneo)
Tranquilo: Sosegado, calmado (≠Ansioso)
Con buen humor: Animado, jovial (≠Malhumorado)
Valiente: Decidido, atrevido (≠Temeroso)
Alegre: Que manifiesta o expresa alegría, animado, contento (≠Triste)
Pacífico: Que no participa ni crea conflicto (≠Agresivo)
Cauto: Cauteloso, precavido (≠Impulsivo)
Empático: Que muestra preocupación por el estado y las necesidades de los demás (≠Cruel)
Creativo: Capaz de producir idas nuevas, solucionar y buscar respuesta a nuevos problemas (≠No creativo)

Article 4. Assessing Eysenck's PEN model to describe personality in chimpanzees

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Assessing Eysenck's PEN model to describe personality in chimpanzees

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ABSTRACT

Questionnaires based on human models can be used to reliably assess personality also in non-human primates. In this study, we used an adapted version of Eysenck's Psychoticism-Extraversion-Neuroticism (PEN) model that focuses on three higher-order personality traits. Extending previous work on a small group of chimpanzees (*Pan troglodytes*), we tested 37 chimpanzees housed at Fundació Mona (Girona, Spain) and the Leipzig Zoo (Germany). We assessed personality with a 12-item questionnaire, which raters scored using a 7-point Likert scale. To identify the personality traits, we conducted data reduction with Principal Components Analysis and Robust Unweighted Least Squares. The ICCs for the single (3, 1) and average (3, k) ratings indicated substantial agreement between raters. Parallel analyses identified two factors to retain, whereas the scree plot inspection and eigenvalues larger than one rule identified three factors. Factor 1 and 2 in our study were identical to the ones previously described for this species (labelled Extraversion and Neuropsychoticism, respectively) and we also obtained a third factor that could be related to Dominance (Fearless Dominance). Thus, our results confirm the potential of the PEN model to describe chimpanzee personality structure.

1. Introduction

In the last three decades, personality assessment in captive animals has become increasingly popular as a non-invasive tool to improve animal management and welfare, while also providing valuable data to the field of animal personality research (Gartner and Weiss, 2017, for a review see: Norman et al., 2021). Understanding inter-individual differences of animals kept in captivity allows us to predict how subjects may respond when they face certain situations. This may be especially useful in zoos and other captive settings, because it can lead to the optimization of husbandry practices and environmental enrichment strategies according to the needs of each individual (Baker, 2012; Goswami et al., 2020; Quintavalle Pastorino et al., 2019). For example, it can help to increase success and decrease risks when forming social groups or transferring individuals to other centres (Gartner and Weiss, 2017). Furthermore, personality can have an impact on subjects' interest and performance in cognitive experiments, which are usually conducted in captive populations (Altschul et al., 2016; Altschul et al., 2017; Herrelko et al., 2012). This may have implications for animal management, but also for the study design. For example, highly neurotic individuals, which may be more likely to show excessive stress or anxiety during testing (Herrelko et al., 2012), may be excluded from the study or chosen to participate last, after seeing other group members performing the experiments.

Non-human primates, and more specifically great apes, are among the most studied animals in the field of animal personality (Freeman and Gosling, 2010; Norman et al., 2021; Weiss et al., 2011b). Historically, there have been two main methodological approaches to the study of animal personality: one based on behavioural ecology, which uses behavioural coding, and one based on human differential psychology, which uses a rating methodology (Weiss and Adams, 2013). Behavioural coding implies direct observations of subjects' spontaneous behaviour (Brandão et al., 2019; Koski, 2011) or their assessment during experimental situations (Massen et al., 2013). By contrast, the rating or

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questionnaire-based approach involves human raters who are familiar with the animals (e.g., keepers, researchers) scoring a list of adjectives or descriptions of behaviours, usually employing a Likert scale (Vazire and Gosling, 2004). Furthermore, some authors have combined the psychological and behavioural approaches by developing questionnaires based on observed behaviours (Stevenson-Hinde and Hinde, 2011; Stevenson-Hinde and Zunz, 1978; Uher, 2008; Uher and Asendorpf, 2008). This "bottom-up" approach contrast the "top-down" approach typically used in comparative psychology, in which questionnaire items are selected from human models.

Both methodologies, behavioural coding and trait rating, have been widely used to assess personality in non-human primates (Blaszczyk, 2020; Freeman et al., 2011; Gosling et al., 2003a; Highfill et al., 2010) and they both have strengths and limitations. For instance, although behavioural coding is assumed to be more objective, human studies have shown that it can also provide unreliable estimates (Borkenau, 1992; Gosling et al., 1998), as single measures of specific behaviours tend to have low cross-situational consistency. By contrast, ratings provide a more global perspective, as they encompass the experience of the raters across time and situations (Gosling et al., 2003a). Another popular criticism regarding the use of questionnaires, especially those based on human models, is the risk of anthropomorphism, which would imply that raters are falsely attributing human features to animals (Weiss et al., 2011b). Nonetheless, studies in the wild and in captivity have showed that great apes have intrinsic personality structures and that similarities with humans can be attributed to our genetic and phylogenetic closeness rather than to anthropomorphism (King et al., 2005; Weiss et al., 2012; Weiss et al., 2017). In fact, it has been extensively demonstrated that questionnaires based on human models provide a reliable approach (Freeman et al., 2013; Freeman and Gosling, 2010; Úbeda and Llorente, 2015; Weiss, 2017; Weiss and Adams, 2013; Weiss et al., 2009; Weiss et al., 2017), and that personality traits similar to those found in humans are expressed, with some modifications, across species (Weiss, 2018). Moreover, the use of questionnaires is especially effective for species that are phylogenetically close to humans, like great apes, as it is possible to more easily interpret their behaviour, rate their personality, and establish direct comparisons with human personality traits (Weiss and Adams, 2013). Some researchers have questioned the validity ratings (Šlipogor et al., 2021; Uher and Asendorpf, 2008; Uher and Visalberghi, 2016), implying that the traits obtained with this method are not descriptive of actual behaviours. However, several studies have found correlations between trait rating and behavioural observations both in monkeys (Ebenau et al., 2020; Iwanicki and Lehmann, 2015; Konečná et al., 2008) and in great apes (Eckardt et al., 2015; Pederson et al., 2005; Schaefer and Steklis, 2014; Vazire et al., 2007), thus revealing that, at least to some extent, traits obtained from questionnaires can estimate behaviour. Finally, it is also worth noting that, in general, questionnaires are easier to implement and less time-consuming than behavioural observations (Freeman et al., 2011).

A common top-down approach to describe non-human primate personality is based on the human Five Factor Model (Goldberg, 1990; McCrae and Costa Jr, 1999; McCrae and John, 1992), a hierarchical model constituted by five higher-order personality traits onto which several related lower-order traits cluster (Digman, 1990). This model has been successfully used to assess personality in chimpanzees (*Pan troglodytes*; King and Figueredo, 1997), bonobos (*Pan paniscus*; Weiss et al., 2015), gorillas (*Gorilla gorilla*; Eckardt et al., 2015; Schaefer and Steklis, 2014) and orangutans (*Pongo pygmeaus*, *P. abelii*; Weiss et al., 2006). The most popular adaptation of the Five Factor Model (FFM) for non-human primates is the Hominoid Personality Questionnaire (HPQ), developed by Weiss and colleagues (2009) and based on the previous attempt by King and Figueredo (1997) to describe chimpanzee personality. Using a larger sample of 146 chimpanzees and a revised version of the questionnaire containing 54 items, Weiss and colleagues (2009) obtained five personality traits homologous to the human traits in the FFM: Neuroticism, Extraversion, Agreeableness, Conscientiousness, and Openness (to Experience), plus the trait Dominance, which was already described in the original study by King and Figueredo (1997).

Besides the FFM, other human models have also been adapted to evaluate personality in non-human primates, such as Eysenck's Psychoticism-Extraversion-Neuroticism (PEN) model (Chamove et al., 1972; Úbeda and Llorente, 2015) or Cattell's 16 Personality Factors (PF) model (Ortín et al., 2019). One of the main advantages of these models is that the adapted questionnaires are shorter (i.e., they contain fewer items to evaluate) than the HPQ, making them more appealing and less time-consuming for raters (Hopper and Cronin, 2018). Furthermore, despite being psychometrically inferior to longer questionnaires, in human personality research, shorter scales have proved to be reliable and valid alternatives (Burisch, 1984, 1997; Føllesdal and Soto, 2022; Gosling et al., 2003b; Gouveia et al., 2021; Nunes et al., 2018; Romero et al., 2012). Eysenck's model (Eysenck, 1967; Eysenck and Eysenck, 1964), in particular, follows a psychobiological approach to personality that focuses on three higher-order traits (Psychoticism, Extraversion and Neuroticism) based on genetic and neurophysiological factors (Eaves et al., 1989; Eysenck, 1967; Eysenck, 1997). The PEN model shares two common dimensions or traits with the FFM (Neuroticism and Extraversion), which have reported to be very similar across models (McCrae and Costa, 1985; Zuckerman et al., 1993) and which have been identified in a wide range of primate species (Freeman and Gosling, 2010). Moreover, according to Eysenck and colleagues (1985), Agreeableness and Conscientiousness in the FFM are facets of the trait Psychoticism, a hypothesis which has been partially supported by later studies (Draycott and Kline, 1995; Goldberg and Rosolack, 1994; Heaven et al., 2013; Ruch et al., 2020; Saggino, 2000). It is also worth noting that, some features of Eysenck's Psychoticism, such as aggressiveness and impulsivity are commonly displayed behaviours by non-human primates, especially in competitive contexts and dominance-related interactions (de Almeida et al., 2015; Fairbanks et al., 2004; Higley et al., 2011). We can therefore conclude that Eysenck's model holds great potential to describe non-human primates' personality.

The first attempt to describe chimpanzee personality using the PEN model was conducted by Úbeda and Llorente (2015) with a small sample of captive chimpanzees. They developed a 12-item questionnaire, in which the items corresponded to primary scales or traits that are integrated into the three higher-order factors described by Eysenck (Eysenck, 1967; Eysenck et al., 1992; Eysenck and Eysenck, 1964, 1991; Eysenck et al., 1985). For each factor (i.e., Extraversion, Neuroticism and Psychoticism), the authors selected four primary scales, ensuring that they were appropriate to characterize chimpanzee personality. After performing factorial analyses, the authors identified three dimensions: Extraversion, Neuropsychoticism and Dominance. The items that loaded onto Extraversion were very similar to those reported for humans in that same dimension, facilitating the interpretation of this trait. The trait Neuropsychoticism was identified as a combination of Neuroticism and Psychoticism, because it included items that in humans load on these two traits. Moreover, the authors identified a third factor, labelled Dominance, which had been already described in other studies evaluating adaptations of human personality models in chimpanzees (Freeman and Gosling, 2010; King and Figueredo, 1997) and other non-human primates (Adams et al., 2015; Weiss et al., 2011b). Finally, personality traits assessed with the PEN model correlated with observational data collected over a 11-year period, supporting convergent validity (Padrell et al., 2020). Nonetheless, these studies assessing Eysenck's model in chimpanzees were strongly limited by the small sample size and the fact that all the chimpanzees were from the same centre and shared a similar background (i.e., they were all former pets or used in the entertainment industry). In this study, we therefore aimed to extend the research by Úbeda and Llorente (2015) and assess Eysenck's PEN model on a larger and more diverse sample (N = 37) of captive chimpanzees from two different sites. We expected that, if the PEN model is a suitable approach to assess personality in chimpanzees, we would find a clear factor structure, with similar dimensions or personality traits (i.e., Extraversion, Neuropsychoticism and Dominance) as compared to previous studies (Úbeda and Llorente, 2015), as well as substantial agreement between raters.

2. Material and methods

2.1. Subjects and study sites

The study sample consisted of 37 chimpanzees (*Pan troglodytes*), 16 males and 21 females, that ranged in age from 3.5 to 53 years at the time of personality assessment (mean age ± SD = 25.76 ± 12.37 years). They were housed at two different centres: 14 chimpanzees lived at Fundació Mona (Girona, Spain), a centre dedicated to the rescue and rehabilitation of primates that have been previously used as pets or for entertainment, and 23 lived at the Wolfgang Köhler Primate Research Centre (WKPRC), also known as Pongoland, at Leipzig Zoo (Germany). Table 1 contains information on the subjects' characteristics and background.

The 14 chimpanzees from Fundació Mona lived in two separate groups (mean age ± SD = 21.64 ± 8.85 years, range = 8–33 years), which have been mostly stable over the years: one group of 5 males and another group of 9 individuals (4 males and 5 females). In 2017, two of the females (África and Waty) from the larger group were moved to the only-males group. The chimpanzees spent most of the day in an outdoor enclosure, divided into two areas (2420 m2 and 3220 m2), one for each group. This enclosure was covered by natural vegetation and it contained enrichment elements such as wooden platforms, towers, and ropes. There were also 140 m2 of indoor facilities, divided into four rooms, to which the chimpanzees had access at nights and during bad weather conditions. The chimpanzees were fed four times a day and water was provided ad libitum in both enclosures. Their diet consisted mainly of seasonal vegetables and fresh fruits, and it also included small portions of dried fruits and nuts, boiled rice and some protein-rich items (e.g., eggs, meat, tofu). Most of the food was distributed along the outdoor area, in order to encourage foraging behaviour. The 23 chimpanzees from the Leipzig Zoo also lived in two separate groups (mean age ± SD = 28.26 ± 13.67 years, range = 3–53 years): a large group including 17 chimpanzees (6 males, 11 females) and a small group of 6 chimpanzees (1 male, 5 females). Each group had two types of enclosures: large outdoor enclosures for summer and hot days (4000 m^2 and 1400 m^2), and inside enclosures for the winter season (430 m^2 and 175 m^2). Both facilities were covered with natural vegetation and included other elements such as rocks and streams. They also had trees, ropes and wooden platforms for climbing and shelter, and environmental enrichment devices, such as artificial termite mounds and food mazes. The chimpanzees were also fed four times a day (twice in the indoor enclosures and twice with food being scattered in the outdoor area) and they had access to water at all times. Their diet predominantly consisted of vegetables and fruits, along with small portions of seeds, grains, and sources of protein (e.g., eggs, meat). Pellets (dry food) were also occasionally provided as rewards directly by the keepers or hidden in enrichment devices.

2.2. Questionnaires

We assessed personality using a questionnaire based on the Psychoticism-Extraversion-Neuroticism (PEN) model of personality (Eysenck, 1967; Eysenck and Eysenck, 1964). This tool was used for the first time in a previous study, in which the authors evaluated the

Table 1
Biographical information on the chimpanzees from the study sample.

Study site	Subject	Sex	Age (at personality assessment)	Origin	Former use	Age of arrival at the centre (years)	Time spent at the centre (years)
Fundació Mona	Africa	F	12	Wild	Pet	10	2
	Bea	F	33	Wild	Entertainment	27	6
	Bongo	M	11	Captive	Entertainment	2	9
	Charly	M	22	Captive	Entertainment	12	10
	Cheeta	F	28	Wild	Entertainment	25	3
	Coco	F	24	Wild	Pet/Entertainment	18	6
	Juanito	M	8	Captive	Pet/Entertainment	2	6
	Marco	M	27	Captive	Entertainment	17	10
	Nico	M	10	Captive	Pet/Entertainment	3	7
	Tico	M	24	Wild	Entertainment	18	6
	Tom	M	33	Wild	Entertainment	26	7
	Toni	M	28	Wild	Entertainment	18	10
	Victor	M	29	Captive	Entertainment	24	5
	Waty	F	14	Captive	Pet/Entertainment	4	10
Leipzig Zoo	Alex	M	18	Captive	Zoo	1	17
	Azibo	M	4	Captive	Zoo	Since birth	4
	Bambari	F	19	Captive	Zoo	16	3
	Corrie	F	43	Captive	Zoo	25	18
	Daza	F	33	Wild	Zoo	27	6
	Dorien	F	39	Captive	Zoo	21	18
	Fraukje	F	43	Captive	Zoo	25	18
	Frederike	F	45	Wild	Zoo	39	6
	Frodo	M	26	Captive	Zoo	8	18
	Hope	F	29	Captive	Zoo	26	3
	Jeudi	F	53	Wild	Zoo	47	6
	Kisha	F	15	Captive	Zoo	9	6
	Lobo	M	15	Captive	Zoo	Since birth	15
	Lome	M	18	Captive	Zoo	Since birth	18
	Maja	F	33	Captive	Zoo	30	3
	Natascha	F	39	Captive	Zoo	21	18
	Ohini	M	3	Captive	Zoo	Since birth	3
	Riet	F	42	Captive	Zoo	24	18
	Robert	M	44	Captive	Zoo	26	18
	Sandra	F	26	Captive	Zoo	8	18
	Swela	F	24	Captive	Zoo	10	14
	Tai	F	17	Captive	Zoo	Since birth	17
	Zira	F	22	Captive	Zoo	19	3

chimpanzees housed at Fundació Mona at that time (Úbeda and Llorente, 2015). The authors developed a 12-item questionnaire, with items corresponding to primary scales that are integrated into the three higher-order factors described by Eysenck (Eysenck and Eysenck, 1964, 1991; Eysenck et al., 1985). Each scale consists of two adjectives representing the opposite pole of the trait. For example, the factor Extraversion was defined by the scales "active-inactive", "social-unsociable" and "assertive-submissive", among others. A complete list of the primary scales and how are integrated into the higher-order factors can be found in Eysenck and colleagues (1992). To develop the questionnaire, the authors selected four descriptive items (i.e., four primary scales) for each factor, considering their suitability and relevance for describing chimpanzee personality. In the questionnaires, each item was also associated with two adjectives representing the two opposite poles of the trait, which raters had to score using a 7-point Likert scale (i.e., they had to select a number between 1 and 7). For instance, for the item "aggressiveness", raters had to provide a score from (1) "pacific" to (7) "aggressive". Additionally, a brief definition for the lower pole (i.e., corresponding to the lower value, 1) of each trait was included at the end of the questionnaire, in order to assist the raters in the interpretation of the traits. The raters at Fundació Mona completed the questionnaires in their native language (Spanish or English). An English version of the questionnaire, including the instructions provided to the raters, can be found in Supplementary Material 1.

To assess the chimpanzees at the Leipzig Zoo we used the same questionnaire previously employed at Fundació Mona, which was translated (and back translated) from English to German, so that the raters could complete it in their native language. Before conducting the statistical analyses, some of the ratings were reversed following the procedure of the previous study (Úbeda and Llorente, 2015). As in the former study, the reversed ratings corresponded to the following pair of adjectives: "social-antisocial", "active-passive", "dominant-submissive", "spontaneous-not spontaneous". For the pair "social-antisocial", for example, low values in the questionnaire (1) corresponded to more social individuals, and high values (7) to more antisocial ones. However, before conducting the analyses, the ratings were reversed, so that higher scores on this pair of items corresponded to more social individuals. This facilitated the comparison between the two studies and the interpretation of the personality structure.

2.3. Raters and ratings

The chimpanzees at Fundació Mona were assessed in two previous studies: 10 subjects were assessed in 2012 (Úbeda and Llorente, 2015) and 4 subjects were later evaluated in 2018 (Padrell et al., 2020). The 10 chimpanzees evaluated in 2012 were assessed by 28 raters (75% women, 25% men), who knew the animals for at least 6 months. The 4 chimpanzees evaluated in 2018 were assessed by 15 raters (73.33% women, 26.67% men) who had been working with the animals for at least 4 months. All raters were highly familiar with the subjects, as they worked as researchers, volunteers or keepers and had daily contact with them. The chimpanzees from the Leipzig Zoo were assessed in 2019 by a total of 8 raters (25% women, 75% men), which had been working as keepers for 4–18 years (mean ± SD = 12.8 ± 5.8 years). However, not all keepers evaluated all chimpanzees, as not all of them worked with all the animals. Thus, each chimpanzee was rated by 6 keepers that were highly familiar with them.

When raters did not answer a question, missing data on the ratings was substituted by a neutral score of 4 (Costa and McCrae, 2008; Weiss et al., 2009). Following the methodology of previous studies (Úbeda and Llorente, 2015; Weiss et al., 2009), we assessed inter-rater reliability by calculating two intraclass correlation coefficients (ICC) (Shrout and Fleiss, 1979): ICC (3,1), which indicates the reliability of the scores for individual single raters, and ICC (3, k), which indicates the reliabilities of scores based on the mean of the total number of raters. To do so, we used the function ICC from the package "psych" version 2.0.8 in R (Revelle, 2020).

2.4. Personality structure

To identify the personality traits or domains we conducted data reduction with two different tools, Principal Components Analysis (PCA) and exploratory factor analysis using a Robust Unweighted Least Squares (RULS) as a method for factor extraction (Ferrando and Lorenzo-Seva, 2017). On the one hand, PCA is a widely used method in current personality research (i.e., Šlipogor et al., 2022; Talbot et al., 2021). On the other hand, regularized exploratory factor analyses such as RULS are commonly applied to extract factors in small samples studies (Jung, 2013; Jung et al., 2020). In both analyses we set an orthogonal normalised Equamax rotation (Lorenzo-Seva and Ferrando, 2019), which generates uncorrelated factors. This rotation needs a previous orthogonal Weighted Equamax rotation, implemented with the Clever Start method, to select the position of the factor axes based on the most stable correlation values in the sample correlation matrix (Browne, 2001; Lorenzo-Seva, 1999). The analysis was based on polychoric correlations (a method adequate to Likert-scale ordinal data with asymmetric or with excess of kurtosis data) to achieve factor simplicity and determine factorial structure and goodness of fit (Lorenzo-Seva and Ferrando, 2019; Muthen and Kaplan, 1992). Correction for robust Chi square was calculated with LOSEFER empirical correction (Lorenzo-Seva and Ferrando, 2022). Following Hair et al. (2010) and Úbeda and Llorente (2015), factor loadings of the rotated loading matrix were considered as salient when they were equal or higher than 0.5. We combined three procedures for determining the number of dimensions. First, the inspection of the scree plot (i.e., factors with eigenvalues above the 95th quantile); second, eigenvalues above 1; and third, the optimal implementation of Parallel analysis based on minimum rank factor analysis (Timmerman and Lorenzo-Seva, 2011) obtaining random correlation matrices with permutation of the raw data (Buja and Eyuboglu, 1992). Finally, we assessed a robust goodness of fit using the Root Mean Square Error of Approximation (RMSEA). RMSEA values below 0.05 are considered excellent fit, while values greater than 0.08 would indicate poor fit (Lloret-Segura et al., 2014). We conducted all the analyses using JASP (version 0.17.2.1; JASP Team, 2023) and FACTOR 12.04.01 softwares (Lorenzo-Seva and Ferrando, 2013).

3. Results

3.1. Inter-rater reliabilities

Considering the 37 chimpanzees, the ICCs for the single (3, 1) and average (3, k) ratings showed substantial agreement between raters, with no unreliable coefficients equal to or less than zero to remove from the analysis. The mean ICC (3, 1) was 0.32 (SD = 0.08; range = 0.21 – 0.47) and the mean ICC (3, k) was 0.95 (SD = 0.02; range = 0.93 – 0.98). The interrater reliabilities for each item are presented in Table 2.

3.2. Personality structure

Parallel analyses identified two factors (Timmerman and Lorenzo-Seva, 2011) to retain, whereas the scree plot and eigenvalues above 1 identified three factors (Table 3), as also suggested by the PCA and the RULS. The three factors accounted for 67.76% of the variance, based on eigenvalues above 1. According to the PCA and the RULS, the value of the Kaiser-Meyer-Olkin (KMO) test was 0.802 (good) [CI 0.744, 0.822] and Bartlett's Test of Sphericity was significant (B=2812.2; df=66, $p < 0.001$), thus indicating the adequacy of the polychoric correlation matrix. Based on the normed MSA (Measure of Sampling Adequacy) all the items obtained values above 0.5, suggesting that they correlated with other items and indicating its adequacy in representing the underlying constructs. Thus, all the items were retained in the factor analysis (Lorenzo-Seva and Ferrando, 2021) (Table 4). RMSEA fit was

Table 2
Intraclass correlation coefficients (ICCs) for the 12 items of the questionnaire. ICC (3, 1) indicates the reliability of the scores for a single rater, and ICC (3, k) indicates the reliabilities of scores based on the mean of the total number of raters.

	ICC (3,1)	ICC (3,K)
Social	0.27	0.95
Active	0.47	0.98
Dominant	0.42	0.97
Spontaneous	0.31	0.96
Anxious	0.32	0.96
Bad-tempered	0.25	0.94
Fearful	0.32	0.96
Sad	0.26	0.94
Aggressive	0.40	0.97
Impulsive	0.33	0.96
Cruel	0.23	0.93
Creative	0.21	0.93
Mean ± SD	**0.32 ± 0.08**	**0.95 ± 0.02**

Note: The table shows the positive pole of each pair of adjectives (e.g., the item “social”, is the positive pole of the pair (1) “antisocial - (7) ”social”).

Table 3
Explained variance based on eigenvalues.

Variable	Eigenvalue	Proportion of the variance	Cumulative proportion
1	4.108	0.342	0.342
2	2.961	0.247	0.589
3	1.062	0.089	0.678
4	0.808	0.067	
5	0.655	0.055	
6	0.541	0.045	
7	0.450	0.038	
8	0.413	0.034	
9	0.303	0.025	
10	0.275	0.023	
11	0.230	0.019	
12	0.195	0.016	

Table 4
Values of the normed Measure of Sampling Adequacy for the PEN items according to the PCA and the RULS.

Items	Normed MSA
Sad	0.865
Bad-tempered	0.839
Cruel	0.809
Aggressive	0.786
Fearful	0.730
Anxious	0.727
Impulsive	0.760
Dominant	0.792
Creative	0.893
Spontaneous	0.862
Active	0.776
Social	0.787

Note: The table shows the positive pole of each pair of adjectives (e.g., the item “social”, is the positive pole of the pair (1) “antisocial - (7) ”social”).

fair (0.071; [Bootstrap 95% CI 0.043, 0.050]) for the RULS and mediocre (0.089; [Bootstrap 95% CI 0.057, 0.062) for the PCA.

The factors extracted by the PCA and the RULS did not differ appreciably, except for one item (“creative”) loading on factor 1 in the PCA, but not in the RULS (see Table 5). In the PCA, the items positively loading on factor 1 were “active”, “social”, ”spontaneous” and “creative”, whereas the items “sad” and “bad-tempered” had negative loadings. In both the PCA and the RULS, the items with positive salient loadings on factor 2 included “aggressive”, “impulsive”, “anxious,” “cruel,” and “bad-tempered”. Finally, the third factor included two items with salient loadings: “fearful” with a negative loading and “dominant” with a positive loading. “Bad-tempered” was the only item with salient loadings on more than one factor (factors 1 and 2) in the PCA and in the RULS, loading higher on factor 2 in both analyses. Table 5 also displays the communalities for each item in the PCA and the RULS (i.e., the proportion of variance in each item accounted for by the underlying factors). Overall, item communalities were above 0.5, suggesting a moderate to high degree of variance explained by the factors, except for the item “creative”.

Finally, to facilitate comparison with previous research on the PEN model in both chimpanzees and humans, Table 6 shows the personality structure obtained in this study and the one reported by Úbeda and Llorente (2015) for chimpanzees, as well as the distribution of the items within the higher-order traits as described by Eysenck and Eysenck (1991) in humans.

4. Discussion

In our study, the personality structures obtained using the two data reduction tools (PCA and RULS) were very similar to each other and highly comparable to the ones described by Úbeda and Llorente (2015) in the first attempt to adapt Eysenck’s PEN model to chimpanzees. As in their study, we obtained three factors, and very similar loadings of adjectives or items for each factor. In particular, the items loading on factors 1 and 2 were identical to those reported in the study by Ubeda and Llorente (2015) (labelled Extraversion and Neuropsychoticism, respectively), and the items loading on factor 3 (i.e., Dominance) differed only slightly in the more restrictive analyses. Therefore, our results provide further support for this three-factor solution and for the existence of a Dominance-related factor, also reported for chimpanzees in the Five Factor Model (King and Figueredo, 1997).

In terms of inter-observer reliability, intraclass correlation coefficients suggested that raters tended to agree in their judgments about personality items. The intraclass correlation coefficients for average ratings (3,k) were all above 0.9, which is indicative of excellent reliability (Koo and Li, 2016). Although the intraclass correlation coefficients for single ratings (3,1) were lower, they were similar to those reported in other studies assessing chimpanzee personality through questionnaires adapted from human models (King and Figueredo, 1997; Ortín et al., 2019; Úbeda and Llorente, 2015; Weiss et al., 2009). Furthermore, they are also in the range of intraclass correlations reported for human models (Costa and McCrae, 1992; McCrae and Costa, 1989; McCrae and Costa, 1987).

In this study, we performed an orthogonal rotation, which assumes that the factors are uncorrelated. Some authors argue that, oblique rotations, which allow factors to correlate, are the most advisable approach (Browne, 2001). In fact, moderate correlations (0.4–0.59) between personality factors have been reported in chimpanzees (King and Figueredo, 1997), barbary macaques (*Macaca sylvanus*; Konečná et al., 2012) and in humans (Borkenau and Ostendorf, 1990; Costa et al., 1991; Graziano and Ward, 1992; Zhang et al., 2022). Nonetheless, orthogonal rotations produce simpler structures, that are easier to interpret and more likely to be replicated in future studies (Kieffer, 1998).

The factors or traits obtained in our analyses are not only comparable with the ones reported in the previous study in chimpanzees (Úbeda and Llorente, 2015) but also with the human dimensions from the PEN model. For example, three of the four items included in factor 1 (Extraversion) according to the RULS (“active”, “social”, “spontaneous”) have also been attributed to Extraversion in humans (Eysenck and Eysenck, 1991; see Table 6. However, in both this and the former study in chimpanzees, the item “sad” loaded on Extraversion, whereas in humans, sadness is considered an aspect of Neuroticism (Eysenck and Eysenck, 1991). This would be in line with the study of King and Figueredo (1997), in which the item “depressed” also had a negative salient loading on Surgency (or Extraversion) and not on Emotionality (or

Table 5
Factor loadings of personality items for PCA and RULS and item communalities.

	Principal Component Analysis				Robust Unweighted Least Squares			
	Component 1	Component 2	Component 3	Item communalities	Factor 1	Factor 2	Factor 3	Item communalities
*Active	**.826**	.144	.258	.770	**.838**	.128	.219	.767
*Social	**.774**	-.012	.159	.639	**.725**	-.134	.128	.562
*Spontaneous	**.713**	.051	.405	.675	**.675**	.019	.373	.595
Sad	**-.717**	.307	-.244	.668	**-.672**	.313	-.228	.602
Creative	**.557**	-.149	-.053	.335	.393	-.182	.062	.192
Aggressive	-.141	**.867**	.216	.819	-.121	**.877**	.227	.836
Impulsive	.303	**.729**	.262	.692	.267	**.637**	.278	.555
Anxious	-.049	**.742**	-.450	.756	-.114	**.636**	-.310	.513
Cruel	-.362	**.683**	.126	.614	-.315	**.629**	.101	.505
Bad-tempered	**-.553**	**.647**	.018	.703	**-.499**	**.626**	.024	.641
Fearful	-.270	.017	**-.835**	.770	-.284	.028	**-.811**	.739
*Dominant	.142	.288	**.766**	.690	.206	.277	**.591**	.468

Note: The table shows the positive pole of each pair of adjectives (e.g., the item "social", is the positive pole of the pair (1) "antisocial - (7) "social"). *Scores on these items were reversed before the factorial analyses following the procedure conducted by Úbeda and Llorente (2015).

Table 6
Comparison of the personality structure obtained in this study with the PEN model in humans (Eysenck and Eysenck, 1991) and with the previous study in chimpanzees (Úbeda and Llorente, 2015).

	Humans (Eysenck and Eysenck, 1991)	Chimpanzees (Úbeda and Llorente, 2015)	Chimpanzees (this study)
Active	Extraversion	Extraversion	Extraversion
Social	Extraversion	Extraversion	Extraversion
Spontaneous	Extraversion	Extraversion	Extraversion
Sad	Neuroticism	Extraversion	Extraversion
Creative	Psychoticism	Extraversion[a]	Extraversion[a]
Aggressive	Psychoticism	Neuropsychoticism	Neuropsychoticism
Impulsive	Psychoticism	Neuropsychoticism	Neuropsychoticism
Anxious	Neuroticism	Neuropsychoticism	Neuropsychoticism
Cruel	Psychoticism	Neuropsychoticism	Neuropsychoticism
Bad-tempered	Neuroticism	Neuropsychoticism	Extraversion/ Neuropsychoticism[c]
Fearful	Neuroticism	Dominance[b]	Fearless Dominance
Dominant	Extraversion	Dominance	Fearless Dominance

[a] The item "creative" yielded a salient loading on Extraversion in the PCA, but not in the more restrictive analyses (REFA in Úbeda and Llorente, 2015 and RULS in this study). [b] In the study by Úbeda and Llorente (2015), the item "fearful" only yielded a salient loading on Dominance in the PCA, but not in the REFA. [c] In the present study, the item "bad-tempered" loaded on both Extraversion and Neuropsychoticism in the PCA and in the RULS, but higher on Neuropsychoticism.

Neuroticism). Moreover, Extraversion in humans has been negatively correlated to sensitivity to negative stimuli (Park et al., 2014) and to depression (Grav et al., 2012; Yu and Hu, 2022).

When comparing the two analyses (PCA and RULS), the only difference in the results was the item "creative", which loaded positively on factor 1 (Extraversion) in the PCA but not in the RULS. This is also in line with the results reported by Úbeda and Llorente (2015), in which "creative" did not load on Extraversion when using a more restrictive analysis (i.e., Regulatory Exploratory Factor Analyses, REFA). According to Eysenck, "creativity" was connected to Psychoticism, because highly psychotic individuals are overinclusive in their thinking (i.e., they have wide associative networks which allow divergent thinking and originality) (Eysenck, 1993; Eysenck, 1995). Later studies also support that manifesting psychotic traits (i.e., cold, unemphatic, aggressive and impulsive) is associated with creativity, and particularly with originality (Abraham et al., 2005; Acar and Runco, 2012; Fink et al., 2014; Fink et al., 2012). Nonetheless, in our analyses, "creative" did not load on Psychoticism and its inclusion within Extraversion was not supported by the more restrictive analyses. It is also worth noting that "creative" exhibited the lowest item communality, revealing that it explains a very small proportion of the variance of the underlying factor (Extraversion). Overall, our findings suggest that, contrary to humans, the item "creative" is not clearly included in any of the higher-order traits in chimpanzees. However, it is also worth noting that creativity is hard to assess in non-human animals (Kaufman and O'Hearn, 2017), and/or on captive environments offering limited opportunities to exhibit innovative behaviours, except when cognitive enrichments like problem-solving tasks are provided (Cronin, 2017; Padrell et al., 2021). Thus, the interpretation of this item may have been challenging for the raters.

As in Úbeda and Llorente (2015), we identified a dimension that included both aspects of Neuroticism and aspects of Psychoticism from the human model (factor 2, see Table 6), which the authors labelled Neuropsychoticism. Considering that the items loading on this factor ("aggressive", "impulsive", "anxious", "cruel" and "bad-tempered") were identical to the ones reported in the former study, our results provide further evidence for this compound dimension in chimpanzees, and suggest that Neuroticism and Psychoticism may not be as distinct in this species as they are in humans. In the first study that compared non-human primates' personality traits with Eysenck's factors, Chamove and colleagues (1972) conducted factor analyses of coded behaviours in rhesus macaques obtaining the traits: Affiliative, Hostile and Fearful, which, according to the authors, were similar to Extraversion, Psychoticism, and Neuroticism found in humans. In our results, the items loading on factor 2 could also be related to hostility (and therefore to human Psychoticism), except for "anxious". In humans, anxiety-related behaviours are clearly attributed to Neuroticism (Eysenck, 1991; Fullerton, 2006). Nonetheless, a link between anxiety and psychotic symptomatology (e.g., schizophrenia) has been reported by several authors (Deng et al., 2020; Hartley et al., 2013; Wigman et al., 2012).

Factor 3 differed from the one described by Úbeda and Llorente (2015) (labelled Dominance), but only in one of the data reduction methods. Particularly, according to the more restrictive analysis (REFA), in the former study factor 3 only included the item "dominant", with a positive and very salient loading (0.97), whereas in the PCA it also included the item "fearful" with a negative loading (−0.68). By contrast, we obtained the same pattern of loadings with both data reduction methods (RULS and PCA), with "fearful" and "dominant" yielding salient loadings on factor 3. In particular, in the RULS we obtained a positive salient loading for "dominant" (0.591) and a negative salient loading for "fearful" (−0.811). Therefore, in our study, factor 3 could also be interpreted as a Dominance-related factor, but considering the high negative loading of "fearful", it could also be identified as Boldness or Confidence. Thus, we decided to combine both elements and name factor 3 Fearless Dominance/Boldness (Crowe et al., 2021). The item "fearful" or "fearfulness" has a negative loading on Dominance across several nonhuman primates' species (Adams et al., 2015; Eckardt et al., 2015; Konečná et al., 2008; Konečná et al., 2012; Manson and Perry, 2013; Morton et al., 2013; Weiss et al., 2011a; Weiss et al., 2015; Wilson et al., 2018), including chimpanzees (King and Figueredo, 1997; Weiss et al., 2009). Although fear in humans is mostly related to the Neuroticism dimension (Eysenck, 1967), in chimpanzees it also plays an important role in dominance-related interactions and relationships. In particular, power conflicts usually involve aggression by more dominant individuals (Noë et al., 1980) and, as a response, submissive animals may display fear through different behaviours (e.g., fleeing, retreating) and by displaying vocal or facial signals (e.g., fear grimace and "bared-teeth" display; Kim et al., 2022; Parr and Waller, 2006).

Finally, our findings support the hypothesis that the Dominance-related factor found in this study may not be directly comparable to any of the human traits described by the PEN model, as it contains items that in humans load on different traits (i.e., Neuroticism and Extraversion). The absence of a Dominance factor in humans may be a consequence of our species having evolved in small-scale egalitarian societies (Weiss, 2022), in contrast to the dominance hierarchies that characterize chimpanzees and other non-human primates, and that are mostly based on agonistic interactions (Bernstein, 1981; Walters and Seyfarth, 1987). Nonetheless, although humans do not have an identifiable Dominance factor, there have been some attempts to develop a dominance scale in our species. For instance, Benning et al., (2003, 2005) defined the trait Fearless Dominance/Boldness in humans using the Psychopathic Personality Inventory (Lilienfeld and Andrews, 1996). Fearless Dominance/Boldness has been identified as an element of psychopathy, describing individuals as resilient to stress and anxiety, social influencers and fearlessness (Crego and Widiger, 2016; Lilienfeld et al., 2016). Further, it is associated with social boldness, egoism, narcissism, and thrill-seeking (Benning et al., 2005) and, according to Weiss (2022), it resembles dominance factors described in chimpanzees, bonobos and orangutans. Thus, factor 3 in our analyses could also be comparable to Fearless Dominance/Boldness in humans (Lilienfeld et al., 2016).

Overall, this study provides further evidence of the possible use of Eysenck's PEN model to describe chimpanzee personality. Eysenck's three higher-order personality traits have been empirically validated in humans (Eysenck and Eysenck, 1994) and they are based on underlying biological mechanisms, including brain activity and hormones (Ergüneş, 2018; Eysenck, 1967; Eysenck, 1983, 1997), which may facilitate inter-species comparison. Another key advantage of using an adaptation of Eysenck's model in non-human primates is that, in contrast to other rating tools, the questionnaire is short and therefore less time-consuming for raters. Furthermore, when the sample size is small, as in this study, fewer items are likely to increase statistical robustness and provide more stable and accurate estimates, because higher subject-to-item ratios are desirable in factorial analyses (Osborne and Costello, 2004). Nonetheless, the PEN model is not without limitations. First, compared to other human models of personality, such as the FFM, or its adaptation to non-human primates, the HPQ, the three factors proposed by Eysenck may not capture some features of non-human primates' personality, such as Openness (to Experience). In addition, the only study that compared behavioural observations with personality ratings obtained with Eysenck's adapted model in chimpanzees reported limited discriminant validity (Padrell et al., 2020). Thus, future research should focus on validating the suitability of the PEN model in chimpanzees and other non-human primates by comparing personality ratings with behavioural measures in different contexts, including spontaneous behaviour, but also behavioural responses under experimental conditions (Massen et al., 2013), which would provide a complementary approach.

5. Conclusions

This study provides further evidence of the potential use of Eysenck's PEN model to assess personality in captive chimpanzees. First, we obtained good reliability between raters, demonstrating that human raters can adequately evaluate the traits from the adapted 12-item questionnaire developed by Úbeda and Llorente (2015). Second, we showed that, using a larger sample, the personality structure and the pattern of loadings for each factor were highly similar to previous research. Overall, our results support the use of shorter questionnaires to evaluate primate personality, especially when assessing small samples, as it increases statistical robustness and accuracy. Furthermore, shorter questionnaires are particularly advantageous for animal keepers in zoos and sanctuaries, who usually have limited time to dedicate to research activities.

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CRediT authorship contribution statement

Maria Padrell: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Visualization, Funding acquisition. **Federica Amici**: Resources, Writing – review & editing, Supervision, Funding acquisition. **Yulán Úbeda:** Investigation, Data curation, Writing – review & editing. **Miquel Llorente**: Conceptualization, Methodology, Formal analysis, Resources, Data curation, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Data Availability

Data will be made available on request.

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Ethics statement

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures involving animals were in accordance with the ethical standards of the institution at which the studies were conducted and with the Spanish Government RD 53/2013. In compliance with the General Data Protection Regulation (RGPD-UE 2016/679), raters were provided with an informed consent in which they were informed that their personal data and their responses to the questionnaires would be used anonymously. This project also received the ethical approval from the Ethics Committee of the Universitat de Girona (Project Code: CEBRU0020–2019).

Declarations of conflict of interest

none.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2023.104909.

References

Abraham, A., Windmann, S., Daum, I., Güntürkün, O., 2005. Conceptual expansion and creative imagery as a function of psychoticism. Conscious. Cogn. 14 (3), 520–534.

Acar, S., Runco, M.A., 2012. Psychoticism and creativity: a meta-analytic review. Psychol. Aesthet., Creat., Arts 6, 341–350. https://doi.org/10.1037/a0027497.

Adams, M., Majolo, B., Ostner, J., Schülke, O., Marco, A., Thierry, B., Engelhardt, A., Widdig, A., Gerald, M.S., Weiss, A., 2015. Personality structure and social style in macaques. J. Personal. Soc. Psychol. 109 (2), 338–353. https://doi.org/10.1037/pspp0000041.

de Almeida, R.M.M., Cabral, J.C.C., Narvaes, R., 2015. Behavioural, hormonal and neurobiological mechanisms of aggressive behaviour in human and nonhuman primates. Physiol. Behav. 143, 121–135. https://doi.org/10.1016/j.physbeh.2015.02.053.

Altschul, D.M., Terrace, H.S., Weiss, A., 2016. Serial cognition and personality in macaques. Anim. Behav. Cogn. 3 (1), 46–64. https://doi.org/10.12966/abc.02.04.2016.

Altschul, D.M., Wallace, E., Sonnweber, R., Tomonaga, M., Weiss, A., 2017. Chimpanzee intellect: personality, performance and motivation with touchscreen tasks. R. Soc. Open Sci. 4 (5), 170169 https://doi.org/10.1098/rsos.170169.

Baker, K. (2012). Personality assessment of three species of captive monkey, Macaca nigra, Macaca sylvanus, and Saimiri sciureus: cross-species comparisons of personality and implications for captive management [Doctoral dissertation, University of Exeter].

Benning, S.D., Patrick, C.J., Hicks, B.M., Blonigen, D.M., Krueger, R.F., 2003. Factor structure of the psychopathic personality inventory: validity and implications for clinical assessment. Psychol. Assess. 15 (3), 340–350. https://doi.org/10.1037/1040-3590.15.3.340.

Benning, S.D., Patrick, C.J., Blonigen, D.M., Hicks, B.M., Iacono, W.G., 2005. Estimating facets of psychopathy from normal personality traits: a step toward community epidemiological investigations. Assessment 12 (1), 3–18. https://doi.org/10.1177/1073191104271223.

Bernstein, I.S., 1981. Dominance: the baby and the bathwater. Behav. Brain Sci. 4 (3), 419–429. https://doi.org/10.1017/S0140525X00009614.

Blaszczyk, M.B., 2020. Primates got personality, too: toward an integrative primatology of consistent individual differences in behavior. Evolut. Anthropol. 29 (2), 56–67. https://doi.org/10.1002/evan.21808.

Borkenau, P., 1992. Implicit personality theory and the five-factor model. J. Personal. 60, 295–327. https://doi.org/10.1111/j.1467-6494.1992.tb00975.x.

Borkenau, P., Ostendorf, F., 1990. Comparing exploratory and confirmatory factor analysis: a study on the 5-factor model of personality. Personal. Individ. Differ. 11 (5), 515–524. https://doi.org/10.1016/0191-8869(90)90065-Y.

Brandão, A., Costa, R., Rodrigues, E., Vicente, L., 2019. Using behaviour observations to study personality in a group of capuchin monkeys (Cebus apella) in captivity. Behaviour 156 (3–4), 203–243. https://doi.org/10.1163/1568539X-00003537.

Browne, M.W., 2001. An overview of analytic rotation in exploratory factor analysis. Multivar. Behav. Res. 36 (1), 111–150.

Buja, A., Eyuboglu, N., 1992. Remarks on parallel analysis. Multivar. Behav. Res. 27 (4), 509–540.

Burisch, M., 1984. You don't always get what you pay for: Measuring depression with short and simple versus long and sophisticated scales. J. Res. Personal. 18, 81–98. https://doi.org/10.1016/0092-6566(84)90040-0.

Burisch, M., 1997. Test length and validity revisited. Eur. J. Personal. 11, 303–315. https://doi.org/10.1002/(SICI)1099-0984(199711)11:4<303::AID-PER292>3.0.CO;2-%23.

Chamove, A.S., Eysenck, H.J., Harlow, H.F., 1972. Personality in monkeys: factor analyses of Rhesus social behaviour. Q. J. Exp. Psychol. 24 (4), 496–504. https://doi.org/10.1080/14640747208400309.

Costa, P.T., McCrae, R.R., 1992. Four ways five factors are basic. Personal. Individ. Differ. 13 (6), 653–665. https://doi.org/10.1016/0191-8869(92)90236-I.

Costa, P.T., McCrae, R.R., 2008. Empirical and theoretical status of the Five-Factor Model of personality traits. In: Gregory, B.J., Matthews, G., Saklofske, D. (Eds.), The SAGE Handbook of Personality Theory and Assessment: Volume 2 — Personality Measurement and Testing. SAGE Publications, pp. 273–294. https://doi.org/10.4135/9781849200479.n9.

Costa, P.T., McCrae, R.R., Dye, D.A., 1991. Facet scales for agreeableness and conscientiousness: a revision of the NEO personality inventory. Personal. Individ. Differ. 12 (9), 887–898. https://doi.org/10.1016/0191-8869(91)90177-D.

Crego, C., Widiger, T.A., 2016. Cleckley's psychopaths: revisited. J. Abnorm. Psychol. 125, 75–87. https://doi.org/10.1037/abn0000130.

Cronin, K.A., 2017. Studying primate cognition in a social setting to improve validity and welfare: A literature review highlighting successful approaches. PeerJ 5, e3649. https://doi.org/10.7717/peerj.3649.

Crowe, M.L., Weiss, B.M., Sleep, C.E., Harris, A.M., Carter, N.T., Lynam, D.R., Miller, J. D., 2021. Fearless Dominance/Boldness is not strongly related to externalizing behaviors: an item response-based analysis. Assessment 28, 413–428. https://doi.org/10.1177/1073191120907959.

Deng, Wisteria Y., Grove, T., Deldin, P., 2020. Anxiety mediates the relationship between psychotic-like experiences and social functioning in the general population. Psychopathology 53 (2), 95–102. https://doi.org/10.1159/000507869.

Digman, J.M., 1990. Personality structure: emergence of the five-factor model. Annu. Rev. Psychol. 41 (1), 417–440.

Draycott, S.G., Kline, P., 1995. The big three or the big five—the EPQ-R vs the NEO-PI: a research note, replication and elaboration. Personal. Individ. Differ. 18 (6), 801–804. https://doi.org/10.1016/0191-8869(95)00010-4.

Eaves, L., Eysenck, H., Martin, N., Jardine, R., Heath, A., Feingold, L., Young, P., Kendler, K., 1989. Genes, Culture and Personality: An Empirical Approach. Academic Press, London.

Ebenau, A., von Borell, C., Penke, L., Ostner, J., Schülke, O., 2020. Integrative personality assessment in wild Assamese macaques (*Macaca assamensis*). J. Comp. Psychol. 134 (1), 27–41. https://doi.org/10.1037/com0000190.

Eckardt, W., Steklis, D.H., Steklis, N.G., Fletcher, A.W., Stoinski, T.S., Weiss, A., 2015. Personality dimensions and their behavioral correlates in wild Virunga mountain gorillas (*Gorilla beringei beringei*). J. Comp. Psychol. 129 (1), 26–41. https://doi.org/10.1037/a0038370.

Ergüneş, H., 2018. The review of five empirical studies: to what extent contemporary findings provide biological evidence for Eysenck's PEN Model? Koç Univ. Undergrad. Psychol. J. 4, 18–24.

Eysenck, H.J. (1967). The biological basis of personality. Thomas.

Eysenck, H.J., 1983. Psychophysiology and personality: Extraversion, neuroticism and psychoticism. In: Gale, A., Edwards, J.A. (Eds.), Individual differences and psychopathology. Academic Press, pp. 13–30. https://doi.org/10.1016/B978-0-12-273903-3.50007-9.

Eysenck, H.J., 1991. Neuroticism, anxiety, and depression. Psychol. Inq. 2 (1), 75–76.

Eysenck, H.J., 1993. Creativity and personality: suggestions for a theory. Psychol. Inq. 4 (3), 147–178. https://doi.org/10.1207/s15327965pli0403_1.

Eysenck, H.J., 1995. Creativity as a product of intelligence and personality. In: Saklofske, D.H., Zeidner, M. (Eds.), International handbook of personality and intelligence. Springer New York, pp. 231–247.

Eysenck, H.J., 1997. Personality and experimental psychology: the unification of psychology and the possibility of a paradigm. J. Personal. Soc. Psychol. 73 (6), 1224–1237.

Eysenck, H.J., Eysenck, S.B.G., 1964. Manual of the Eysenck Personality Inventory. University of London Press. https://books.google.es/books?id=LJRaDQEACAAJ.

Eysenck, H.J., Eysenck, S.B.G., 1991. Manual of the Eysenck Personality Scales (EPS Adult), Comprising the EPQ-revised (EPQ-R) (including Addiction and Criminality Scales) EPQ-R Short Scale Impulsiveness (IVE) Questionnaire (impulsiveness/venturesomeness/empathy). Hodder and Stoughton. https://books.google.es/books?id=LAzUjwEACAAJ.

Eysenck, H.J., Eysenck, S.B.G., 1994. Manual of the Eysenck personality questionnaire: (EPQ-R Adult). EdITS/Educational and Industrial Testing Service.

Eysenck, H.J., Barrett, P., Wilson, G., Jackson, C., 1992. Primary trait measurement of the 21 components of the PEN system. Eur. J. Psychol. Assess. 8 (2), 109–117.

Eysenck, S.B.G., Eysenck, H.J., Barrett, P., 1985. A revised version of the psychoticism scale. Personal. Individ. Differ. 6 (1), 21–29. https://doi.org/10.1016/0191-8869(85)90026-1.

Fairbanks, L.A., Jorgensen, M.J., Huff, A., Blau, K., Hung, Y.Y., Mann, J.J., 2004. Adolescent impulsivity predicts adult dominance attainment in male vervet monkeys. Am. J. Primatol.: Off. J. Am. Soc. Primatol. 64 (1), 1–17.

Ferrando, P.J., Lorenzo-Seva, U., 2017. Program FACTOR at 10: origins, development and future directions. Psicothema 29 (2), 236–240. https://doi.org/10.7334/psicothema2016.304.

Fink, A., Slamar-Halbedl, M., Unterrainer, H.F., Weiss, E.M., 2012. Creativity: genius, madness, or a combination of both. Psychol. Aesthet., Creat., Arts 6 (1), 11–18. https://doi.org/10.1037/a0024874.

Fink, A., Benedek, M., Unterrainer, H.-F., Papousek, I., Weiss, E.M., 2014. Creativity and psychopathology: are there similar mental processes involved in creativity and in psychosis-proneness. ? [Opin.]. Front. Psychol. 5, 1211. https://doi.org/10.3389/fpsyg.2014.01211.

Føllesdal, H., Soto, C.J., 2022. The Norwegian adaptation of the big five inventory-2 [Original Research]. Front. Psychol. 13, 858920 https://doi.org/10.3389/fpsyg.2022.858920.

Freeman, H.D., Gosling, S.D., 2010. Personality in nonhuman primates: a review and evaluation of past research. Am. J. Primatol. 72 (8), 653–671. https://doi.org/10.1002/ajp.20833.

Freeman, H.D., Gosling, S.D., Schapiro, S.J., 2011. Comparison of methods for assessing personality in nonhuman primates. In: Weiss, A., King, J.E., Murray, L. (Eds.), *Personality* and *temperament in* nonhuman *primates*. Springer Science + Business Media, pp. 17–40. https://doi.org/10.1007/978-1-4614-0176-6_2.

Freeman, H.D., Brosnan, S.F., Hopper, L.M., Lambeth, S.P., Schapiro, S.J., Gosling, S.D., 2013. Developing a comprehensive and comparative questionnaire for measuring personality in chimpanzees using a simultaneous top-down/bottom-up design. Am. J. Primatol. 75 (10), 1042–1053. https://doi.org/10.1002/ajp.22168.

Fullerton, J., 2006. New approaches to the genetic analysis of neuroticism and anxiety. Behav. Genet. 36 (1), 147–161. https://doi.org/10.1007/s10519-005-9000-4.

Gartner, M., Weiss, A., 2017. Studying primate personality in zoos: implications for the management, welfare and conservation of great apes. Int. Zoo. Yearb. 52, 79–91. https://doi.org/10.1111/izy.12187.

Goldberg, L.R., 1990. An alternative "description of personality": the big-five factor structure. J. Personal. Soc. Psychol. 59 (6), 1216–1229. https://doi.org/10.1037/0022-3514.59.6.1216.

Goldberg, L.R., Rosolack, T.K., 1994. The Big Five factor structure as an integrative framework: An empirical comparison with Eysenck's P-E-N model. In: Halverson, J. C.F., Kohnstamm, G.A., Martin, R.P. (Eds.), The developing structure of temperament and personality from infancy to adulthood. Lawrence Erlbaum Associates, Inc, pp. 7–35.

Gosling, S.D., John, O.P., Craik, K.H., Robins, R.W., 1998. Do people know how they behave? Self-reported act frequencies compared with on-line codings by observers. J. Personal. Soc. Psychol. 74 (5), 1337–1349. https://doi.org/10.1037/0022-3514.74.5.1337.

Gosling, S.D., Lilienfeld, S.O., Marino, L., 2003a. Personality. In: Maestripieri, D. (Ed.), Primate psychology. Harvard University Press, pp. 254–288.

Gosling, S.D., Rentfrow, P.J., Swann, W.B., 2003b. A very brief measure of the Big-Five personality domains. J. Res. Personal. 37 (6), 504–528. https://doi.org/10.1016/S0092-6566(03)00046-1.

Goswami, S., Tyagi, P.C., Malik, P.K., Pandit, S.J., Kadivar, R.F., Fitzpatrick, M., Mondol, S., 2020. Effects of personality and rearing-history on the welfare of captive Asiatic lions (*Panthera leo persica*). e8425-e8425 PeerJ 8. https://doi.org/10.7717/peerj.8425.

Gouveia, V., de Carvalho Rodrigues Araújo, R., Oliveira, I., Gonçalves, M., Milfont, T., Lins de Holanda Coelho, G., Santos, W., Medeiros, E., Silva Soares, A., Monteiro, P., Andrade, R., Cavalcanti, J., Nascimento, T., Gouveia, B., 2021. A short version of the big five inventory (BFI-20): evidence on construct validity (R.). Rev. Interam. De. Psicol. /Interam. J. Psychol. 55. https://doi.org/10.30849/ripijp.v55i1.1312.

Grav, S., Stordal, E., Romild, U.K., Hellzen, O., 2012. The relationship among neuroticism, extraversion, and depression in the HUNT Study: in relation to age and gender. Issues Ment. Health Nurs. 33 (11), 777–785. https://doi.org/10.3109/01612840.2012.713082.

Graziano, W.G., Ward, D., 1992. Probing the big five in adolescence: personality and adjustment during a developmental transition. J. Pers. 60 (2), 425–439. https://doi.org/10.1111/j.1467-6494.1992.tb00979.x.

Hair, J.F., Black, W.C., Babin, B.J., Anderson, R.E., 2010. Multivariate data analysis, seventh ed. Prentice Hall, Pearson.

Hartley, S., Barrowclough, C., Haddock, G., 2013. Anxiety and depression in psychosis: a systematic review of associations with positive psychotic symptoms. Acta Psychiatr. Scand. 128 (5), 327–346. https://doi.org/10.1111/acps.12080.

Heaven, P.C., Ciarrochi, J., Leeson, P., Barkus, E., 2013. Agreeableness, conscientiousness, and psychoticism: distinctive influences of three personality dimensions in adolescence. Br. J. Psychol. 104 (4), 481–494. https://doi.org/10.1111/bjop.12002.

Herrelko, E.S., Vick, S.J., Buchanan-Smith, H.M., 2012. Cognitive research in zoo-housed chimpanzees: Influence of personality and impact on welfare. Am. J. Phys. Anthropol. 74 (9), 828–840. https://doi.org/10.1002/ajp.22036.

Highfill, L., Hanbury, D., Kristiansen, R., Kuczaj, S., Watson, S., 2010. Rating vs. coding in animal personality research. Zoo. Biol. 29 (4), 509–516. https://doi.org/10.1002/zoo.20279.

Higley, J.D., Suomi, S.J., Chaffin, A.C., 2011. Impulsivity and Aggression as Personality Traits in Nonhuman Primates. In: Weiss, A., King, J.E., Murray, L. (Eds.), Personality and Temperament in Nonhuman Primates. Springer New York, pp. 257–283. https://doi.org/10.1007/978-1-4614-0176-6_10.

Hopper, L.M., Cronin, K.A., 2018. A multi-institutional assessment of a short-form personality questionnaire for use with macaques. Zoo. Biol. 37 (5), 281–289. https://doi.org/10.1002/zoo.21439.

Iwanicki, S., Lehmann, J., 2015. Behavioral and trait rating assessments of personality in common marmosets (*Callithrix jacchus*). J. Comp. Psychol. 129 (3), 205–217. https://doi.org/10.1037/a0039318.

Jung, S., 2013. Exploratory factor analysis with small sample sizes: a comparison of three approaches. Behav. Process. 97, 90–95. https://doi.org/10.1016/j.beproc.2012.11.016.

Jung, S., Seo, D.G., Park, J., 2020. Regularized exploratory bifactor analysis with small sample sizes. Front. Psychol. *11*. https://doi.org/10.3389/fpsyg.2020.00507.

Kaufman, A.B., O'Hearn, W.J., 2017. Creativity in Non-Human Animals. In: Kaufman, J. C., Baer, J., Glăveanu, V.P. (Eds.), The Cambridge Handbook of Creativity across Domains. Cambridge University Press, pp. 492–506 https://doi.org/DOI: 10.1017/9781316274385.027.

Kieffer, K.M. (1998). Orthogonal versus Oblique Factor Rotation: A Review of the Literature regarding the Pros and Cons. Annual Meeting of the Mid-South Educational Research Association, New Orleans.

Kim, Y., Vlaeyen, J.M.R., Heesen, R., Clay, Z., Kret, M.E., 2022. The association between the bared-teeth display and social dominance in captive chimpanzees (*Pan troglodytes*). *Affective*. Science 3 (*4*), 749–760. https://doi.org/10.1007/s42761-022-00138-1.

King, J.E., Figueredo, A.J., 1997. The five-factor model plus dominance in chimpanzee personality. J. Res. Personal. 31 (2), 257–271. https://doi.org/10.1006/jrpe.1997.2179.

Konečná, M., Lhota, S., Weiss, A., Urbánek, T., Adamová, T., Pluháček, J., 2008. Personality in free-ranging Hanuman langur (*Semnopithecus entellus*) males: Subjective ratings and recorded behavior. J. Comp. Psychol. 122 (4), 379. https://doi.org/10.1037/a0012625.

Konečná, M., Weiss, A., Lhota, S., Wallner, B., 2012. Personality in Barbary macaques (*Macaca sylvanus*): Temporal stability and social rank. J. Res. Personal. 46 (5), 581–590. https://doi.org/10.1016/j.jrp.2012.06.004.

Koo, T.K., Li, M.Y., 2016. A guideline of selecting and reporting intraclass correlation coefficients for reliability research. J. Chiropr. Med. 15 (2), 155–163. https://doi.org/10.1016/j.jcm.2016.02.012.

Koski, S.E., 2011. Social personality traits in chimpanzees: temporal stability and structure of behaviourally assessed personality traits in three captive populations. Behav. Ecol. Sociobiol. 65 (11), 2161–2174. https://doi.org/10.1007/s00265-011-1224-0.

Lilienfeld, S.O., Andrews, B.P., 1996. Development and preliminary validation of a self-report measure of psychopathic personality traits in noncriminal populations. J. Personal. Assess. 66 (3), 488–524. https://doi.org/10.1207/s15327752jpa6603_3.

Lilienfeld, S.O., Smith, S.F., Sauvigné, K.C., Patrick, C.J., Drislane, L.E., Latzman, R.D., Krueger, R.F., 2016. Is boldness relevant to psychopathic personality? Meta-analytic relations with non-psychopathy checklist-based measures of psychopathy. Psychol. Assess. 28, 1172–1185. https://doi.org/10.1037/pas0000244.

Lloret-Segura, S., Ferreres-Traver, A., Hernández-Baeza, A., Tomás-Marco, I., 2014. El Análisis Factorial Exploratorio de los Ítems: una guía práctica, revisada y actualizada. An. De. Psicol. 30, 1151–1169. http://scielo.isciii.es/scielo.php?script=sci_arttext&pid=S0212-97282014000300040&nrm=iso.

Lorenzo-Seva, U., 1999. Promin: a method for oblique factor rotation. Multivar. Behav. Res. 34, 347–365. https://doi.org/10.1207/S15327906MBR3403_3.

Lorenzo-Seva, U., Ferrando, P.J., 2013. Factor 9.2: a comprehensive program for fitting exploratory and semiconfirmatory factor analysis and IRT models. Appl. Psychol. Meas. 37, 497–498. https://doi.org/10.1177/0146621613487794.

Lorenzo-Seva, U., Ferrando, P.J., 2019. Robust Promin: a method for diagonally weighted factor rotation. Lib. Rev. Peru. De. Psicol. 25 (1), 99–106.

Lorenzo-Seva, U., Ferrando, P.J., 2021. MSA: The forgotten index for identifying inappropriate items before computing exploratory item factor analysis. Methodology 17 (4), 296–306. https://doi.org/10.5964/meth.7185.

Lorenzo-Seva, U., Ferrando, P.J. (2022). *A simulation-based scaled test statistic for assessing model-data fit in least-squares unrestricted factor-analysis solutions*.

Manson, J.H., Perry, S., 2013. Personality structure, sex differences, and temporal change and stability in wild white-faced capuchins (*Cebus capucinus*). J. Comp. Psychol. 127 (3), 299–311. https://doi.org/10.1037/a0031316.

Massen, J.J., Antonides, A., Arnold, A.M., Bionda, T., Koski, S.E., 2013. A behavioral view on chimpanzee personality: exploration tendency, persistence, boldness, and tool-orientation measured with group experiments. Am. J. Primatol. 75 (9), 947–958. https://doi.org/10.1002/ajp.22159.

McCrae, R.R., Costa, P., 1989. Different points of view: Self-reports and ratings in the assessment of personality. In: Forgas, J., Innes, M. (Eds.), Recent Advances in Social Psychology. An International Perspective, North-Holland, pp. 429–439.

McCrae, R.R., Costa, P.T., 1985. Comparison of EPI and psychoticism scales with measures of the five-factor model of personality. Personal. Individ. Differ. 6 (5), 587–597. https://doi.org/10.1016/0191-8869(85)90008-X.

McCrae, R.R., Costa Jr., P.T., 1987. Validation of the five-factor model of personality across instruments and observers. J. Personal. Soc. Psychol. 52 (1), 81–90. https://doi.org/10.1037//0022-3514.52.1.81.

McCrae, R.R., Costa Jr, P.T., 1999. A Five-Factor theory of personality. In: Pervin, L.A., John, O.P. (Eds.), Handbook of personality: Theory and research, second. Guilford Press, pp. 139–153.

McCrae, R.R., John, O.P., 1992. An introduction to the five-factor model and its applications. J. Personal. 60 (2), 175–215. https://doi.org/10.1111/j.1467-6494.1992.tb00970.x.

Morton, B.F., Lee, P.C., Buchanan-Smith, H.M., Brosnan, S.F., Thierry, B., Paukner, A., de Waal, F.B.M., Widness, J., Essler, J.L., Weiss, A., 2013. Personality structure in brown capuchin monkeys (*Sapajus apella*): Comparisons with chimpanzees (*Pan troglodytes*), orangutans (*Pongo spp.*), and rhesus macaques (*Macaca mulatta*). J. Comp. Psychol. 127 (3), 282–298. https://doi.org/10.1037/a0031723.

Muthen, B., Kaplan, D., 1992. A comparison of some methodologies for the factor analysis of non-normal Likert variables: a note on the size of the model. Br. J. Math. Stat. Psychol. 45 (1), 19–30.

Noë, R., Waal, F., van Hooff, J., 1980. Types of dominance in a chimpanzee colony. Folia Primatol. 34, 90–110. https://doi.org/10.1159/000155949.

Norman, M., Rowden, L.J., Cowlishaw, G., 2021. Potential applications of personality assessments to the management of non-human primates: a review of 10 years of study. PeerJ 9, e12044. https://doi.org/10.7717/peerj.12044.

Nunes, A., Limpo, T., Lima, C.F., Castro, S.L., 2018. Short scales for the assessment of personality traits: development and validation of the Portuguese Ten-Item Personality Inventory (TIPI). [Brief. Res. Rep.]. *Front. Psychol. 9*. https://doi.org/10.3389/fpsyg.2018.00461.

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

Osborne, J., Costello, W., 2004. Sample size and subject to item ratio in principal components analysis (A., B.). Pract. Assess., Res. Eval. 9 (11), 1–9. https://www.ingentaconnect.com/content/doaj/15317714/2004/00000009/00000011/art00001.

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

Padrell, M., Amici, F., Córdoba, M.P., Giberga, A., Broekman, A., Almagro, S., Llorente, M., 2021. Artificial termite-fishing tasks as enrichment for sanctuary-housed chimpanzees: behavioral effects and impact on welfare. Animals 11 (10), 2941. https://doi.org/10.3390/ani11102941.

Park, M.S., Lee, K.H., Sohn, S., Eom, J.S., Sohn, J.H., 2014. Degree of extraversion and physiological responses to physical pain and sadness. Scand. J. Psychol. 55 (5), 483–488. https://doi.org/10.1111/sjop.12144.

Parr, L.A., Waller, B.M., 2006. Understanding chimpanzee facial expression: insights into the evolution of communication. Soc. Cogn. Affect. Neurosci. 1 (3), 221–228. https://doi.org/10.1093/scan/nsl031.

Pederson, A.K., King, J.E., Landau, V.I., 2005. Chimpanzee (*Pan troglodytes*) personality predicts behavior. J. Res. Personal. 39 (5), 534–549. https://doi.org/10.1016/j.jrp.2004.07.002.

Quintavalle Pastorino, G., Preziosi, R., Faustini, M., Curone, G., Albertini, M., Nicoll, D., Moffat, L., Pizzi, R., Mazzola, S., 2019. Comparative personality traits assessment of three species of communally housed captive penguins. Animals 9 (6), 376. https://doi.org/10.3390/ani9060376.

Revelle, W. (2020). psych: Procedures for Personality and Psychological Research, Northwestern University. Version 2.0.8. In https://CRAN.R-project.org/package=psych.

Romero, E., Villar, P., Gómez-Fraguela, J.A., López-Romero, L., 2012. Measuring personality traits with ultra-short scales: a study of the Ten Item Personality

Inventory (TIPI) in a Spanish sample. Personal. Individ. Differ. 53 (3), 289–293. https://doi.org/10.1016/j.paid.2012.03.035.

Ruch, W., Heintz, S., Gander, F., Hofmann, J., Platt, T., Proyer, R., 2020. The long and winding road: a comprehensive analysis of 50 years of Eysenck instruments for the assessment of personality. Personal. Individ. Differ. 169 https://doi.org/10.1016/j.paid.2020.110070.

Saggino, A., 2000. The big three or the big five? A replication study. Personal. Individ. Differ. 28 (5), 879–886. https://doi.org/10.1016/S0191-8869(99)00146-4.

Schaefer, S., Steklis, H., 2014. Personality and subjective well-being in captive male western lowland gorillas living in bachelor groups. Am. J. Primatol. 76 (9), 879–889. https://doi.org/10.1002/ajp.22275.

Šlipogor, V., Massen, J.J., Schiel, N., Souto, A., Bugnyar, T., 2021. Temporal consistency and ecological validity of personality structure in common marmosets (*Callithrix jacchus*): a unifying field and laboratory approach. Am. J. Primatol. 83 (2), e23229.

Šlipogor, V., Graf, C., Massen, J.J.M., Bugnyar, T., 2022. Personality and social environment predict cognitive performance in common marmosets (*Callithrix jacchus*). Sci. Rep. 12 (1), 6702. https://doi.org/10.1038/s41598-022-10296-8.

Stevenson-Hinde, J., Hinde, C.A., 2011. Individual characteristics: Weaving psychological and ethological approaches. Personality and temperament in nonhuman primates. Springer Science + Business Media, pp. 3–14. https://doi.org/10.1007/978-1-4614-0176-6_1.

Stevenson-Hinde, J., Zunz, M., 1978. Subjective assessment of individual rhesus monkeys. Primates 19, 473–482.

Talbot, S., Freire, R., Wassens, S., 2021. Identifying behavioural traits and underlying personality dimensions in domestic ferrets (*Mustela putorius furo*). Animals 11 (8), 2173. https://www.mdpi.com/2076-2615/11/8/2173.

Timmerman, M.E., Lorenzo-Seva, U., 2011. Dimensionality assessment of ordered polytomous items with parallel analysis. Psychol. Methods 16, 209–220. https://doi.org/10.1037/a0023353.

Úbeda, Y., Llorente, M., 2015. Personality in sanctuary-housed chimpanzees: a comparative approach of psychobiological and penta-factorial human models. Evolut. Psychol. 13 (1), 1959364992. https://doi.org/10.1177/147470491501300111.

Uher, J., 2008. Comparative personality research: methodological approaches. Eur. J. Personal. 22 (5), 427–455. https://doi.org/10.1002/per.680.

Uher, J., Asendorpf, J.B., 2008. Personality assessment in the Great Apes: Comparing ecologically valid behavior measures, behavior ratings, and adjective ratings. J. Res. Personal. 42 (4), 821–838. https://doi.org/10.1016/j.jrp.2007.10.004.

Uher, J., Visalberghi, E., 2016. Observations versus assessments of personality: a five-method multi-species study reveals numerous biases in ratings and methodological limitations of standardised assessments. J. Res. Personal. 61, 61–79. https://doi.org/10.1016/j.jrp.2016.02.003.

Vazire, S., Gosling, S., 2004. Personality and temperament: A comparative perspective. In: Bekoff, M. (Ed.), Encyclopedia of animal behavior. Greenwood Publishing Group, pp. 818–822.

Vazire, S., Gosling, S.D., Dickey, A.S., Schapiro, S.J., 2007. Measuring personality in nonhuman animals. In: Robins, R.W., Fraley, R.C., Krueger, R.F. (Eds.), Handbook of research methods in personality psychology. Guilford Press, pp. 190–206.

Walters, J., Seyfarth, R.M., 1987. Conflict and cooperation. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., Struhsaker, T.T. (Eds.), Primate societies. University of Chicago Press Chicago, pp. 306–317.

Weiss, A. (2017). A human model for primate personality. Proceedings of the Royal Society B, *284*(1864), 20171129. https://doi.org/10.1098/rspb.2017.1129.

Weiss, A., 2018. Personality traits: a view from the animal kingdom. J. Personal. 86 (1), 12–22. https://doi.org/10.1111/jopy.12310.

Weiss, A., Adams, M.J., 2013. Differential behavioral ecology. The structure, life history and evolution of primate personality. In: Carere, C.M., Dario (Eds.), Animal personalities: behavior, physiology and evolution. The University of Chicago Press, pp. 96–123.

Weiss, A., King, J.E., Perkins, L., 2006. Personality and subjective well-being in orangutans (*Pongo pygmaeus* and *Pongo abelii*). J. Personal. Soc. Psychol. 90 (3), 501–5011. https://doi.org/10.1037/0022-3514.90.3.501.

Weiss, A., Inoue-Murayama, M., Hong, K.W., Inoue, E., Udono, T., Ochiai, T., Matsuzawa, T., Hirata, S., King, J.E., 2009. Assessing chimpanzee personality and subjective well-being in Japan. Am. J. Primatol. 71 (4), 283–292. https://doi.org/10.1002/ajp.20649.

Weiss, A., Adams, M.J., Widdig, A., Gerald, M.S., 2011a. Rhesus macaques (*Macaca mulatta*) as living fossils of hominoid personality and subjective well-being. J. Comp. Psychol. 125 (1), 72–83. https://doi.org/10.1037/a0021187.

Weiss, A., King, J.E., Murray, L., 2011b. Personality and temperament in nonhuman primates. Springer, New York. https://doi.org/10.1007/978-1-4614-0176-6.

Weiss, A., Staes, N., Pereboom, J.J.M., Inoue-Murayama, M., Stevens, J.M.G., Eens, M., 2015. Personality in bonobos. Psychol. Sci. 26 (9), 1430–1439. https://doi.org/10.1177/0956797615589933.

Weiss, A., Wilson, M.L., Collins, A.D., Mjungu, D., Kamenya, S., Foerster, S., Pusey, A.E., 2017. Personality in the chimpanzees of Gombe National Park. Sci. Data 4, 170146. https://doi.org/10.1038/sdata.2017.146.

Wigman, J.T., van Nierop, M., Vollebergh, W.A., Lieb, R., Beesdo-Baum, K., Wittchen, H. U., van Os, J., 2012. Evidence that psychotic symptoms are prevalent in disorders of anxiety and depression, impacting on illness onset, risk, and severity–implications for diagnosis and ultra-high risk research. Schizophr. Bull. 38 (2), 247–257. https://doi.org/10.1093/schbul/sbr196.

Wilson, V.A.D., Inoue-Murayama, M., Weiss, A., 2018. A comparison of personality in the common and Bolivian squirrel monkey (*Saimiri sciureus* and *Saimiri boliviensis*). J. Comp. Psychol. 132, 24–39. https://doi.org/10.1037/com0000093.

Yu, T., Hu, J., 2022. Extraversion and Neuroticism on college freshmen's depressive symptoms during the COVID-19 pandemic: the mediating role of social support [Original Research]. Front. Psychiatry 13, 822699. https://doi.org/10.3389/fpsyt.2022.822699.

Zhang, B., Li, Y.M., Li, J., Luo, J., Ye, Y., Yin, L., Chen, Z., Soto, C.J., John, O.P., 2022. The big five inventory–2 in china: a comprehensive psychometric evaluation in four diverse samples. Assessment 29 (6), 1262–1284. https://doi.org/10.1177/10731911211008245.

Zuckerman, M., Kuhlman, D., Joireman, J., Teta, P., Kraft, M., 1993. A comparison of three structural models for personality: the big three, the big five, and the alternative five. J. Personal. Soc. Psychol. 65, 757–768. https://doi.org/10.1037/0022-3514.65.4.757.

Supplementary Materials

Supplementary Material 1. English version of the personality questionnaire used in this study (as provided to the raetrs)

PERSONALITY QUESTIONNAIRE FOR CHIMPANZEES

INSTRUCTIONS:

- Please answer the questionnaire individually, without discussing it with other keepers, volunteers or researchers.

- Evaluate each personality trait by assigning a numerical value on a scale of 1 to 7, depending on whether the subject is better identified with one end of the scale or the other. Example for a subject considered "social":

Social 1 2 3 4 5 [✓ 6] 7 Antisocial

1: Very social 2: Social 3: Slightly social 4: Neutral 5: Slightly antisocial
6: Antisocial 7: Very antisocial

- It is important to evaluate all the adjectives for all the subjects. Some traits might be difficult to assess, and some may be very similar. However, in order to obtain a complete personality profile of each individual, it is highly desirable that you evaluate all adjectives. Nevertheless, if you experience a great difficulty assessing a certain adjective, you can leave it blank.

- Each item should be evaluated by focusing on the two opposite adjectives. If necessary, at the end of the document you will find explanatory definitions for all the adjectives used (with their antonyms in brackets), in order to facilitate the assessment.

- Traits involving social aspects can refer to how subjects behave with humans or with their conspecifics (other chimpanzees), and assessment of these traits should include both. Nevertheless, if the subject behaves differently with humans than with other chimpanzees, the evaluation should focus on its relationships with conspecifics.

NAME OF THE CHIMPANZEE:

Social	1 2 3 4 5 6 7	Antisocial
Active	1 2 3 4 5 6 7	Passive
Dominant	1 2 3 4 5 6 7	Submissive
Spontaneous	1 2 3 4 5 6 7	Not spontaneous
Calm	1 2 3 4 5 6 7	Anxious
Good-tempered	1 2 3 4 5 6 7	Bad-tempered
Brave	1 2 3 4 5 6 7	Fearful
Cheerful	1 2 3 4 5 6 7	Sad
Pacific	1 2 3 4 5 6 7	Aggressive
Cautious	1 2 3 4 5 6 7	Impulsive
Empathic	1 2 3 4 5 6 7	Cruel
Not creative	1 2 3 4 5 6 7	Creative

ADJECTIVES’ DEFINITIONS:

Social: The subject enjoys interacting with others (≠Antisocial)
Active: Energetic, engaging in physical activity (≠Passive)
Dominant: The subject exercises power over the other individuals (≠Submissive)
Spontaneous: The subject has an open, natural and uninhibited behaviour (≠Not spontaneous)
Calm: The subject does not show tension or anger (≠Anxious)
Good-tempered: Naturally friendly and pleasant (≠Bad-tempered)
Brave: Determined, daring (≠Fearful)
Cheerful: The subject expresses joy and happiness (≠Sad)
Pacific: The subject does not start conflicts, nor participates in them (≠Aggressive)
Cautious: Forehanded, thoughtful (≠Impulsive)
Empathic: The subject shows concern for the states and needs of others (≠Cruel)
Creative: The subject is able to produce new ideas, solve and find answers to new problems (≠Not creative).

Chapter 4. General discussion, conclusions and future research directions

Photograph by Miquel Llorente

This thesis comprised two primary research questions, both related to the use of cognitive challenges by captive chimpanzees: one focused on investigating the effects of cognitive challenges on chimpanzee behavior and welfare, while the other aimed to assess how individual differences in personality might influence the outcomes of these activities. Specifically, Articles 1 and 2 explored the relationship between cognitive challenges, behavior and welfare in the context of enrichment, and Article 3 assessed the link between personality and cognitive performance in a non-invasive research context. Furthermore, Article 3 compared behavioral measures with personality traits obtained with questionnaires based on Eysenck's model. Finally, Article 4 provided further evidence supporting the use of this model in chimpanzees.

Our main hypotheses were that: (1) we would find individual differences in chimpanzees' interest and performance in cognitive tasks; (2) these differences would be predicted by sex, age and personality; (3) exposing chimpanzees to cognitively demanding activities would enhance their level of welfare, by increasing the frequency of species-typical behaviors while reducing the frequency of undesirable behaviors; and (4) Eysenck's model would prove to be an effective tool to describe chimpanzee personality.

Throughout the four studies of this thesis, we obtained evidence supporting the previous hypotheses. Nonetheless, we also found some unexpected results and faced several limitations. In this final section, we provide an overview of our main findings across the different studies, we discuss the limitations of our work, and we provide recommendations for future research.

4.1. Discussion

4.1.1. Factors affecting participation and performance in the cognitive challenges:

In this doctoral thesis, we studied three different cognitive challenges in a group of captive chimpanzees. Specifically, two of these challenges, the artificial termite-fishing task and the food maze were designed as tool-based enrichment activities and have been discussed in Articles 1 and 2, respectively. On the other hand, the third challenge was part of a cognitive research project, involving a series of problem-solving tasks (i.e., puzzle boxes), as detailed in Article 3. Throughout the triad of studies, we investigated the potential influence of individual factors like sex and age on subjects' participation in these cognitive tasks. For the puzzle boxes we also tested whether personality could predict differences in participation and success, to shed light on the link between specific personality traits and chimpanzees' problem-solving skills. Finally, for the two enrichment activities we assessed whether participation, and its effects on behavior, were consistently maintained across sessions. This longitudinal approach allowed us to understand the sustainability and effectiveness of these enrichment activities over time. By exploring the diversity of factors influencing chimpanzees' performance during cognitive challenges, this thesis aimed to provide new insights into chimpanzees' cognitive complexity, and to outline the importance of providing cognitively stimulating activities to ensure their welfare in captivity. Table 1 summarizes the findings of Articles 1, 2 and 3 regarding participation and success in the cognitive challenges.

Table 1

Summary of the main findings of Articles 1, 2 and 3 about participation and success in the cognitive challenges presented

		Artificial termite-fishing task (Article 1)	**Food maze (Article 2)**	**Puzzle boxes (Article 3)**
Sample size (N chimpanzees)		14	14	14
Chimpanzees interacting with the tasks at least once		10 (71.4%)	14 (100%)	14 (100%)
Participation[a] (mean±SD, range)		5.65±5.97%, (0.00-18.25%)	8.92±15.27%, (0.22-53.52%)	81±22% (35-100%)
Success[b] (%)		100%	14.28%	91%
Participation is predicted by…	Sex	No	Yes (♀ > ♂)	No
	Age	No	No	No
	Time of the day	Yes (morning > afternoon)	Yes (morning > afternoon)	-
	Personality	-	-	No
Success is predicted by…	Personality	-	-	Yes
Participation in the enrichment…	Decreased across sessions	No, it increased	Yes	-
	Predicted an increase in:	Tool use Feeding Social proximity	Tool use Aggression-related behaviors Self-directed behaviors[c]	-
	Predicted a decrease in:	Inactivity	Inactivity	-
	Predicted no variation in:	Abnormal behaviors Affiliation-related behaviors Aggression-related behaviors Self-directed behaviors	Abnormal behaviors Affiliation-related behaviors Social proximity	-

Note. [a] Participation in the artificial termite-fishing task and the food maze was estimated as the proportion of scans in which the chimpanzees interacted with the enrichment, while participation in the puzzle boxes was calculated as the proportion of trials in which subjects engaged in the task. [b] Success in the artificial termite-fishing task and the food maze represents the proportion of subjects who were successfully retrieved food from the enrichment, while success in the puzzle boxes was estimated as the proportion of successful trials across all tasks. [c] Self-directed behaviors increased only when the subject actively interacted with the device using tools (not just exploring it or being in contact to it).

Providing animals with the opportunity to make choices is considered one of the key elements to create a favorable captive environment (Whitham & Wielebnowski, 2013). In line with this, the two enrichment activities assessed in this thesis were provided in the chimpanzees' usual enclosures, allowing the animals to actively decide whether to engage with the tasks. In contrast, solving the puzzle boxes required temporarily isolating the chimpanzees from their social group in adjacent enclosures, where keepers encouraged their participation in the experimental sessions. Nonetheless, they could still choose not to enter the enclosures or not to interact with the devices. Despite that experimental isolation may potentially induce stress in non-human primates (Fagot & Paleressompoulle, 2009), some studies involving cognitive tests in monkeys have demonstrated that voluntary participation and short periods of isolation do not negative impact their welfare (Ruby & Buchanan-Smith, 2015; Whitehouse et al., 2013). In the puzzle boxes study, we did not assess welfare indicators during the experimental sessions and therefore we cannot make assumptions regarding whether the isolation or the task challenge were stressful for the chimpanzees. However, the higher rates of participation in the puzzle boxes suggest that chimpanzees were interested in the tasks and perceived them as positive stimuli. Similarly, all the individuals from our sample engaged in the food maze at least once, and 10 out of 14 chimpanzees interacted with the termite-fishing task. The high interest towards the cognitive challenges exhibited by the chimpanzees was not unexpected, considering their inherent curiosity towards novel objects (Paquette & Prescott, 1988) and their highly developed manipulative skills (Paquette & Prescott, 1988; Torigoe, 1985). Furthermore, previous research has shown that these animals find cognitive challenges rewarding, even in the absence of preferred food rewards (Brooks et al., 2021; Clark & Smith, 2013).

The proportion of chimpanzees in the group interacting with the tasks at least once was high for the three cognitive activities. Participation in the puzzle boxes was not directly comparable with participation in the cognitive enrichment tasks, as they were measured differently (i.e., in the puzzle boxes it was measured as a proportion of sessions and, in the cognitive enrichment tasks, as a proportion of scans). Nonetheless, our results show that participation was very high for the puzzle boxes (mean = 81% of the sessions) and moderate for the two cognitive tasks, considering that chimpanzees spent, on average, between 5.65% (termite-fishing task) and 8.92% (food maze) of the scans interacting with the enrichment activities. Nonetheless, in all three cognitive activities there was important variation in participation across individuals, with some chimpanzees engaging more than others in the tasks (see individual values for participation in Supplementary Materials Table S3, Article 1; Supplementary Information Table S2, Article 2 and Supplemental Information Table S4A, Article 3). Additionally, in the two more cognitively demanding activities —the food maze and the puzzle boxes—, we observed differences in subjects' ability to solve the tasks. In contrast, in the termite-fishing task, all subjects that engaged with the enrichment successfully obtained the food rewards. This supports previous research showing that, similar to their wild counterparts, chimpanzees are capable to manufacture tools by gathering materials from their environment and use them to successfully retrieve food rewards from tasks that simulate termite-fishing (Celli et al., 2003; Hopper et al., 2015; Llorente & Campi, 2014; Nash, 1982). Inter-individual variation in participation and performance has been previously reported in other studies assessing cognitive challenges in great apes (Clark et al., 2019; Clark & Smith, 2013; Tarou et al., 2004) and monkeys (Jacobson et al. 2019; Polgár et al. 2017). These differences have been attributed to multiple variables, including sex, age, cognitive skills and personality (Altschul et al., 2017; Celli et al., 2003; Clark & Smith, 2013; Herrelko et al., 2012; Hopper et al., 2014; Šlipogor et al., 2022). In the study assessing the food maze, we observed that females were much more likely to engage in the enrichment than males, and the only two individuals able to master the task were females. These results are consistent with previous studies evaluating tool-based activities in captive chimpanzees, which have consistently reported that females exhibit higher interest and use tools more effectively than males (Brent & Eichberg, 1991; Herrelko et al., 2012; Yamanashi et al., 2016). Furthermore, this female-biased tool-use behavior has been consistently observed in wild chimpanzees (Boesch and Boesch 1981, 1990; Lonsdorf 2005; Lonsdorf et al. 2004; McGrew 1979; Pruetz et al. 2015), but also in wild and captive bonobos (Samuni et al. 2022; Boose et al. 2013; Gruber et al. 2010). Nonetheless, in the study assessing the artificial termite-fishing task, we found no sex differences in participation. This might be attributed to the food maze requiring more complex tool-use abilities than the termite-fishing task, thereby accentuating sex differences in the food maze. Additionally, research in captivity suggests that female chimpanzees have higher cognitive flexibility (Cantwell et al., 2022), which could also account for the observed higher success of females in our study compared to males.

In the puzzle boxes, the relationship between personality and performance was, in some cases, modulated by sex. For instance, higher Neuropsychoticism predicted higher success in females, but not in males. Sex differences in the relationship between personality and performance in experimental tasks have been rarely explored in chimpanzees (Hopper et al., 2014). However, assessing the modulating effect of sex in this species might be especially important, as sex differences in the expression of personality traits are known in chimpanzees and appear to be stronger than in other species, like humans and orangutans (King et al., 2008; Rawlings et al., 2020; Weiss & King, 2015). Finally, despite the importance of considering sex differences in the context of cognitive challenges in this species, the results of our studies should be interpreted with caution, due to the particularly small number of females in our sample (N=5). Likewise, the absence of a significant effect of age on participation in all the three cognitive challenges is likely attributable to the narrow age range of our sample.

Our statistical models also explored differences in the use of enrichment activities throughout the day. Since both the termite-fishing tasks and the food maze were loaded with food in the morning, before the chimpanzees entered their outdoor enclosures, a consistent trend emerged in both cases: participation was higher in the morning (between 10:30h and 14:00h) than in the afternoon (between 15:00h and 17:30h). Although participation declined through the day, chimpanzees still engaged with the enrichment activities in the afternoon, suggesting that some food rewards remained available throughout the day. This was particularly evident for the food maze, as extracting the rewards was more challenging than in the termite-fishing task, and therefore more rewards were accessible throughout the entire day. In addition to the availability of the rewards, the higher use of the enrichment in the morning may also be attributed to the chimpanzees' higher hunger during the early hours of the day. Prior to entering the outdoor enclosures in the morning, they were only provided with a light breakfast. Therefore, they were likely hungrier in the morning than in the afternoon, when they had already been fed twice (morning and midday).

In the puzzle boxes, we used the probability to stop interacting with the task during the experimental session as an indicator of lack of motivation. We found some interesting relationships between this variable and personality. For instance, higher Neuropsychoticism predicted higher probability of losing contact with the task. This was not surprising, considering that the puzzle boxes required patience and persistency, qualities that contrast the attributes that described this personality dimension (e.g., anxiety and impulsivity). In the studies assessing the artificial termite-fishing task and the food maze, motivation was not assessed as such (i.e., we did not record how many times subjects lost contact with the enrichment while interacting with it). Nonetheless, in our models we investigated whether participation changed across sessions, as a decrease in participation across sessions could reflect changes in chimpanzees' interest (i.e., the chimpanzees were no longer curious towards the tasks) or motivation (i.e., the chimpanzees were unwilling to maintain the necessary effort to solve the tasks). In our studies, we observed an increase in participation across sessions in the artificial termite-fishing task, while participation in the food maze decreased.

Previous research has shown that non-human primates tend to lose interest in food-based enrichments and puzzle feeders after a few hours of exposure (Bloomstrand et al., 1986; Csatádi et al., 2008; Gilloux et al., 1992). Nonetheless, more complex devices are supposed to promote engagement for longer time periods (Clark, 2011; Taylor et al., 1994). Our results seem to contradict these findings, as for the more complex task, the food maze, we found a decrease in participation through time. We hypothesize that this could depend on the fact that most of the chimpanzees were unable to master the more complex task, and therefore, although they were curious during the first sessions, they experienced frustration and loss of motivation after repeatedly failing to extract the rewards (Toates, 1986). Conversely, despite being a less complex and not entirely novel task, participation in the artificial termite-fishing task increased across sessions, and so did tool use behavior. These findings suggest that, after years of not being exposed to this enrichment, the chimpanzees perceived the termite-fishing task as a rewarding challenge, and became more proficient at using tools to extract the foods.

A critical aspect when providing cognitive challenges to non-human animals is to achieve an appropriate level of challenge or cognitive stimulation. A task must offer sufficient stimulation to drive animals' motivation, while avoiding excessive difficulty that may lead to frustration (Meehan & Mench, 2007). The high proportion of success (91%) exhibited by chimpanzees in the puzzle boxes show that they made considerable effort to solve them, and that the level of task difficulty was suitable. Similarly, all the chimpanzees who interacted with the artificial termite-fishing task were able to successfully extract the honey from the tubes. In the food maze, however, the fact that only two individuals mastered the task may indicate that either the task was too complex for this particular group, or the study duration was too short.

Considering that wild non-human primates require extensive time to master tool-use activities like ant-dipping or nut-cracking (Boesch & Boesch-Achermann, 2000; Matsuzawa et al., 2001; Ottoni & Izar, 2008), it is possible that the chimpanzees in our study, by lacking previous experience with these devices, would have required additional time and practice to learn to effectively retrieve the food rewards from the maze.

Furthermore, all the chimpanzees in our study were naïve to the food maze task, so that social learning was not possible, at least at the beginning of the study period. Social learning plays a crucial role in the acquisition of tool-use activities in chimpanzees, both in the wild (Gruber et al., 2009; Hobaiter et al., 2014; Inoue-Nakamura & Matsuzawa, 1997) and in captivity (Nagell et al., 1993; Yamamoto et al., 2013). In line with this, wild chimpanzees provide greater opportunities for social learning to their conspecifics in populations where termite-fishing is a more complex task (Musgrave et al., 2020). Additionally, all the chimpanzees in our sample were adults, and previous research has shown that adult captive chimpanzees tend to exhibit behavioral conservatism when provided with opportunities to use tools (Neadle et al., 2020). Some researchers have also suggested the existence of sensitive learning periods during which the acquisition of tool-use skills is optimal for chimpanzees (Biro et al., 2003; Neadle et al., 2020). For instance, for nut-cracking, this optimal learning window is thought to occur between 3 and 7 years of age (Inoue-Nakamura & Matsuzawa, 1997), while the acquisition of termite-fishing skills begins at 1.5 years and can continue developing until 10-11 years (Musgrave & Lonsdorf, 2021). Although adult chimpanzees and other great apes can successfully innovate and individually learn to solve novel tool-use tasks (Motes-Rodrigo & Tennie, 2022), it is possible that the inclusion of younger chimpanzees in our study sample would have led to different findings.

Finally, differences in food preferences or food motivation among subjects may have had an influence on their participation in the cognitive tasks. Chimpanzees show individual differences in their food preferences (Brosnan et al., 2008; Slocombe & Zuberbühler, 2006), but, in general, they tend to favor foods high in non-starch sugars (Remis, 2002), such as the rewards offered in this thesis (e.g., dried fruits, honey). Thus, we consider that the selected food items were appropriate to motivate the animals.

Overall, our findings on participation and performance in the cognitive challenges suggest that, when implementing these activities in captive non-human primates, individual differences may play an important role and should, therefore, be taken into consideration. First, individual differences other than subjects' cognitive abilities may explain part of the variation in performance in a cognitive research context. Second, when cognitive challenges are provided as enrichment activities, not all subjects may obtain the same welfare benefits (Coleman & Novak, 2017; Costa et al., 2018; Izzo et al., 2011).

4.1.2. Behavioral and welfare implications of cognitive challenges

To achieve optimal welfare, captive animals should be given the opportunity to engage in species-typical behaviors, addressing their "ethological needs" (Browning, 2019; Hughes & Duncan, 1988). Furthermore, they need to be provided with choices and rewarding challenges that elicit positive affective states, contributing to a life that is meaningful and enriching (Bernstein-Kurtycz, 2015; Mellor, 2016). Due to their behavioral, cognitive, and social complexity, ensuring optimal conditions and welfare-promoting environments to captive non-human primates is a particularly challenging endeavor (Talbot et al., 2023). In the wild, non-human primates inhabit complex environments where they constantly encounter challenges related to finding food, competing for resources, avoiding predators, and establishing social hierarchies (Nishida et al., 2010). Great apes, and chimpanzees specifically, are known for their remarkable cognitive skills, enabling them to solve complex problems and to exhibit a wide range of sophisticated behaviors, including tool use. Nonetheless, captive settings often fall short in replicating the complexity of their natural environments. Therefore, environmental enrichment has become a key tool for improving animal welfare by providing opportunities for physical, affective, and cognitive stimulation (Fernández & Martin, 2021; Hoy et al., 2010).

Several authors have suggested that providing cognitively demanding tasks to captive great apes can be an effective way to promote species-typical behaviors and improve their welfare (Clark, 2011, 2017; Meehan & Mench, 2007). In line with this, extractive foraging devices requiring tool use have been commonly used as environmental enrichment for chimpanzees. Nonetheless, only a few studies have extensively explored this topic. For instance, studies assessing the welfare outcomes of devices that simulate ant- or termite-fishing have mainly focused on the effects of this tasks on solitary behaviors (Celli et al., 2003). However, given that these tasks are usually provided in a social setting, the influence they may have on social behaviors and group dynamics should also be considered. Furthermore, researchers usually compare the frequency of behaviors in the presence versus in the absence of the enrichment, but they rarely consider individual differences in participation and temporal variation (e.g., whether the effects of the enrichment are maintained over time).

In this thesis, we evaluated the behavioral and welfare impact of two cognitive enrichment activities requiring tool use in a group of captive chimpanzees: an artificial termite-fishing task and a double-sided food maze. Our statistical models assessed whether participation in the tasks, rather than the mere presence of the enrichment, would predict changes in chimpanzee behavior and whether these changes would remain consistent over time (i.e., across enrichment sessions). In both studies, we found similar results regarding the effects of enrichment activities on solitary behaviors. For instance, participation in the enrichment predicted an increase in tool use and a decrease in inactivity, while promoting foraging behavior. In their natural habitats, non-human primates dedicate a substantial proportion of time to foraging and feeding, accounting for approximately 18.8% to 60% of chimpanzee activity budget (Boesch & Boesch-Achermann, 2000; Doran, 1997; Inoue & Shimada, 2020; Pruetz & McGrew, 2001; Yamanashi & Hayashi, 2011). Conversely, in captive environments, food resources are directly supplied to the animals and chimpanzees spend much less time foraging compared to their wild counterparts (Inoue & Shimada, 2020; Yamanashi & Hayashi, 2011). This is problematic, because the time that ought to be allocated to foraging may be dedicated to undesirable behaviors, such as inactivity or self-directed and abnormal behaviors. To address this issue, it is thus crucial to provide challenges to captive animals that encourage and stimulate their natural foraging behavior. Nonetheless, food-based enrichments usually consist of simple objects (e.g., boxes, pipes, tubes, balls) that do not require sophisticated cognitive skills to be solved, and result in limited engagement time (Dutton et al., 2018). In contrast, the termite-fishing task and the food maze required the chimpanzees to locate, modify, and use tools to extract food, thus providing a higher level of cognitive stimulation. This aligns with the definition of cognitive enrichment as stated by Buchanan-Smith and colleagues (2016), which emphasizes that cognitive enrichment should "engage animals' evolved cognitive skills, rather than simply occupy them".

Similarly to foraging, inactivity levels are typically higher in captive chimpanzees than in their wild counterparts, and therefore, a decrease in inactivity is generally considered a positive welfare outcome (Kurtycz et al., 2014; Neal Webb & Schapiro, 2023). Conversely, elevated levels of inactivity in captive animals are considered an indicator of compromised welfare (Fureix & Meagher, 2015). In line with these findings and with the outcomes of our studies, several authors have reported a reduction in inactivity when providing environmental enrichment to great apes (Baker, 2004; Baker & Aureli, 1997; Bloomsmith et al., 1991; Brent, 1992; Celli et al., 2003; Csatádi et al., 2008; Gilloux et al., 1992) and other primates (Baker et al., 2014; Wowk & Behie, 2023). It should be noted that a decrease in inactivity does not necessarily imply an increase in locomotion (i.e., walking, climbing, hanging) (Neal Webb &

Schapiro, 2023). This is because, instead of being inactive (i.e., resting), chimpanzees may display behaviors that do not necessarily imply physical movement between locations, like interacting with the enrichment. Thus, in our studies, the decrease in inactivity when participating in the two enrichment activities could be interpreted as an indicator of engagement or cognitive stimulation (Kurtycz et al., 2014; Poole, 1988).

Contrary to our predictions, participation in the enrichment activities did not predict a decrease in chimpanzees' abnormal behaviors. One possible explanation is that abnormal behaviors were relatively rare in our study sample, constituting only 1%-2.5% of the total scans. This prevalence contrast with the 2.9-7.6% of time spent engaging in abnormal behaviors, as reported in studies involving other captive chimpanzee colonies (Bradshaw et al., 2008). It is worth noting that our sampling methodology, employing instantaneous scan sampling every two minutes, may have led to an underestimation of the occurrence of abnormal behaviors, especially those with short durations (Altmann, 1974). Despite this potential limitation, it is essential to highlight that various studies have validated the reliability of instantaneous scan sampling as a method to monitor multiple animals and behaviors concurrently (Brereton et al., 2022; Martin & Bateson, 2007; Pullin et al., 2017). This suggests that the observed discrepancy in abnormal behaviors may be reflective of genuine patterns within our study population rather than an artifact of the sampling approach.

Several studies have explored the effects of tool-based enrichment devices and puzzle boxes on the frequency of abnormal and stereotypic behaviors in non-human primates, but the results were not unequivocal. Certain studies have documented a decrease in abnormal and stereotypic behaviors during or after exposure to enrichment (Brent & Eichberg, 1991; Maki et al., 1989; Yamanashi et al., 2016; Zaragoza et al., 2011), while others have reported no significant changes or even an increase (Camargo & Mendes, 2016; Gottlieb et al., 2011; Lutz & Novak, 2005; Rooney & Sleeman, 1998). Moreover, although abnormal behaviors have traditionally been considered a reliable indicator of poor welfare, recent studies in non-human primates have raised questions about this association (Birkett & Newton-Fisher, 2011; Hopper et al., 2016; Jacobson et al., 2016). In fact, understanding the etiology of abnormal behaviors in chimpanzees and interpreting its relationship with welfare has proven to be a challenging issue (Bloomsmith et al., 2020). For instance, research has demonstrated that the occurrence of abnormal behaviors in captive chimpanzees is influenced by multiple factors, including sex, age, early rearing history, genetic predisposition, group size, or personality (Bloomsmith et al., 2020; Lutz & Coleman, 2022). It is also worth noting that chimpanzees show high inter-individual variation not only in the frequency and duration of abnormal behaviors but also in their specific behavioral repertoires. Some abnormal behaviors are common in certain individuals but absent in others (Goldsborough et al., 2023). In this thesis, we did not delve into investigating the diversity of abnormal behaviors within our chimpanzee sample, nor did we explore individual differences in the occurrence of these behaviors. Nonetheless, considering the life experiences of our chimpanzees, we can assume that multiple variables may have contributed to differences in the emergence of abnormal behaviors, also explaining why some of these behaviors may be difficult to eradicate. For example, chimpanzees that experienced separation from their mothers and spent years in impoverished environments, as observed in some individuals within our study sample, may persist in engaging in stereotypical or abnormal behaviors even years after their rescue (Lopresti-Goodman et al., 2012; Martin, 2023). Thus, it is plausible that some chimpanzees in our study sample adopted and maintained certain abnormal behaviors as adaptive coping mechanisms developed in response to the deprived conditions they encountered at different points of their lives (Lutz & Coleman, 2022). This insight underscores the long-lasting impact of early-life experiences on the behavioral repertoire of captive chimpanzees and the challenges associated with mitigating abnormal behaviors in such populations.

The enrichment presence was not linked to an increase in the rate of self-directed behaviors (i.e., rubs and scratches) in neither of the two tasks, suggesting that the mere presence of the enrichment did not induce stress. Additionally, self-directed behaviors increased as a function of participation in the food maze, but not in the termite-fishing task. This difference could be attributed to variations in the complexity and cognitive demands associated with each task. While the termite-fishing task presented an easier and less time-consuming challenge, already familiar to the chimpanzees, the food maze introduced a completely novel challenge and more demanding task, requiring fine motor skills, precise coordination, and advanced cognitive abilities such as planning and understanding of the physical properties of objects (Völter & Call, 2014). Similarly to our findings, several authors have reported an increase in self-directed behaviors when primates face novel or challenging situations (Clark & Smith, 2013; Elder & Menzel, 2001; Itakura, 1993; Leavens et al., 2004; Leavens et al., 2001; Yamanashi & Matsuzawa, 2010). Consequently, we can infer that the increase in self-directed behaviors during interactions with the food maze was not indicative of stress or anxiety but rather reflected emotional arousal in a challenging context (Baker & Aureli, 1997; Maestripieri et al., 1992), which might not be necessarily linked to negative emotions. Nonetheless, we cannot dismiss the possibility that some of the chimpanzees lacked the necessary cognitive skills to cope with the challenge, potentially leading to anxiety and, consequently, an increase in the rate of self-directed behaviors (Clark, 2017).

Overall, engaging in the cognitive enrichment tasks had no major effects on chimpanzee social behavior. The fact that affiliative behaviors remained unaffected by any of the enrichment activities could be considered as a positive outcome, suggesting that chimpanzees did not allocate more time to a solitary activity (i.e., participating in the enrichment) at the cost of diminishing positive social interactions. However, two behaviors changed as a function of participation: engaging in the artificial termite-fishing task increased proximity to conspecifics, whereas interacting with the food maze increased aggression-related behaviors. We expected that participation would predict an increase in proximity in both tasks, as both could be used by more than one chimpanzee at the same time and chimpanzees might be curious about enrichments and gather around them. Furthermore, we predicted an increase in aggression-related behaviors as a result of competition over access to the devices and food rewards, as in other studies providing cognitive tasks in a social setting (Jacobson et al., 2019; Maki et al., 1989; Tarou et al., 2004). Nonetheless, there were significant differences between the two tasks that could explain the contrasting results for social proximity and aggression-related behaviors. For instance, the termite-fishing tasks had multiple holes, enabling two or more animals to engage in the enrichment simultaneously, whereas the food maze contained two independent mazes that could be used by maximum two animals. Thus, the termite-fishing task allowed for more animals to interact with the enrichment simultaneously, which could explain the increase in proximity as a function of participation. Furthermore, in the artificial termite-fishing task the chimpanzees could see each other while interacting with the task, whereas two animals simultaneously engaging in the food maze were at the opposite sides of the device, without seeing each other. This impossibility to see their conspecifics might have increased tension and potentially contributed to an increase in aggressive behavior for those engaging in the food maze. At the same time, this could explain why the termite-fishing task was frequently used by several animals at a time, while the food maze was mostly monopolized by one single chimpanzee.

Another possible explanation for the raise in aggression-related behaviors during the food maze is that retrieving food rewards in this task required more time and effort, as compared to the termite-fishing task, and indeed none of the males mastered the task. Wild male chimpanzees are known to be dominant to all females (Reynolds, 2005), often displaying higher rates of aggression towards them (Goodall, 1986; Muller & Mitani, 2005; Newton-

Fisher, 2006). Thus, it is possible that, in our study, the females who engaged with the food maze and retrieved the food were also more likely to receive aggression from the males. However, in captivity, females can sometimes dominate over males (Noë et al., 1980) and, in some contexts (i.e. during social integrations), males can display more submissive behaviors than females (Fultz et al., 2022). Additionally, wild female chimpanzees have also been reported to be aggressive towards males in the context of feeding competition (Muller & Mitani, 2005). Thus, although we did not investigate sex-differences in aggression-related behaviors, it is possible that both males and females were involved in these behaviors.

Finally, aggression-related behaviors in our behavioral catalogue included aggressive behaviors (e.g., physical aggression, charging displays), but also agonistic behaviors that did not involve physical aggression (e.g., displacements) and submissive behaviors (e.g., avoidance, bared-teeth, hand-to mouth). Submissive behaviors are a way to appease dominant individuals and can help reducing social tension and prevent aggression, and are therefore highly desirable in captive groups. Moreover, while excessive aggression is generally considered a negative welfare indicator in captive environments, agonistic interactions, including aggression, play a crucial role in the social lives of chimpanzees Furthermore, it has been demonstrated that non-human primates frequently engage in friendly interactions with former opponents after a conflict involving physical aggression (de Waal, 2000). This further supports the hypothesis that aggression is an integral part of non-human primates' social life, serving as tool during competition and negotiation (de Waal, 1992, 2000). Although enrichment tasks in a social setting may enhance intragroup competition, this does not necessarily need to be negative, as this scenario is more similar to natural conditions and increases ecological validity (Cronin, 2017).

Our statistical models further assessed whether the behavioral effects of enrichment activities were maintained over time (i.e., across enrichment sessions), allowing us to further investigate whether the frequency and duration of the enrichment was adequate. In general, we found that behavioral changes were maintained across sessions, suggesting that the enrichment activities were effective throughout our study period. Nonetheless, to ensure that a particular enrichment activity remains effective in the long-term, subjects' interest and behavior should be ideally monitored over longer time frames.

Overall, the results of the two studies assessing cognitive enrichment tasks (Articles 1 and 2) supported our third hypothesis that cognitive challenges contribute to improving chimpanzee welfare. In particular, these enrichment tasks (1) promoted the expression of species-typical behaviors such as foraging and tool-use, (2) reduced periods of inactivity, and (3) provided chimpanzees with the opportunity to engage in cognitively stimulating activities, creating learning opportunities that simulate aspects of their natural environment (Young et al., 2020).

4.1.3. Applying Eysenck's model to chimpanzees

In this thesis we employed a questionnaire based on Eysenck's Psychoticism-Extraversion-Neuroticism (PEN) model to assess chimpanzee personality in two captive settings: Fundació Mona (Girona, Spain) and the Leipzig Zoo (Leipzig, Germany). In Article 3, we compared the personality traits obtained from the 14 chimpanzees at Fundació Mona to behavioral measures obtained through observations of spontaneous behavior. Additionally, this chapter assessed the possible relationship between personality and performance in tasks that required problem-solving skills. Article 4 expanded our research goals by applying the same personality questionnaire to a broader sample of 23 chimpanzees housed at the Leipzig Zoo. In Article 4 we conducted factorial analysis on a total sample of 37 chimpanzees, including individuals from both research locations (Fundació Mona and the Leipzig Zoo). Considering chimpanzee phylogenetic closeness to humans, and building upon the promising results of previous studies assessing this model in chimpanzees, our hypothesis was that Eysenck's model would prove as a reliable tool to assess personality in this species.

When employing human models for the evaluation of animal personality, two key indicators of their suitability are inter-rater reliability and validity. Inter-rater reliability refers to the level of agreement between raters and, in personality research, is commonly measured using intraclass correlation coefficients (Shrout and Fleiss, 1979). In this thesis, we achieved good results for inter-rater reliability, both when exclusively assessing the small sample of chimpanzees at Fundació Mona and when incorporating the chimpanzees at the Leipzig Zoo into the analysis.

Validity refers to the degree to which a measurement accurately captures the specific trait it aims to assess (Gosling, 2001). In personality research, the correlation between traits and behavioral observations is commonly considered a measure of validity (Freeman & Gosling, 2010). This assessment usually encompasses two essential aspects of validity: convergent validity (whether a trait correlates with conceptually related behaviors) and discriminant validity (whether a trait is not correlated with unrelated behaviors). In Article 3, we obtained several expected correlations between chimpanzee behavior and personality traits based on Eysenck's model, providing evidence of convergent validity. For instance, Extraversion exhibited positive correlations with the overall relative frequency of affiliative behaviors (including grooming, social play, sexual behavior and other affiliative behaviors), as well as independent positive correlations with grooming and social play. Furthermore, Dominance correlated with the relative frequency of agonistic dominant behavior and Neuropsychoticism correlated with the relative frequency of agonistic interactions (including agonistic dominance, agonistic submission and other agonistic behaviors). Nonetheless, some behaviors were associated with two traits (e.g., the relative frequency of agonistic dominance correlated with both Dominance and Extraversion), thus revealing limited discriminant validity for the model. As extensively discussed in Article 3, these results were largely expected. Studies comparing trait rating and behavioral observations in primates have also reported limited discriminant validity (Pederson et al., 2005; Šlipogor et al., 2020). Furthermore, the relationship between traits and behaviors is not always straightforward, as some behaviors may be predicted by the combination of multiple traits (Capitanio, 2004). Finally, it is worth noting that the correlation between Dominance and Neuropsychoticism in Article 3 was close to significance, indicating a moderate association between the traits. Therefore, it was not surprising that some behaviors correlated with both traits. Moderate correlations (0.4-0.59) between personality factors have also been reported in various species, including chimpanzees (King and Figueredo, 1997), barbary macaques (*Macaca sylvanus*; Konečná et al. 2012) and humans (Borkenau and Ostendorf, 1990; Costa et al., 1991; Graziano and Ward, 1992; Zhang et al., 2022). Nonetheless, to ensure the independency of personality factors, we conducted a methodological adjustment in the factorial analysis in Article 4. Instead of the oblique rotation employed by Úbeda and Llorente (2019), which provided the factor structure used to compute personality scores in Article 3, we performed an orthogonal rotation in Article 4. This adjustment aimed for a more rigorous analysis, as orthogonal rotations assume that factors are uncorrelated and yield more straightforward structures that are more likely to be replicated (Kieffer, 1998). Despite this modification in the analysis, the personality structure we obtained in Article 4 was highly similar to the one previously reported by Úbeda and Llorente (2019). This confirmed the existence of three independent factors: Extraversion, Neuropsychoticism and Fearless Dominance. However, the issue of the limited discriminant validity of our model should not be dismissed, emphasizing the need for further research to confirm that these three traits can successfully predict behavioral outcomes in chimpanzees.

Validity also refers to the informativeness of a personality structure about a species (Weiss, 2017b). In this thesis, we assessed chimpanzees from two different captive environments: a zoological institution and a rehabilitation and rescue center. Including chimpanzees from the Leipzig Zoo in the factorial analysis did not alter the personality structure obtained when only considering the chimpanzees at Fundació Mona. These findings indicate that the chimpanzees in our sample shared the same personality domains, and confirm previous research showing that human-based personality questionnaires can reveal similar personality structure in chimpanzees from different captive settings (King et al., 2005; Weiss et al., 2007). Additionally, our results align with previous research (Weiss et al., 2009), indicating that potential cultural differences between raters from different countries (Spain and Germany) did not affect the personality structure that emerged from the ratings.

Two of the traits obtained in our analysis, Extraversion and Dominance/Fearless Dominance, have been extensively documented in both captive and wild chimpanzees (Dutton, 2008; King & Figueredo, 1997; Weiss et al., 2009; Weiss et al., 2007; Weiss et al., 2017) and their descriptions and interpretations are straightforward. However, Neuropsychoticism, as identified in our factorial analysis, is a more intricate dimension. According to our results, Neuropsychoticism is a combination of Eysenck's traits Neuroticism and Psychoticism. Neuroticism has been described in chimpanzees (Dutton, 2008; King & Figueredo, 1997; Weiss et al., 2009; Weiss et al., 2017) and other non-human primates (Gosling, 2001), but it tends to exhibit lower inter-rater reliability as compared to other dimensions (see Weiss et al., 2017). This suggests that identifying and assessing this trait may be more challenging for human raters. Regarding Psychoticism, this dimension has seldom been explored in non-human primates. In a landmark study assessing Eysenck's model in Rhesus macaques, Chamove and colleagues (1972) identified the dimensions Hostility and Fearful, which resembled human Psychoticism and Neuroticism, respectively. Furthermore, using a questionnaire-based methodology, Lilienfeld and colleagues (1999) found a psychopathy construct in chimpanzees, with positive associations between this trait and behavioral measures of agonism, daring behaviors, gentle teasing, displays, and temper tantrums. They also found a negative correlation between the psychopathic construct and repetitive movements (i.e., rocking, clasping) associated with anxiety. This would be in line with the notion that psychopathy in humans is usually associated with lack of anxiety (Cleckley, 1951). However, this would contradict our results, because, in our sample, being “aggressive”, “impulsive” and “cruel” (i.e., items that in humans load onto Psychoticism) fell into the same personality domain as “anxious” and “bad-tempered” (i.e., items that in humans load onto Neuroticism). Nonetheless, studies in humans have questioned the traditional believe that psychopathy is linked to low anxiety, revealing a complex relationship between these two traits (Derefinko, 2015; Hofmann et al., 2021; Kubak & Salekin, 2009; Sandvik et al., 2015; Schmitt & Newman, 1999).

In chimpanzees, the dimension Neuroticism has been positively associated with aggressiveness (Weiss et al., 2007). Furthermore, neurogenetic research in non-human primates has revealed that genetic diversity affecting reward sensitivity, impulsiveness and levels of anxiety can contribute to individual differences in aggressive behavior (Barr & Driscoll, 2014). Similarly, in humans, aggression and violence are likely to develop as a result of a generally disturbed emotional regulation, which can manifest as either abnormally high or low levels of anxiety (Neumann et al., 2010). Based on findings from both human and animal studies, it can thus be concluded that anxiety and aggression are interrelated and share common neural pathways, but the precise nature of their complex interplay remains a topic of ongoing investigation (Honess & Marin, 2006a; Neumann et al., 2010).

Another possible explanation for the interrelation between aggression and anxiety in non-human primates may provide additional arguments for the compound nature of Neuropsychoticism in our analysis. Several studies in non-human primates have shown that aggressive interactions trigger the expression of anxiety-related behaviors, such as self-scratching and other self-directed behaviors (Arnold & Aureli, 2007; Fraser et al., 2008;

Kutsukake & Castles, 2001; Maestripieri et al., 1992). Interestingly, this increase in anxiety-related behaviors is not only observed in the recipients of aggression, but also in those who initiate the conflict (i.e., the aggressors) (Aureli, 1997; Castles & Whiten, 1998; Romero et al., 2009; Schino et al., 2007). Thus, it is possible that chimpanzees rated as being more impulsive, aggressive and cruel were also perceived as being more anxious.

The concept of validity also implies that personality traits should predict meaningful life outcomes (Gosling et al., 2003a; Weiss, 2017b). This is a critical consideration in understanding the relevance of personality traits in non-human primates and their implications for various aspects of primate life. In alignment with this notion, numerous studies have established connections between personality and key aspects of primate life, including health and longevity (Altschul et al., 2018; Capitanio et al., 1999; Gottlieb et al., 2018; Jin et al., 2013; Robinson et al., 2018; Weiss et al., 2013), welfare (Costa et al., 2020; Fernández-Lázaro et al., 2019; Inoue-Murayama et al., 2018; Robinson & Weiss, 2023), social relationships (Massen & Koski, 2014; Verspeek & Staes, 2019; Weinstein & Capitanio, 2012), and cognitive performance (Altschul et al., 2016; Altschul et al., 2017; Herrelko et al., 2012; Hopper et al., 2014; Morton et al., 2013a; Šlipogor et al., 2022). In Article 3, the evaluation of the relationship between personality traits and chimpanzee performance in the puzzle boxes did not aim to specifically evaluate the validity of our personality assessment method. However, in line with the hypothesis that personality traits should predict real-word outcomes, our dimensions were linked with differences in performance measures. For instance, as expected, higher Neuropsychoticism predicted an increase in the probability of losing contact with the task. Chimpanzees scoring higher on this trait would be more aggressive, impulsive and anxious, traits that are not desirable in a testing situation and that would explain our findings.

Finally, from a practical point of view, the personality questionnaire employed in this thesis offers a distinct advantage: its brevity. One significant drawback of personality questionnaires designed for non-human primates lies in the extensive item count, making the rating process time-consuming, especially in scenarios where a large number of animals need to be assessed. For instance, the widely used Hominoid Personality Questionnaire (HPQ) (Weiss, 2017a; Weiss et al., 2009) is composed of 54 adjectives, and the first questionnaire based on the Five Factor Model used to assess chimpanzee personality contained 43 adjectives. In contrast, the early adaptation of Eysenck's model for chimpanzees revealed its potential to effectively describe personality with a concise set of items (Úbeda & Llorente, 2015). In this thesis we used the same questionnaire developed by Úbeda and Llorente (2015), consisting of 12 items corresponding to Eysenck's primary scales, which are integrated into three higher-order factors. Some authors have raised concerns about the use of brief personality inventories in humans, suggesting potential compromises in precision and consistency (Chapman & Elliot, 2019; Weiss & Costa, 2014). However, other studies argue that short scales can be reliable and valid alternatives (Burisch, 1984, 1997; Føllesdal & Soto, 2022; Gosling et al., 2003b; Gouveia et al., 2021; Nunes et al., 2018; Romero et al., 2012). This perspective is supported by successful applications of shorter questionnaires in describing non-human primates' personality (Hopper & Cronin, 2018). For instance, in a recent study with captive chimpanzees, Murray and colleagues (2023) successfully applied the Ten Item Personality Inventory (TIPI; Gosling et al., 2003b), which includes 10 items to measure the five personality dimensions of the Five Factor Model. Furthermore, the authors found associations between chimpanzee facial expressions and four of the personality dimensions obtained with this model (Extraversion, Agreeableness, Conscientiousness and Emotional stability). While the length of a questionnaire might seem trivial to researchers, it holds critical significance in zoological institutions and other captive settings where caretakers, who often have limited time for research activities, serve as the primary raters. Consequently, the adoption of shorter questionnaires emerges as an appealing and time-efficient alternative in these practical contexts (Hopper & Cronin, 2018).

4.2. Limitations and recommendations for future research directions

The research outlined in this thesis has several limitations and constraints which warrant careful consideration. This section will address them and suggest prospective avenues for future research in the domains of cognitive enrichment (Articles 1 and 2), cognitive testing (Article 3), and the application of Eysenck's model to describe chimpanzee personality traits, thereby investigating potential links with cognitive performance (Articles 3 and 4). Finally, we will sum up the general limitations inherent of our study and provide broader recommendations for future research.

4.2.1. Cognitive enrichment studies

Our findings from both studies assessing cognitive enrichment activities (Articles 1 and 2) suggest that the relatively short study period and limited number of sessions did not allow us to adequately evaluate the long-term effectiveness of the enrichment interventions. Notably, in the termite-fishing task, participation increased across sessions, while in the food maze it decreased. Therefore, extending the study period would have allowed us to confirm that chimpanzee interest in the termite-fishing task remained high over time and that the frequency of administration (1-2 times per week) was appropriate. Conversely, prolonged exposure to the food maze might have resulted in enhanced proficiency among the chimpanzees, potentially leading to increased participation and a more uniform distribution of engagement across subjects. Thus, we recommend for future studies assessing enrichment activities —either novel or familiar— to consider monitoring subjects' interest and performance over more extended periods of time. Additionally, employing multiple data collection events, spaced over weeks, months, and even years, holds promise for yielding a more nuanced understanding of the enduring impact of such activities.

In both cognitive enrichment tasks, morning sessions consistently exhibited higher participation rates compared to the afternoon, suggesting a potential influence of diminishing food rewards as the day progressed. To maintain a consistent supply of food rewards throughout the day, a potential improvement for enrichment devices, particularly food mazes, could involve incorporating a timed dispenser mechanism. This innovation would enable the gradual dispensation of rewards, also preventing the risk of chimpanzees monopolizing the device during a single session. Consequently, such a modification would likely broaden participation across a diverse range of animals and promote engagement throughout the day.

Overall, the use of enrichment showed no significant effect on the occurrence of abnormal behaviors, and the influence on self-directed behaviors was inconsistent across tasks. These findings lend support to the hypothesis that abnormal behaviors might not serve as the most reliable indicators of welfare in captive chimpanzees (Birkett & Newton-Fisher, 2011; Bloomsmith et al., 2020; Hopper et al., 2016; Jacobson et al., 2016). Consequently, future studies should explore alternative behavioral indicators. Particularly, in the context of enrichment, a more appropriate approach would involve emphasizing positive behavioral indicators, such as the total time animals engage with the task or the impact of enrichment on desirable behaviors (e.g., locomotion, exploration, feeding). Furthermore, to comprehensively evaluate the welfare effects of the cognitive enrichment tasks, it would be advisable to categorize self-directed behaviors and analyze them independently, considering not only their type (rubs, scratches) but also incorporating other variables such as target (body, face) or laterality (right side, left side), as suggested by Laméris and colleagues (2022) In addition, future studies should consider other anxiety-related behaviors that could be monitored while animals are engaged with the tasks, such as excessive vigilance or fear-related facial expressions and vocalizations, as these might provide important measures of emotional well-being and psychological stress in captive environments (Coleman & Pierre, 2014; Lutz &

Baker, 2023). Finally, non-invasive techniques for assessing physiological indicators of anxiety in non-human primates, such as measuring cortisol levels from samples of hair, saliva or urine samples, offer promising avenues for investigation (Ash et al., 2018; Novak et al., 2013; Verspeek et al., 2021). There is evidence supporting that stress can impact the hypothalamic-pituitary-adrenocortical (HPA) axis in non-human primates, although the specific effects of environmental enrichment on HPA axis activity remain inadequately understood (Novak et al., 2013). Therefore, when evaluating novel cognitive enrichment or tasks, integrating these physiological indicators could provide a complementary approach to behavioral indicators in assessing anxiety levels.

The food maze assessed in this thesis featured a double-sided design, allowing two chimpanzees to simultaneously interact with two independent mazes. The primary rationale behind this design stemmed from financial constraints of the center. Nonetheless, the maze was purposely designed so that the inner structure (i.e., the wooden shelves) was completely removable, and therefore could be modified or replaced by other types of mazes or cognitive activities. This flexibility offers the opportunity to design activities wherein two chimpanzees can engage simultaneously with the same maze, facilitating, for instance, the investigation of cooperative and competitive behaviors. In our study, however, although the two mazes were independent, the device was often monopolized by a single individual, and the increased levels of aggression-related behaviors linked to participation suggest that the maze inadvertently encouraged competition. To gain a deeper understanding of this phenomenon, we recommend more precise monitoring of competitive behavior and aggressive interactions when introducing new enrichment activities. Nonetheless, our current findings strongly advocate for the provision of multiple devices strategically placed around the enclosures to reduce potential aggressive competition (Honess & Marin, 2006b).

Another limitation of our enrichment studies is the absence of exploration into the specific cognitive skills triggered by the enrichment activities, coupled with a lack of measurement for the level of cognitive stimulation induced. Although there is no consensus on how to evaluate the level of cognitive stimulation and thus the effectiveness of a particular cognitive enrichment, Meehan and Mench (2007) and Clark (2017, 2023) propose some innovative criteria. For example, Meehan and Mench (2007) introduced the concept of “flow”, which refers to “the positive emotional state of satisfaction and pleasure that an animal experiences when applying a high-level skill to master a high-level task*”* (Clark, 2017, p.58*)*. “Flow” could be inferred, for instance, by measuring how easily an animal is “distracted” from a cognitive task (Clark, 2011). Furthermore, Ŝpinka and Wemelsfelder (2011) proposed the term “competence” to describe the range of cognitive skills that an animal employs to address unfamiliar situations (i.e., exploration, problem-solving). Our enrichment activities implied exploration and problem-solving, but also searching, modifying and using tools from the environments. Additionally, the food maze required the application of fine motor skills, precise hand movements, and likely more advanced cognitive skills, such as planning and understanding of the physical properties of objects (Völter & Call, 2014). Despite this, the cognitive abilities required to solve the food maze were not systematically assessed in this thesis. However, future investigations could undertake this analysis by examining video-recorded sessions. Furthermore, as noted before, the maze allows the implementation of other tasks or activities that could tackle specific cognitive abilities. Finally, our data collection method (scan sampling) did not allow recording the total time subjects spent engaging with the enrichment tasks, nor perseverance (e.g., how long chimpanzees remained engaged with the tasks before giving up when they were unsuccessful). As suggested by Clark (2017), however, these types of measurements may provide crucial information on the benefits of being cognitively engaged for long periods of time.

Finally, the novel food maze created an opportunity to investigate the likelihood of social learning within our chimpanzee groups. While this aspect fell outside the primary scope of this thesis, the fact that the enrichment sessions were videotaped allows the potential assessment of social learning in the future.

4.2.2. Cognitive research study

In the study assessing puzzle boxes (Article 3), chimpanzees were tested in an adjacent enclosure and encouraged by the keepers to participate in the experimental sessions. This was a requirement of the original study (Riba, 2016) to prevent other group members to interfere and to evaluate each chimpanzee independently. Although subjects could decide whether to enter the adjacent enclosure and engage with the task, future studies should explore alternative experimental settings for a better assessment of subjects' interest. For instance, a more effective approach could involve allowing the animals to voluntarily depart from the group and access individual research areas, where others are not allowed to enter before the testing session concludes (Ruby & Buchanan-Smith, 2015). If possible, conducting cognitive experiments in a social setting should also be considered as an alternative to subjects' isolation. Although this approach introduces challenges, such as a potential increase in intragroup competition, it offers an environment more closely resembling natural conditions, thus increasing ecological validity (Cronin, 2017).

Several authors have outlined the potential advantages of conducting primate cognition research in socially-housed primates living in zoos, animal centers, and sanctuaries (Hopper, 2017; McEwen et al., 2022; Ross & Leinwand, 2020). There is general consensus among researchers regarding the benefits of non-invasive and voluntary cognitive challenges for the welfare of these animals (Cronin, 2017; Egelkamp & Ross, 2019; Macdonald & Ritvo, 2016). Additionally, studying primates in environments that closely emulate their natural habitats offers a better understanding of their lives, yields more reliable outcomes, and minimizes potential adverse effects on their welfare (Lopresti-Goodman & Villatoro-Sorto, 2023). In our investigation with puzzle boxes, we provided chimpanzees with opportunities to engage in novel tasks and overcome challenges, which is crucial for captive primates and especially great apes (Clark, 2011, 2017). However, one significant limitation of our study lies in the omission of an assessment of the welfare impact of the puzzle boxes, as we did for the cognitive enrichment activities. This limitation was partly due to the limited visibility of the subjects in the video recordings of the experimental sessions, which did not allow behavioral coding. Nonetheless, considering the growing awareness among the general public regarding animal welfare, and the increasing demand for zoos and other captive settings to ensure the highest standards of animal welfare, it is imperative for researchers investigating animals' cognitive skills to assess the welfare implications of these activities (Cronin, 2017; Ross, 2010). This evaluation could be achieved, for instance, by monitoring positive and negative behavioral indicators of welfare during animal interactions with the tasks, as well as before and after the experimental sessions (Herrelko et al., 2012; Ruby & Buchanan-Smith, 2015; Whitehouse et al., 2013).

4.2.3. The use of Eysenck's model to describe chimpanzee personality and establish links with cognitive performance

Some of the limitations of Eysenck's model to describe chimpanzee personality are also common to the human model. For instance, when compared to other human models of personality, such as the Five Factor Model, or its adaptation to non-human primates, the Hominoid Personality Questionnaire, the three factors proposed by Eysenck may not comprehensively capture certain aspects of personality in non-human primates, such as Openness (to Experience). Furthermore, according to Eysenck (Eysenck et al., 1985), the

Agreeableness and Conscientiousness factors in the Five Factor Model are facets of the trait Psychoticism. Nonetheless, critics of Eysenck's model argue that Psychoticism shows low reliability and that, given its association with the two traits of the Five Factor Model, its interpretation as a unique and independent trait is questionable (Goldberg & Rosolack, 1994). It is also worth noting that Openness (to Experience) and Conscientiousness have been linked to cognitive performance in non-human primates (Altschul et al., 2017; Herrelko et al., 2012; Hopper et al., 2014; Morton et al., 2013a; Reamer et al., 2014) and to academic achievement and job performance in humans (Hurtz & Donovan, 2000; Mount et al., 1999; Noftle & Robins, 2007; Rrick & Mount, 1991; von Stumm et al., 2011). Therefore, in order to continue exploring these associations and gain a deeper understanding of the relationship between personality and performance, it would be advisable to consider personality models that encompass dimensions resembling Openness (to Experience) and Conscientiousness, as they are closely aligned with cognitive performance.

In this thesis, the link between chimpanzee personality and cognitive performance was assessed in a small sample of individuals housed at the same facility. Additionally, most of these animals had been exposed to traumatic experiences in their past, likely affecting both their personality (Ortín et al., 2019) and behavior (Crailsheim et al., 2020). The chimpanzees the Leipzig Zoo allowed us to work with a larger sample size when assessing Eysenck's model as detailed in Article 4. Nonetheless, other personality questionnaires, such as the Hominid Personality Questionnaire, have been applied to substantially larger chimpanzee cohorts (N>500), including animals from several facilities worldwide (Altschul et al., 2018), as well as large samples (N<100) of wild chimpanzees (Weiss et al., 2017). Thus, to validate Eysenck's model in chimpanzees and assess the possible link between Eysenck's traits and cognitive performance, broader and more diverse samples need to be considered.

It is important to clarify that the objective of this thesis was not to study the association between chimpanzee personality and a specific cognitive skill. The puzzle boxes we employed were originally designed for a different research purpose and were not tailored for the current study. In the future, it would be crucial to identify which cognitive skills underly individual performance in a task. This preliminary step is essential to establish the consistency of performance across time and contexts, which is basic to understand the relationship between personality and cognition (Griffin et al., 2015). To achieve this, tasks should be purposefully developed and thoroughly planned in advance.

Regarding the correlations between the three personality traits identified in our factorial analyses and behavioral observations, our results revealed limited discriminant validity for Eysenck's model. This constraint may be partly attributed to the broad categories within our behavioral catalogue, which for instance did not distinguish between aggressive and non-aggressive dominant interactions. In the future, more detailed behavioral catalogues would be advisable to further investigate the validity of Eysenck's model in chimpanzees or other non-human primates. Furthermore, beyond assessing spontaneous behavior, it might be useful to use complementary approaches (e.g., behavioral observations in controlled testing environments) to test the validity of our model (Massen et al., 2013).

Finally, one controversial aspect of our personality questionnaire is the emergence of a dimension termed Neuropsychoticism in the factorial analysis, encompassing elements of both human Neuroticism and Psychoticism. This complicates interpretation and hinders the straightforward comparisons between chimpanzees and humans. To address this issue, further research is needed to explore Eysenck's model in other non-human primates, shedding light on whether analogous dimensions might be identified in other species.

4.2.4. General limitations and future research directions

A general limitation across all our studies was the small sample size. The use of small limited sample sizes is a frequent challenge in primate research conducted within zoos and other captive settings, potentially hindering the generalizability of results (Gartner & Weiss, 2018). Additionally, at Fundació Mona, our sample exhibited uneven sex distribution, with only few females. One alternative to overcome limitations like small sample sizes is to replicate studies across different facilities using standardized data collection methodologies (Garcia-Pelegrin et al., 2022; Rose et al., 2019). Software applications like ZooMonitor, for instance, facilitate this process by quickly enabling behavioral data collection with the same procedures (Ross et al., 2016; Wark et al., 2019; https://zoomonitor.org). Subsequently, data can be stored and exported into electronic formats, thereby simplifying subsequent analyses and promoting data sharing (van der Marel et al., 2022). In line with this, the data collection methodology and the software employed in this thesis could serve as a valuable resource for assessing similar cognitive enrichment devices in other facilities.

Recently, to address the challenges with small samples sizes and to better account for methodological and site-specific differences, a significant effort has been made by the ManyPrimates project. ManyPrimates has established a large-scale collaboration infrastructure in the field of primate cognition research, bringing together multiple research groups to produce reproducible and replicable results (ManyPrimates et al., 2019a; ManyPrimates et al., 2019b). These extensive collaborations among researchers and institutions, known as big team science (BTS), have gained increased popularity over the past decade (Coles et al., 2022). In the future, the fields of animal welfare and animal personality research might also benefit from this type of initiatives.

In this thesis, we found individual differences in both participation and performance in the cognitive enrichment activities and in the puzzle boxes. To understand this individual variation, we considered subjects' characteristics such as sex or age. Furthermore, for the puzzle boxes, we explored the role of personality. Nonetheless, it is important to acknowledge that there are multiple other variables that we did not consider, which could have had a significant impact on chimpanzee participation and performance in the cognitive challenges. For instance, social hierarchy or rank was not factored in due to the limited number of dyadic agonistic interactions in our chimpanzee groups. However, previous research assessing enrichment in a social context showed that higher-ranking individuals usually have priority access to the enrichment devices (Celli et al., 2003). Thus, studies involving larger primate groups with well-stablished social hierarchies should take rank into consideration when designing and implementing enrichment activities in a social environment.

Other factors that may influence subjects' participation and performance in cognitive tasks include rearing history (Russell et al., 2011), early life experiences and exposure to humans (Tomasello & Call, 2004) or genetic predisposition (Hopkins et al., 2014; Hopkins & Sherwood, 2022). Additionally, a recent study by Forss and colleagues (2020) showed that chimpanzees' problem-solving skills were influenced by housing facility, captive care duration, and prior experiences with cognitive tasks. The available information about the life history of the chimpanzees at Fundació Mona is mostly incomplete and inaccurate. Nonetheless, several general variables should be considered in the future, including origin (wild, captive), years spent at the center, housing condition during infancy (e.g., social or isolated) and former use (pet or entertainment industry) (Crailsheim et al., 2020).

Finally, it should be acknowledged that this thesis explored the role of personality on subjects' interest and performance in cognitive tasks, but not in the cognitive enrichment activities. Originally, this was one of our objectives during the research stay at the Leipzig Zoo, where animals are exposed to similar cognitive enrichment devices than those provided at Fundació Mona. Additionally, the larger sample size at the Leipzig Zoo would have yielded increased statistical power as compared to the sample from Fundació Mona. Although we collected behavioral data when animals engaged with cognitive enrichment devices at the Leipzig Zoo, this research remains unpublished due to time constraints. Nonetheless, we plan to continue investigating whether personality plays a role in how individuals interact and benefit from enrichment activities. Other researchers have already recognized that the effectiveness of an enrichment may also depend on animals' personalities (Franks et al., 2013; Gartner & Weiss, 2018). In addition, subjects' response to a particular enrichment could serve as a measure for assessing and quantifying aspects of their personality (Gartner & Powell, 2012; Massen et al., 2013). Crucially, acknowledging the potential influence of personality on the effectiveness of enrichment strategies may lead to a more individualized approach and, ultimately, to better welfare (Carere & Locurto, 2011; Gartner & Weiss, 2018).

4.3. Conclusions

In this section we will: (1) summarize the most relevant findings of this thesis, organizing them in three sections that mirror the structure of the discussion and the specific objectives of the thesis, (2) provide overall conclusions relative to the main hypotheses and (3) provide applied recommendations for chimpanzee captive management based on our findings.

4.3.1. Factors affecting participation and performance in the cognitive challenges

- The majority of the chimpanzees engaged with the three cognitive tasks (i.e., puzzle boxes, artificial termite-fishing task and food maze), thus suggesting that they were interested in these activities and that they perceived them as positive stimuli. Nonetheless, there was considerable individual variation in participation and performance, especially in the two more cognitively demanding tasks (i.e., food maze and puzzle boxes).

- There were no sex differences in participation in the artificial termite-fishing task, but females participated more and were more successful at retrieving rewards from the food maze. This could be attributed to the food maze requiring more complex tool-use abilities, supporting previous findings in captivity and in the wild suggesting that female chimpanzees use tools more often and more effectively than males.
- Age did not predict differences in participation across any of the cognitive challenges, likely due to the limited variability within our sample.
- In the puzzle boxes, the link between personality and performance was partially modulated by subjects' sex. However, these findings should be interpreted with caution due to the low number of females in our sample.
- In the artificial termite-fishing task, participation increased across sessions, while in the food maze, it decreased. The first finding indicates that chimpanzees' interest was sustained across sessions, and despite previous exposure to this task, they continued to find the artificial termite-fishing task rewarding. In contrast, the decrease in participation in the food maze likely depended on the complexity of this task, with the majority of chimpanzees struggling to master it. Consequently, these animals likely experienced increasing frustration and loss of motivation over time.
- The high proportion of success observed in both the puzzle boxes and the artificial termite-fishing task indicate that the cognitive activities offered an appropriate level of challenge. By contrast, the fact that only two individuals were able to master the food maze task suggests that this task was overly complex, or perhaps that chimpanzees required additional time to learn how to retrieve the rewards effectively.

4.3.2. Behavioral and welfare implications of cognitive challenges

The tool-based cognitive enrichment tasks assessed in this study constitute effective enrichment activities for captive chimpanzees for the following reasons:

- They offered cognitive stimulation and provided learning opportunities that simulate their natural environments where animals encounter challenging situations (e.g., locating and obtaining food) that often require complex behavioral and cognitive abilities, like exploration or problem solving.
- They had a positive impact on welfare, by promoting species-typical behaviors (e.g., tool use and foraging) and reducing undesirable behaviors (e.g., inactivity). Nonetheless, in contrast to our predictions, participation in the cognitive enrichment tasks did not predict a reduction in abnormal or self-directed behaviors.
- In general, their behavioral effects remained consistent across sessions, indicating their effectiveness throughout the study period. Nonetheless, to further investigate their long-term effectiveness, it would be advisable to evaluate these types of activities over extended durations.
- The absence of significant changes in abnormal behaviors might be attributed to their limited occurrence within our study sample. However, it is also plausible that, as suggested by other researchers, abnormal behaviors and other negative indicators do not reliably reflect the welfare of captive chimpanzees and other non-human primates.
- The presence of the cognitive enrichment tasks did not predict an increase in self-directed behaviors (i.e., rubs and scratches), and neither did interaction with the artificial termite-fishing tasks. However, these behaviors increased when chimpanzees actively interacted with the novel food maze. This suggests that the mere presence of the enrichment activities did not induce stress, and that self-directed behaviors tended to rise in challenging situations, likely as a result of higher emotional arousal.

- Overall, the cognitive enrichment tasks did not have a negative impact on chimpanzee social behavior. Interestingly, the termite-fishing task seemed to act as a “gathering point”, with social proximity increasing for individuals that participated in the task. Nonetheless, participation in the novel food maze was linked to an increase in aggression-related behaviors, possibly as a result of higher intragroup competition.

4.3.3. Applying Eysenck’s model to chimpanzees

- The 12-item questionnaire based on Eysenck’s model demonstrated good levels of inter-rater reliability when assessing chimpanzee personality. This suggests that the selected items were readily understood and interpreted by human evaluators.
- The correlations observed between personality traits derived from Eysenck’s model and behavioral observations provided some evidence for convergent validity but limited discriminant validity. These results align with previous research and support the hypothesis that the interplay between personality traits and distinct behaviors is complex and still poorly understood. Nonetheless, the low discriminant validity of our model suggests that results should be taken with caution, and that additional research is needed to validate these three traits in chimpanzees.
- After assessing a larger and more diverse sample of chimpanzees and making methodological adjustments to the factorial analysis, we obtained a three-factor structure that closely resembled the one initially reported in the first study assessing Eysenck’s model in chimpanzees.
- Two traits obtained in our analysis, Extraversion and Dominance/Fearless Dominance, have been thoroughly documented in both captive and wild chimpanzees, and are straightforward to describe and interpret. In contrast, the third trait, Neuropsychoticism, represents a more intricate dimension, as it includes items that in humans load both onto

Neuroticism (e.g., anxious, bad-tempered) and Psychoticism (e.g., impulsive, aggressive, cruel).

- Research conducted in both humans and other primates has reported an interrelation between anxiety and psychotic traits that offers a potential explanation for the composite nature of Neuropsychoticism in our analyses. Furthermore, chimpanzee aggressive interactions have been associated to the expression of anxiety-related behaviors.
- Consistently with the assumption that personality traits should predict real-word outcomes, the three traits based on Eysenck's model predicted differences in chimpanzee performance in cognitive tasks.
- A relevant advantage of the questionnaire employed in this thesis is its brevity in comparison to the typically lengthier questionnaires used in non-human primates. Therefore, it may be more appealing and less time-consuming for raters, particularly when they need to assess a large number of animals and are constrained by limited time for research activities.

4.3.4. Overall conclusions

In conclusion, regarding the main hypotheses of this thesis, our findings can be summarized as follows: (1) chimpanzees exhibit individual differences in their interest and performance in cognitive tasks, both in enrichment and research contexts; (2) this individual variation in interest and performance is linked to sex and personality; (3) cognitive challenges are effective enrichment activities for captive chimpanzees, offering opportunities for engaging in cognitively stimulating activities that simulate aspects of their natural habitats, all the while promoting species-typical behaviors (i.e., foraging and tool-use) and reducing some undesirable behaviors (i.e., inactivity); and (4) while Eysenck's model may represent an alternative approach to assess personality in chimpanzees, additional research is needed to confirm its validity in this species.

4.3.5. Recommendations for professional animal care managers

Based on the findings of this thesis, presented below is a summary of recommendations for the care and management of captive chimpanzees. We trust that these suggestions may prove valuable for professionals involved in chimpanzee welfare.

Cognitive enrichment:

- Incorporating cognitively challenging activities as enrichment for captive chimpanzees can improve their welfare by promoting species-typical behaviors while increasing their sense of control over the environment (Badihi, 2006; Dawkins, 2003; Morgan & Tromborg, 2007; Sambrook & Buchanan-Smith, 1997; Whitham & Wielebnowski, 2013).
- For a comprehensive understanding of the enduring effects of enrichment activities, it is crucial to monitor subjects' interest, performance, and behavior for extended periods. This is especially important for evaluating new and challenging tasks that may take time for animals to learn.
- Abnormal behaviors and self-directed behaviors (rubs and scratches) might not serve as the most reliable indicators to assess welfare in the context of enrichment. We would recommend focusing on positive behavioral indicators, such as frequency or duration of device use, as well as on the increase of desirable behaviors (i.e., exploration or foraging). Additionally, we suggest assessing other potential negative behavioral indicators (i.e., vigilance, fear-related facial expressions and vocalizations) while also incorporating physiological measures (i.e., cortisol levels).

- Self-directed behaviors (rubs and scratches) are a sign of emotional arousal, but it is unclear whether this arousal can be attributed to positive emotions (i.e., excitement) or negative emotions (i.e., anxiety) experienced during the cognitive enrichment. To gain a deeper understanding of the nature of these behaviors in a challenging context, we suggest including additional variables in the study, such as differentiating between rough and gentle actions and considering the target and laterality (Laméris et al., 2022).
- When cognitive enrichment is provided in a social context, multiple devices should be strategically placed around the enclosures to facilitate engagement by all individuals and prevent potential aggression (Honess & Marin, 2006b). Furthermore, to ensure the availability of food rewards throughout the day, enrichment devices could be upgraded with a timed dispenser mechanism.
- Studies involving large primate groups with well-stablished social hierarchies should also take rank into consideration when designing and implementing cognitive challenges activities in a social environment, as higher-ranking individuals usually have priority of access to the enrichment devices (Celli et al., 2003).
- Software applications like ZooMonitor (Ross et al., 2016; Wark et al., 2019) or Boris (Friard & Gamba, 2016) are automated, efficient, and user-friendly data collection tools which provide valuable assistance for evaluating enrichment activities in captive environments.

Cognitive research:

- This thesis outlines the importance of considering personality and sex differences when assessing participation and performance in cognitive challenges. If possible, future studies should also assess the role of additional variables on performance during cognitive challenges, including housing facility, duration of captive care, prior exposure to cognitive tasks, rearing history, early life experiences with humans, and genetic predisposition (Forss et al., 2020; Russell et al., 2011; Tomasello & Call, 2004; Hopkins et al., 2014; Hopkins & Sherwood, 2022).

- For a precise assessment of subjects' interest in a task, animals should have the freedom to choose to leave the group and participate, rather than being called or prompted. Additionally, to enhance ecological validity, researchers should consider conducting cognitive experiments in a social setting rather than isolating subjects (Cronin, 2017).
- Researchers studying animals' cognitive abilities must prioritize welfare assessment (Cronin, 2017; Ross, 2010). This can involve observing both positive and negative behaviors related to welfare before, during, and after experimental sessions (Herrelko et al., 2012; Ruby & Buchanan-Smith, 2015; Whitehouse et al., 2013).

Personality assessment

- Short personality questionnaires, such as the one employed in this thesis, can effectively evaluate chimpanzee personality without imposing excessive time demands on the raters (Hopper & Cronin, 2018).
- Recognizing individual differences in chimpanzee personality can shed light on multiple reactions and outcomes within testing and enrichment contexts, facilitating better-informed decisions regarding chimpanzee management (Carere & Locurto, 2011; Gartner & Weiss, 2018).
- To more accurately assess the validity of personality questionnaires, tailored behavioral catalogues are essential, alongside complementary approaches, such as behavioral observations in experimental contexts (Massen et al., 2013). Additionally, it will be crucial to include larger sample sizes and other primate species.

4.4. Final thought

The majority of chimpanzees living under human care spend their entire lives in captivity. Re-introducing them to their natural habitats is extremely challenging, even in rescue and rehabilitation centers in their countries of origin. Hence, it is our moral obligation to ensure optimal welfare conditions for these animals. To achieve this, it is essential not only to understand their ethological needs but also to acknowledge and account for their individual differences. This thesis represents a first modest contribution to this critical endeavor, emphasizing the necessity for further research to guarantee that chimpanzees and other non-human primates living in captivity are finally provided with the opportunity to live a life "worth living".

References

Acar, S., & Runco, M. A. (2012). Psychoticism and creativity: A meta-analytic review. *Psychology of Aesthetics, Creativity, and the Arts*, *6*(4), 341–350. https://doi.org/10.1037/a0027497

Ackerman, P. L., & Heggestad, E. D. (1997). Intelligence, personality, and interests: Evidence for overlapping traits. *Psychological Bulletin*, *121*(2), 219–245. https://doi.org/10.1037/0033-2909.121.2.219

Adams, C., & Huntingford, F. (2005). Behavioural syndromes in farmed fish: implications for production and welfare. *Behaviour*, *142*(9–10), 1207–1221. https://doi.org/10.1163/156853905774539382

Adams, M., Majolo, B., Ostner, J., Schülke, O., Marco, A., Thierry, B., Engelhardt, A., Widdig, A., Gerald, M. S., & Weiss, A. (2015). Personality structure and social style in macaques. *Journal of Personality and Social Psychology*, *109*(2), 338–353. https://doi.org/10.1037/pspp0000041

Adolphs, R., Mlodinow, L., & Barrett, L. F. (2019). What is an emotion? *Current Biology*, *29*(20), R1060–R1064. https://doi.org/10.1016/j.cub.2019.09.008

Alkalay, S., Mizrachi, Y., & Agasi, E. (2022). Toward a biological basis of the FFM Meta-traits: Associations between the Fisher Type Indicator (FTI) temperament construct and the hierarchical Five Factor Model (FFM) of personality. *Personality and Individual Differences*, *185*, Article 111266. https://doi.org/10.1016/j.paid.2021.111266

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

Altschul, D. M., Hopkins, W. D., Herrelko, E. S., Inoue-Murayama, M., Matsuzawa, T., King, J. E., Ross, S. R., & Weiss, A. (2018). Personality links with lifespan in chimpanzees. *eLife*, *7*, Article e33781. https://doi.org/10.7554/eLife.33781

Altschul, D. M., Terrace, H., & Weiss, A. (2016). Serial cognition and personality in macaques. *Animal Behavior and Cognition*, *3*(1), 46–64. https://doi.org/10.12966/abc.02.04.2016

Altschul, D. M., Wallace, E., Sonnweber, R., Tomonaga, M., & Weiss, A. (2017). Chimpanzee intellect: personality, performance and motivation with touchscreen tasks. *Royal Society Open Science*, *4*(5), Article 170169. https://doi.org/10.1098/rsos.170169

Anderson, J. R., Ang, M. Y. L., Lock, L. C., & Weiche, I. (2019). Nesting, sleeping, and nighttime behaviors in wild and captive great apes. *Primates*, *60*(4), 321–332. https://doi.org/10.1007/s10329-019-00723-2

Anderson, J. R., Gillies, A., & Lock, L. C. (2010). Pan thanatology. *Current Biology*, *20*(8), R349–R351. https://doi.org/10.1016/j.cub.2010.02.010

Ape Alliance (2018). *Chimpanzees in Chinese captive wild animal facilities*. https://4apes.com/news/ape-alliance/item/download/16_e2e31f754becbe5182a04972dbb9cb20

Arcadi, A. C. (2018). Chimpanzee fission–fusion social organization and its conservation implications. In A. C. Arcadi (Ed.), *Wild chimpanzees: Social behavior of an endangered species* (pp. 27–32). Cambridge University Press. https://doi.org/10.1017/9781108178303.004

Arndt, S. S., Goerlich, V. C., & van der Staay, F. J. (2022). A dynamic concept of animal welfare: The role of appetitive and adverse internal and external factors and the animal's ability to adapt to them. *Frontiers in Animal Science*, *3*, Article 908513. https://doi.org/10.3389/fanim.2022.908513

Arnold, K., & Aureli, F. (2007). Postconflict reconciliation. In S. Bearder, C. Campbell, A. Fuentes, K. C. McKinnon, & M. Panger (Eds.), *Primates in perspective* (1st ed., Vol. 2, pp. 608–625). Oxford University Press.

Ash, H., Smith, T. E., Knight, S., & Buchanan-Smith, H. M. (2018). Measuring physiological stress in the common marmoset (*Callithrix jacchus*): Validation of a salivary cortisol collection and assay technique. *Physiology & behavior*, *185*, 14–22. https://doi.org/10.1016/j.physbeh.2017.12.018

Aureli, F. (1997). Post-conflict anxiety in nonhuman primates: The mediating role of emotion in conflict resolution. *Aggressive Behavior*, *23*(5), 315–328. https://doi.org/10.1002/(SICI)1098-2337(1997)23:5<315::AID-AB2>3.0.CO;2-H

Baayen, R. H. (2008). *Analyzing linguistic data: A practical introduction to statistics using R*. Cambridge University Press. https://doi.org/10.1017/CBO9780511801686

Badihi, I. (2006). *The effects of complexity, choice and control on the behaviour and the welfare of captive common marmosets (Callithrix jacchus)* [Doctoral dissertation, University of Stirling]. Stirling Online Research Repository. http://hdl.handle.net/1893/120

Bakeman, R., & Quera, V. (2011). *Sequential analysis and observational methods for the behavioral sciences*. Cambridge University Press. https://doi.org/10.1017/CBO9781139017343

Baker, K. (2012). *Personality assessment of three species of captive monkey, Macaca nigra, Macaca sylvanus, and Saimiri sciureus: cross-species comparisons of personality and implications for captive management* [Doctoral dissertation, University of Exeter]. https://core.ac.uk/download/pdf/12826804.pdf

Baker, K. C. (1997). Straw and forage material ameliorate abnormal behaviors in adult chimpanzees. *Zoo Biology*, *16*(3), 225–236. https://doi.org/10.1002/(SICI)1098-2361(1997)16:3<225::AID-ZOO3>3.0.CO;2-C

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

Baker, K. C., & Aureli, F. (1997). Behavioural indicators of anxiety: An empirical test in chimpanzees. *Behaviour*, *134*(13/14), 1031–1050. https://doi.org/10.1163/156853997X00386

Baker, K. C., Bloomsmith, M. A., Oettinger, B., Neu, K., Griffis, C., & Schoof, V. A. (2014). Comparing options for pair housing rhesus macaques using behavioral welfare measures. *American Journal of Primatology*, *76*(1), 30–42. https://doi.org/10.1002/ajp.22190

Baker, K. C., & Easley, S. P. (1996). An analysis of regurgitation and reingestion in captive chimpanzees. *Applied Animal Behaviour Science*, *49*(4), 403–415. https://doi.org/10.1016/0168-1591(96)01061-1

Balcombe, J. (2009). Animal pleasure and its moral significance. *Applied Animal Behaviour Science*, *118*(3–4), 208–216. https://doi.org/10.1016/j.applanim.2009.02.012

Bandini, E., & Harrison, R. A. (2020). Innovation in chimpanzees. *Biological Reviews*, *95*(5), 1167–1197. https://doi.org/10.1111/brv.12604

Banwell, S. (2023). Granting nonhuman animals legal personhood: The implications for human and nonhuman animals. In S. Banwell (Ed.), *The war against nonhuman animals: A non-speciesist understanding of gendered reproductive violence* (pp. 47–85). Springer International Publishing. https://doi.org/10.1007/978-3-031-30430-9_2

Barr, C. S., & Driscoll, C. (2014). Neurogenetics of aggressive behavior: Studies in primates. In K. A. Miczek & A. Meyer-Lindenberg (Eds.), *Neuroscience of aggression* (pp. 45–71). Springer Berlin Heidelberg. https://doi.org/10.1007/7854_2013_267

Barr, D. J. (2008). Analyzing ‘visual world’eyetracking data using multilevel logistic regression. *Journal of Memory and Language*, *59*(4), 457–474. https://doi.org/10.1016/j.jml.2007.09.002

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Barth, J., & Call, J. (2006). Tracking the displacement of objects: A series of tasks with great apes (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, and *Pongo pygmaeus*) and young children (*Homo sapiens*). *Journal of Experimental Psychology: Animal Behavior Processes*, *32*(3), 239–252. https://doi.org/10.1037/0097-7403.32.3.239

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bech, P. (2020). Psychoticism (Eysenck's Theory). In V. Zeigler-Hill & T. K. Shackelford (Eds.), *Encyclopedia of Personality and Individual Differences* (pp. 4235–4237). Springer International Publishing. https://doi.org/10.1007/978-3-319-24612-3_1103

Bentea, C. C., & Anghelache, V. (2012). Comparative aspects concerning the effects of extraversion on performance in a cognitive task in competitive and cooperative conditions. *Procedia - Social and Behavioral Sciences*, *33*, 558–562. https://doi.org/10.1016/j.sbspro.2012.01.183

Bernstein-Kurtycz, L. (2015, 11/01). *Choice and control for animals in captivity*. Retrieved from https://www.bps.org.uk/psychologist/choice-and-control-animals-captivity

Berridge, K. C., & Robinson, T. E. (2003). Parsing reward. *Trends in Neurosciences*, *26*(9), 507–513. https://doi.org/10.1016/S0166-2236(03)00233-9

Binding, S., Farmer, H., Krusin, L., & Cronin, K. (2020). Status of animal welfare research in zoos and aquariums: Where are we, where to next? *Journal of Zoo and Aquarium Research*, *8*(3), 166–174. https://doi.org/10.19227/jzar.v8i3.505

Birkett, L. P., & Newton-Fisher, N. E. (2011). How abnormal is the behaviour of captive, zoo-living chimpanzees? *PLOS ONE*, *6*(6), Article e20101. https://doi.org/10.1371/journal.pone.0020101

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal cognition*, *6*(4), 213–223. https://doi.org/10.1007/s10071-003-0183-x

Blaszczyk, M. B. (2020). Primates got personality, too: Toward an integrative primatology of consistent individual differences in behavior. *Evolutionary anthropology*, *29*(2), 56–67. https://doi.org/10.1002/evan.21808

Bloomsmith, M., Clay, A., Ross, S., Lutz, C., Breaux, S., Pietsch, R., Fultz, A., Lammey, M., Jacobson, S., & Perlman, J. (2020). Chimpanzees in us zoos, sanctuaries, and research facilities: A survey-based comparison of atypical behaviors. In L. M. Hopper & S. R. Ross (Eds.), *Chimpanzees in context* (pp. 481–508). University of Chicago Press. https://doi.org/10.7208/chicago/9780226728032.003.0021

Bloomsmith, M. A., Brent, L. Y., & Schapiro, S. J. (1991). Guidelines for developing and managing an environmental enrichment program. *Laboratory Animal Science*, *41*(4), 372–377.

Bloomsmith, M. A., Clay, A. W., Lambeth, S. P., Lutz, C. K., Breaux, S. D., Lammey, M. L., Franklin, A. N., Neu, K. A., Perlman, J. E., Reamer, L. A., Mareno, M. C., Schapiro, S. J., Vazquez, M., & Bourgeois, S. R. (2019). Survey of behavioral indices of welfare in research chimpanzees (*Pan troglodytes*) in the United States. *Journal of the American Association for Laboratory Animal Science*, *58*(2), 160–177. https://doi.org/10.30802/aalas-jaalas-18-000034

Bloomstrand, M., Riddle, K., Alford, P., & Maple, T. L. (1986). Objective evaluation of a behavioral enrichment device for captive chimpanzees (*Pan troglodytes*). *Zoo Biology*, *5*(3), 293–300. https://doi.org/10.1002/zoo.1430050307

Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour*, *48*(3), 653–667. https://doi.org/10.1006/anbe.1994.1285

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

Boesch, C., & Boesch, H. (1981). Sex differences in the use of natural hammers by wild chimpanzees: A preliminary report. *Journal of Human Evolution*, *10*(7), 585–593. https://doi.org/10.1016/S0047-2484(81)80049-8

Boesch, C., & Boesch, H. (1983). Optimisation of nut-cracking with natural hammers by wild chimpanzees. *Behaviour*, *83*(3–4), 265–286. https://doi.org/10.1163/156853983X00192

Boesch, C., & Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia primatologica*, *54*(1–2), 86–99. https://doi.org/10.1159/000156428

Boesch, C., Bolé, C., Eckhardt, N., & Boesch, H. (2010). Altruism in forest chimpanzees: The case of adoption. *PLOS ONE*, *5*(1), Article e8901. https://doi.org/10.1371/journal.pone.0008901

Boissy, A., Manteuffel, G., Jensen, M. B., Moe, R. O., Spruijt, B., Keeling, L. J., Winckler, C., Forkman, B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I., & Aubert, A. (2007). Assessment of positive emotions in animals to improve their welfare. *Physiology & behavior*, *92*(3), 375–397. https://doi.org/10.1016/j.physbeh.2007.02.003

Bonnie, K. E., Ang, M. Y., & Ross, S. R. (2016). Effects of crowd size on exhibit use by and behavior of chimpanzees (*Pan troglodytes*) and Western lowland gorillas (*Gorilla*

gorilla) at a zoo. *Applied Animal Behaviour Science*, *178*, 102–110. https://doi.org/10.1016/j.applanim.2016.03.003

Bono, R., Alarcón, R., & Blanca, M. J. (2021). Report quality of generalized linear mixed models in psychology: A systematic review. *Frontiers in Psychology*, *12*, Article 666182. https://doi.org/10.3389/fpsyg.2021.666182

Boogert, N. J., Madden, J. R., Morand-Ferron, J., & Thornton, A. (2018). Measuring and understanding individual differences in cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), Article 20170280. https://doi.org/10.1098/rstb.2017.0280

Boose, K. J., White, F. J., & Meinelt, A. (2013). Sex differences in tool use acquisition in bonobos (*Pan paniscus*). *American Journal of Primatology*, *75*(9), 917–926. https://doi.org/10.1002/ajp.22155

Borkenau, P. (1992). Implicit personality theory and the Five-Factor Model. *Journal of Personality*, *60*(2), 295–327. https://doi.org/10.1111/j.1467-6494.1992.tb00975.x

Borkenau, P., & Ostendorf, F. (1990). Comparing exploratory and confirmatory factor analysis: A study on the 5-factor model of personality. *Personality and Individual Differences*, *11*(5), 515–524. https://doi.org/10.1016/0191-8869(90)90065-Y

Bortolato, T., Friederici, A. D., Girard-Buttoz, C., Wittig, R. M., & Crockford, C. (2023). Chimpanzees show the capacity to communicate about concomitant daily life events. *iScience*, *26*(11), Article 108090. https://doi.org/10.1016/j.isci.2023.108090

Bouchard, A., & Zuberbühler, K. (2022). An intentional cohesion call in male chimpanzees of Budongo Forest. *Animal cognition*, *25*(4), 853–866. https://doi.org/10.1007/s10071-022-01597-6

Bracke, M. B., & Hopster, H. (2006). Assessing the importance of natural behavior for animal welfare. *Journal of Agricultural and Environmental Ethics*, *19*(1), 77–89. https://doi.org/10.1007/s10806-005-4493-7

Bradshaw, G. A., Capaldo, T., Lindner, L., & Grow, G. (2008). Building an inner sanctuary: Complex PTSD in chimpanzees. *Journal of Trauma & Dissociation*, *9*(1), 9–34. https://doi.org/10.1080/15299730802073619

Brambell, F. W. R. (1965). *Report of the Technical Committee to enquire into the welfare of animals kept under intensive livestock husbandry systems*. Technical Committee to enquire into the Welfare of Animals kept under Intensive Livestock Husbandry Systems. https://archive.org/details/b3217276x

Brandão, A., Costa, R., Rodrigues, E., & Vicente, L. (2019). Using behaviour observations to study personality in a group of capuchin monkeys (*Cebus apella*) in captivity. *Behaviour*, *156*(3–4), 203–243. https://doi.org/10.1163/1568539X-00003537

Bray, J., Murray, C. M., Gilby, I. C., & Stanton, M. A. (2021). Immature male chimpanzees' (*Pan troglodytes schweinfurthii*) social relationships with adult males, but not peers, persist into adulthood. *International Journal of Primatology*, *42*(5), 701–721. https://doi.org/10.1007/s10764-021-00235-1

Brent, L. (1992). Woodchip bedding as enrichment for captive chimpanzees in an outdoor enclosure. *Animal Welfare*, *1*(3), 161–170. https://doi.org/10.1017/S0962728600014986

Brent, L. (2007). Life-long well being: applying animal welfare science to nonhuman primates in sanctuaries. *Journal of Applied Animal Welfare Science*, *10*(1), 55–61. https://doi.org/10.1080/10888700701277626

Brent, L., & Belik, M. (1997). The response of group-housed baboons to three enrichment toys. *Lab Anim*, *31*(1), 81–85. https://doi.org/10.1258/002367797780600305

Brent, L., & Eichberg, J. W. (1991). Primate puzzleboard: A simple environmental enrichment device for captive chimpanzees. *Zoo Biology*, *10*(4), 353–360. https://doi.org/10.1002/zoo.1430100409

Brereton, J., & Rose, P. (2023). An evaluation of the role of 'biological evidence' in zoo and aquarium enrichment practices. *Animal Welfare*, *31*(1), 13–26. https://doi.org/10.7120/09627286.31.1.002

Brereton, J. E., Tuke, J., & Fernandez, E. J. (2022). A simulated comparison of behavioural observation sampling methods. *Scientific Reports*, *12*(1), Article 3096. https://doi.org/10.1038/s41598-022-07169-5

Brooker, J. S., Webb, C. E., & Clay, Z. (2022). Primate empathy: a flexible and multi-componential phenomenon. In M. J. Beran, & B. L. Schwartz (Eds.), *Primate Cognitive Studies* (pp. 505–531). Cambridge University Press. https://doi.org/10.1017/9781108955836.020

Brooker, J.S., Webb, C.E., de Waal, F.B.M. & Clay, Z. (2024). The expression of empathy in human's closest relatives, bonobos and chimpanzees: current and future directions. *Biological Reviews of the Cambridge Philosophical Society*. Advance online publication. https://doi.org/10.1111/brv.13080

Brooks, J., Yoshimura, H., & Taki, Y. (2021). Knowledge-based enrichment: Development of a novel enrichment device for captive chimpanzees. *Zoo Biology*, *40*(5), 398–406. https://doi.org/10.1002/zoo.21617

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal*, *9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Broom, D.M. (2001). Coping, stress and welfare. In D.M. Broom (Ed.), *Coping with Challenge: Welfare in Animals including Humans, Proceedings of Dahlem Conference* (*pp. 1–9)*. Dahlem University Press.

Broom, D. M. (1986). Indicators of poor welfare. *British Veterinary Journal*, *142*(6), 524–526. https://doi.org/10.1016/0007-1935(86)90109-0

Broom, D. M. (1991). Animal welfare: concepts and measurement. *Journal of Animal Science*, *69*(10), 4167–4175. https://doi.org/10.2527/1991.69104167x

Broom, D. M. (2014). Welfare assessment. In D. M. Broom (Ed.), *Sentience and animal welfare* (pp. 90–107). CABI International. https://doi.org/10.1079/9781780644035.0090

Brosnan, S. F., Grady, M. F., Lambeth, S. P., Schapiro, S. J., & Beran, M. J. (2008). Chimpanzee autarky. *PLOS ONE*, *3*(1), Article e1518. https://doi.org/10.1371/journal.pone.0001518

Browning, H. (2019). The natural behavior debate: Two conceptions of animal welfare. *Journal of Applied Animal Welfare Science*, *23*(3), 325–337. https://doi.org/10.1080/10888705.2019.1672552

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

Bründl, A., Girard-Buttoz, C., Bortolato, T., Samuni, L., Grampp, M., Löhrich, T., Tkaczynski, P., Wittig, R., & Crockford, C. (2022). Maternal effects on the development of vocal communication in wild chimpanzees. *iScience*, *25*, Article 105152. https://doi.org/10.1016/j.isci.2022.105152

Buchanan-Smith, H. M., Vick, S.-J., Morton, F. B., & Herrelko, E. S. (2016, 18–20 August 2016). *Environmental enrichment: Our cognitive challenges* [Abstract]. Chimpanzees in Context, Chicago, IL: Lincoln Park Zoo. https://www.chimpsymposium.org/abstracts/

Buirski, P., Plutchik, R., & Kellerman, H. (1978). Sex differences, dominance, and personality in the chimpanzee. *Animal Behaviour*, *26*(1), 123–129. https://doi.org/10.1016/0003-3472(78)90011-8

Burisch, M. (1984). You don't always get what you pay for: Measuring depression with short and simple versus long and sophisticated scales. *Journal of Research in Personality*, *18*(1), 81–98. https://doi.org/10.1016/0092-6566(84)90040-0

Burisch, M. (1997). Test length and validity revisited. *European Journal of Personality*, *11*, 303–315. https://doi.org/10.1002/(SICI)1099-0984(199711)11:4<303::AID-PER292>3.0.CO;2-%23

Cacchione, T., & Rakoczy, H. (2017). Comparative metaphysics: Thinking about objects in space and time. In *APA handbook of comparative psychology: Perception, learning, and cognition* (pp. 579–599). American Psychological Association.

Caldecott, J. O., & Miles, L. (2005). *World atlas of great apes and their conservation* (1st ed.). University of California Press.

Call, J. (2013). Three ingredients for becoming a creative tool user. In C. Boesch, C. M. Sanz, & J. Call (Eds.), *Tool use in animals: Cognition and ecology* (pp. 3–20). Cambridge University Press. https://doi.org/10.1017/CBO9780511894800.002

Call, J., Burghardt, G. M., Pepperberg, I. M., Snowdon, C. T., & Zentall, T. (2017). *APA handbook of comparative psychology: Basic concepts, methods, neural substrate, and behavior* (Vol. 1). American Psychological Association. https://doi.org/10.1037/0000011-000

Call, J., & Tomasello, M. (2007). *The gestural communication of apes and monkeys* (1st ed.). Psychology Press.

Camargo, M. R., & Mendes, F. D. C. (2016). Induced tool use as environmental enrichment for captive capuchin monkeys (*Sapajus libidinosu*s). *Psicologia: Teoria e Pesquisa*, *32*, Article e32ne21. https://doi.org/10.1590/0102-3772e32ne21

Cantlon, J. F. (2012). Math, monkeys, and the developing brain. *Proceedings of the National Academy of Sciences*, *109*(Suppl 1), 10725–10732. https://doi.org/10.1073/pnas.1201893109

Cantwell, A., Buckholtz, J. W., Atencia, R., & Rosati, A. G. (2022). The origins of cognitive flexibility in chimpanzees. *Developmental science*, *25*(5), Article e13266. https://doi.org/10.1111/desc.13266

Capitanio, J. (2004). Personality factors between and within species. In B. Thierry, M. Singh, & W. Kaumanns (Eds.), *Macaque societies: A model for the study of social organization* (pp. 13–33). Cambridge University Press.

Capitanio, J. P., Mendoza, S. P., & Baroncelli, S. (1999). The relationship of personality dimensions in adult male rhesus macaques to progression of simian immunodeficiency virus disease. *Brain, Behavior, and Immunity*, *13*(2), 138–154. https://doi.org/10.1006/brbi.1998.0540

Carere, C., Caramaschi, D., & Fawcett, T. W. (2010). Covariation between personalities and individual differences in coping with stress: converging evidence and hypotheses. *Current Zoology*, *56*(6), 728–740. https://doi.org/10.1093/czoolo/56.6.728

Carere, C., & Locurto, C. (2011). Interaction between animal personality and animal cognition. *Current Zoology*, *57*(4), 491–498. https://doi.org/10.1093/czoolo/57.4.491

Carere, C., & Maestripieri, D. (2013). Animal personalities: who cares and why? In C. Carere & D. Maestripieri (Eds.), *Animal Personalities: Behavior, Physiology, and Evolution* (pp. 1–9). University of Chicago Press. https://doi.org/10.7208/chicago/9780226922065.003.0001

Carlsen, F., & De Jongh, T. (2015). *European studbook for the chimpanzee Pan troglodytes*. 2014 – 1st edition of joint EEP studbook. European Association of Zoos and Aquaria (EAZA) and Ex situ Programmes (EEP). https://docplayer.net/53480624-European-studbook-chimpanzee-1st-edition-of-joint-eep-studbook-frands-carlsen-copenhagen-zoo-tom-de-jongh-burgers-zoo.html

Carlsen, F., de Jongh, T., & Pluháčková, J. (2022). *EAZA Best practice guidelines for chimpanzees (Pan troglodytes)*. European Association of Zoos and Aquaria (EAZA). https://www.eaza.net/assets/Uploads/CCC/BPG-2022/Chimpanzee-BPG22.pdf

Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlishaw, G. (2014). Personality predicts the propensity for social learning in a wild primate. *PeerJ*, *2*, Article e283. https://doi.org/10.7717/peerj.283

Castanheira, M., Herrera, M., Costas, B., Conceição, L. E. C., & Martins, C. I. M. (2013). Can we predict personality in fish? Searching for consistency over time and across contexts. *PLOS ONE*, *8*(4), Article e62037. https://doi.org/10.1371/journal.pone.0062037

Castles, D. L., & Whiten, A. (1998). Post-conflict behaviour of wild olive baboons. II. Stress and self-directed behaviour. *Ethology*, *104*(2), 148–160. https://doi.org/10.1111/j.1439-0310.1998.tb00058.x

Cattell, H. E., & Mead, A. D. (2008). The Sixteen Personality Factor Questionnaire (16PF). In G. J. Boyle, G. Matthews, & D. H. Saklofske (Eds.), *The SAGE handbook of personality theory and assessment. Personality measurement and testing* (Vol. 2, pp. 135–159). Sage Publications, Inc. https://doi.org/10.4135/9781849200479.n7

Cattell, R. B. (1945). The description of personality: Principles and findings in a factor analysis. *The American Journal of Psychology*, *58*(1), 69–90. https://doi.org/10.2307/1417576

Celli, M. L., Tomonaga, M., Udono, T., Teramoto, M., & Nagano, K. (2003). Tool use task as environmental enrichment for captive chimpanzees. *Applied Animal Behaviour Science*, *81*(2), 171–182. https://doi.org/10.1016/S0168-1591(02)00257-5

Ciardelli, L. E., Weiss, A., Powell, D. M., & Reiss, D. (2017). Personality dimensions of the captive California sea lion (*Zalophus californianus*). *Journal of Comparative Psychology*, *131*(1), 50–58. https://doi.org/10.1037/com0000054

Claridge, G. S. (1967). *Personality and arousal: A psychophysiological study of psychiatric disorder*. Pergamon Press.

Claridge, G. S., & Birchall, P. M. (1973). The biological basis of psychoticism: A study of individual differences in response to dexamphetamine. *Biological Psychology*, *1*(2), 125–137. https://doi.org/10.1016/0301-0511(73)90004-5

Claridge, G. S., & Chappa, H. J. (1973). Psychoticism: A study of its biological basis in normal subjects. *British Journal of Social and Clinical Psychology*, *12*(2), 175–187. https://doi.org/10.1111/j.2044-8260.1973.tb00864.x

Clark, F. E. (2011). Great ape cognition and captive care: Can cognitive challenges enhance well-being? *Applied Animal Behaviour Science*, *135*(1–2), 1–12. https://doi.org/10.1016/j.applanim.2011.10.010

Clark, F. E. (2017). Cognitive enrichment and welfare: Current approaches and future directions. *Animal Behavior and Cognition*, *4*(1), 52–71. https://doi.org/10.12966/abc.05.02.2017

Clark, F. E. (2023). In the zone: Towards a comparative study of flow state in primates. *Animal Behavior and Cognition*, *10*(1), 62–88. https://doi.org/10.26451/abc.10.01.04.2023

Clark, F. E., Gray, S. I., Bennett, P., Mason, L. J., & Burgess, K. V. (2019). High-tech and tactile: Cognitive enrichment for zoo-housed gorillas. *Frontiers in Psychology*, *10*, Article 1574. https://doi.org/10.3389/fpsyg.2019.01574

Clark, F. E., & Smith, L. J. (2013). Effect of a cognitive challenge device containing food and non-food rewards on chimpanzee well-being. *American Journal of Primatology*, *75*(8), 807–816. https://doi.org/10.1002/ajp.22141

Clay, A. W., Ross, S. R., Lambeth, S., Vazquez, M., Breaux, S., Pietsch, R., Fultz, A., Lammey, M., Jacobson, S. L., Perlman, J. E., & Bloomsmith, M. A. (2023). Chimpanzees (*Pan troglodytes*) in U.S. zoos, sanctuaries, and research facilities: A survey-based comparison of species-typical behaviors. *Animals*, *13*(2), Article 251. https://doi.org/10.3390/ani13020251

Clay, Z., Webb, C. E., Romero, T., & de Waal, F. B. M. (2022). Comparative perspectives of empathy development: Insights from chimpanzees and bonobos. In D. Dukes, A. C. Samson, & E. A. Walle (Eds.), *The Oxford Handbook of Emotional Development* (pp. 277–290). Oxford University Press. https://doi.org/10.1093/oxfordhb/9780198855903.013.30

Cleckley, H. M. (1951). The mask of sanity. *Postgraduate medicine*, *9*(3), 193–197. https://doi.org/10.1080/00325481.1951.11694097

Cole, J., & Fraser, D. (2018). Zoo animal welfare: The human dimension. *Journal of Applied Animal Welfare Science*, *21*(sup1), 49–58. https://doi.org/10.1080/10888705.2018.1513839

Coleman, K., & Novak, M. A. (2017). Environmental enrichment in the 21st century. *ILAR journal*, *58*(2), 295–307. https://doi.org/10.1093/ilar/ilx008

Coleman, K., & Pierre, P. J. (2014). Assessing anxiety in nonhuman primates. *ILAR journal*, *55*(2), 333–346. https://doi.org/10.1093/ilar/ilu019

Coleman, K., Tully, L., & McMillan, J. L. (2005). Temperament correlates with training success in adult rhesus macaques. *American Journal of Primatology*, *65*(1), 63–71. https://doi.org/10.1002/ajp.20097

Coles, N. A., Hamlin, J. K., Sullivan, L. L., Parker, T. H., & Altschul, D. (2022). Build up big-team science. *Nature*, *601*(7894), 505–507. https://doi.org/10.1038/d41586-022-00150-2

Colzato, L. S., Slagter, H. A., van den Wildenberg, W. P. M., & Hommel, B. (2009). Closing one's eyes to reality: Evidence for a dopaminergic basis of Psychoticism from spontaneous eye blink rates. *Personality and Individual Differences*, *46*(3), 377–380. https://doi.org/10.1016/j.paid.2008.10.017

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

Corr, P. J. (2003). Personality and dual-task processing: Disruption of procedural learning by declarative processing. *Personality and Individual Differences*, *34*(7), 1245–1269. https://doi.org/10.1016/S0191-8869(02)00112-5

Costa, P. T., & McCrae, R. R. (1992). Reply to Eysenck. *Personality and Individual Differences*, *13*(8), 861–865. https://doi.org/0.1016/0191-8869(92)90002-7

Costa, P. T., & McCrae, R. R. (1995a). Domains and facets: Hierarchical personality assessment using the Revised NEO Personality Inventory. *Journal of Personality Assessment*, *64*, 21–50. https://doi.org/10.1207/s15327752jpa6401_2

Costa, P. T., & McCrae, R. R. (1995b). Primary traits of Eysenck's PEN system: Three-and five-factor solutions. *Journal of Personality and Social Psychology*, *69*(2), 308–317. https://doi.org/10.1037//0022-3514.69.2.308

Costa, P. T., McCrae, R. R., & Dye, D. A. (1991). Facet scales for agreeableness and conscientiousness: A revision of the neo personality inventory. *Personality and Individual Differences*, *12*(9), 887–898. https://doi.org/10.1016/0191-8869(91)90177-D

Costa, R., Sousa, C., & Llorente, M. (2018). Assessment of environmental enrichment for different primate species under low budget: A case study. *Journal of Applied Animal Welfare Science*, *21*, 1–15. https://doi.org/10.1080/10888705.2017.1414606

Costa, T. S. O., Nogueira-Filho, S. L. G., De Vleeschouwer, K. M., Oliveira, L. C., de Sousa, M. B. C., Mendl, M., Catenacci, L. S., & Nogueira, S. S. C. (2020). Individual behavioral differences and health of golden-headed lion tamarins (*Leontopithecus chrysomelas*). *82*(5), Article e23118. https://doi.org/10.1002/ajp.23118

Cox-Fuenzalida, L.-E., Angie, A., Holloway, S., & Sohl, L. (2006). Extraversion and task performance: A fresh look through the workload history lens. *Journal of Research in Personality*, *40*(4), 432–439. https://doi.org/10.1016/j.jrp.2005.02.003

Craig, L. E., & Vick, S.-J. (2021). Engaging zoo visitors at chimpanzee (*Pan troglodytes*) exhibits promotes positive attitudes toward chimpanzees and conservation. *Anthrozoös*, *34*(1), 1–15. https://doi.org/10.1080/08927936.2021.1874110

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

Cravens-Brown, L. M. (2002). *Eysenck and antisocial behavior: An analysis of the associations between personality styles and problems with conduct* [Doctoral dissertation, Ohio State University]. OhioLINK Electronic Theses and Dissertations Center. http://rave.ohiolink.edu/etdc/view?acc_num=osu1038457465

Crawford, M. P. (1938). A behavior rating scale for young chimpanzees. *Journal of Comparative Psychology*, *26*(1), 79–92. https://doi.org/10.1037/h0054503

Crockford, C., Samuni, L., Vigilant, L., & Wittig, R. M. (2020). Postweaning maternal care increases male chimpanzee reproductive success. *Science Advances*, *6*(38), Article eaaz5746. https://doi.org/10.1126/sciadv.aaz5746

Cronin, K., & Ross, S. (2020). When is "natural" better? The welfare implications of limiting reproduction in captive chimpanzees. In L. M. Hopper & S. R. Ross (Eds.), *Chimpanzees in Context* (pp. 509–523). University of Chicago Press. https://doi.org/10.7208/chicago/9780226728032.003.0022

Cronin, K. A. (2017). Studying primate cognition in a social setting to improve validity and welfare: A literature review highlighting successful approaches. *PeerJ*, *5*, Article e3649. https://doi.org/10.7717/peerj.3649

Csatádi, K., Leus, K., & Pereboom, J. J. (2008). A brief note on the effects of novel enrichment on an unwanted behaviour of captive bonobos. *Applied Animal Behaviour Science*, *112*(1–2), 201–204. https://doi.org/10.1016/j.applanim.2007.09.001

Cussen, V. A., & Mench, J. A. (2015). The relationship between personality dimensions and resiliency to environmental stress in orange-winged amazon parrots (*Amazona amazonica*), as indicated by the development of abnormal behaviors. *PLOS ONE*, *10*(6), Article e0126170. https://doi.org/10.1371/journal.pone.0126170

Chamorro-Premuzic, T., & Furnham, A. (2006). Intellectual competence and the intelligent personality: A third way in differential psychology. *Review of General Psychology*, *10*(3), 251–267. https://doi.org/10.1037/1089-2680.10.3.251

Chamorro-Premuzic, T., & Furnham, A. (2014). *Personality and intellectual competence*. Psychology Press. https://doi.org/10.4324/9781410612649

Chamorro-Premuzic, T., & Furnham, A. (2003). Personality traits and academic examination performance. *European Journal of Personality*, *17*(3), 237–250. https://doi.org/10.1002/per.473

Chamove, A. S. (1974). A new primate social behaviour category system. *Primates*, *15*, 85–99. https://doi.org/10.1007/BF01749595

Chamove, A. S., Eysenck, H. J., & Harlow, H. F. (1972). Personality in monkeys: Factor analyses of rhesus social behaviour. *Quarterly Journal of Experimental Psychology*, *24*(4), 496–504. https://doi.org/10.1080/14640747208400309

Chaplin, W. F. (2005). Factor analysis of personality measures. In B. S. Everitt & D. C. Howell (Eds.), *Encyclopedia of statistics in behavioral science* (pp. 628–636). Wiley. https://doi.org/10.1002/0470013192.bsa219

Chapman, B. P., & Elliot, A. J. (2019). Brief report: How short is too short? An ultra-brief measure of the big-five personality domains implicates "agreeableness" as a risk for all-cause mortality. *Journal of Health Psychology*, *24*(11), 1568–1573. https://doi.org/10.1177/1359105317720819

Chernus, L. A. (2008). "Separation/abandonment/isolation trauma:" An application of psychoanalytic developmental theory to understanding its impact on both chimpanzee and human children. *Journal of Emotional Abuse*, *8*(4), 447–468. https://doi.org/10.1080/10926790802480356

ChimpCARE. (2020). *Chimpanzees in the U.S.* Retrieved 26/10/2023 from https://chimpcare.org/map

Chotard, H., Bard, K. A., Micheletta, J., & Davila-Ross, M. (2023). Testing for personality consistency across naturally occurring behavioral contexts in sanctuary chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *85*(1), Article e23451. https://doi.org/10.1002/ajp.23451

Daoud, J. I. (2017). Multicollinearity and regression analysis. *Journal of Physics: Conference Series*, *949*(1), Article 012009. https://doi.org/10.1088/1742-6596/949/1/012009

Davison, R. J., & Gurven, M. D. (2021). Human uniqueness? Life history diversity among small-scale societies and chimpanzees. *PLOS ONE*, *16*(2), Article e0239170. https://doi.org/10.1371/journal.pone.0239170

Dawkins M. S. (2003). Behaviour as a tool in the assessment of animal welfare. *Zoology*, *106*(4), 383–387. https://doi.org/10.1078/0944-2006-00122

de Almeida, R. M. M., Cabral, J. C. C., & Narvaes, R. (2015). Behavioural, hormonal and neurobiological mechanisms of aggressive behaviour in human and nonhuman primates. *Physiology & behavior*, *143*, 121–135. https://doi.org/10.1016/j.physbeh.2015.02.053

de Azevedo, C. S., & Young, R. J. (2021). Animal personality and conservation: Basics for inspiring new research. *Animals*, *11*(4), Article 1019. https://doi.org/10.3390/ani11041019

de Marco, A., Cozzolino, R., & Thierry, B. (2022). Coping with mortality: responses of monkeys and great apes to collapsed, inanimate and dead conspecifics. *Ethology Ecology & Evolution*, *34*(1), 1–50. https://doi.org/10.1080/03949370.2021.1893826

de Vere, A. J., & Kuczaj, S. A. (2016). Where are we in the study of animal emotions? *Wiley interdisciplinary reviews. Cognitive science*, *7*(5), 354–362. https://doi.org/10.1002/wcs.1399

de Waal, F. B. M. (1992). Aggression as a well-integrated part of primate social relationships: A critique of the seville statement on violence. In J. Silverberg & J. P. Gray (Eds.), *Aggression and peacefulness in humans and other primates* (pp. 37–56). Oxford Academic. https://doi.org/10.1093/oso/9780195071191.003.0002

de Waal, F. B. M. (2000). Primates--A natural heritage of conflict resolution. *Science*, *289*(5479), 586–590. https://doi.org/10.1126/science.289.5479.586

de Waal, F. B. M. (2007). *Chimpanzee politics: Power and sex among apes* (25th anniversary edition ed.). Johns Hopkins University Press.

de Waal, F. B. M., & Andrews, K. (2022). The question of animal emotions. *Science*, *375*(6587), 1351–1352. https://doi.org/10.1126/science.abo2378

Debusscher, J., Hofmans, J., & De Fruyt, F. (2016). Do personality states predict momentary task performance? The moderating role of personality variability. *Journal of Occupational and Organizational Psychology*, *89*(2), 330–351. https://doi.org/10.1111/joop.12126

Derefinko, K. J. (2015). Psychopathy and low anxiety: Meta-analytic evidence for the absence of inhibition, not affect. *Journal of Personality*, *83*(6), 693–709. https://doi.org/10.1111/jopy.12124

DeYoung, C. (2014). Cybernetic Big Five Theory. *Journal of Research in Personality*, *56*, 33–58. https://doi.org/10.1016/j.jrp.2014.07.004

DeYoung, C. G., Hirsh, J. B., Shane, M. S., Papademetris, X., Rajeevan, N., & Gray, J. R. (2010). Testing predictions from personality neuroscience. Brain structure and the big five. *Psychological Science*, *21*(6), 820–828. https://doi.org/10.1177/0956797610370159

Dingemanse, N. J., & Réale, D. (2005). Natural selection and animal personality. *Behaviour*, *142*(0–10), 1159–1184. https://doi.org/10.1163/156853905774539445

Directive 86/609/EEC. *Directive 86/609/EEC of 24 November 1986 on the approximation of laws, regulations and administrative provisions of the Member States regarding the protection of animals used for experimental and other scientific purposes*. http://data.europa.eu/eli/dir/1986/609/oj

Directive 98/58/EC. *Directive 98/58/EC of 20 July 1998 concerning the protection of animals kept for farming purposes*. http://data.europa.eu/eli/dir/1998/58/oj

Directive 1999/22/EC. *Directive 1999/22/EC of 29 March 1999 relating to the keeping of wild animals in zoos. Official Journal L, 094, 09/04/1999, 0024–002.* http://data.europa.eu/eli/dir/1999/22/oj

Directive 2010/63/EU. *Directive 2010/63/EU of the European Parliament and of the Council of 22 September 2010 on the Protection of Animals Used for Scientific Purposes*. http://data.europa.eu/eli/dir/1999/22/oj

DiVincenti, L., McDowell, A., & Herrelko, E. S. (2023). Integrating individual animal and population welfare in zoos and aquariums. *Animals*, *13*(10), Article 1577. https://doi.org/10.3390/ani13101577

Dobson, A. J., & Barnett, A. G. (2002). *An introduction to generalized linear models*. Chapman & Hall/CRC.

Dobson, P. (2000). An investigation into the relationship between neuroticism, extraversion and cognitive test performance in selection. *International Journal of Selection and Assessment*, *8*(3), 99–109. https://doi.org/10.1111/1468-2389.00140

Doran, D. (1997). Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Tai chimpanzees. *International Journal of Primatology*, *18*(2), 183–206. https://doi.org/10.1023/A:1026368518431

Dougherty, L. R., & Guillette, L. M. (2018). Linking personality and cognition: A meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), Article 20170282. https://doi.org/10.1098/rstb.2017.0282

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

Draycott, S. G., & Kline, P. (1995). The Big Three or the Big Five—the EPQ—R vs the NEO-PI: A research note, replication and elaboration. *Personality and Individual Differences*, *18*(6), 801–804. https://doi.org/10.1016/0191-8869(95)00010-4

Drea, C. M. (2006). Studying primate learning in group contexts: Tests of social foraging, response to novelty, and cooperative problem solving. *Methods*, *38*(3), 162–177. https://doi.org/10.1016/j.ymeth.2005.12.001

Duncan, I. J., & Petherick, J. C. (1991). The implications of cognitive processes for animal welfare. *Journal of Animal Science*, *69*(12), 5017–5022. https://doi.org/10.2527/1991.69125017x

Duncan, I. J. H. (2004). A concept of welfare based on feelings. In G. J. Benson & B. E. Rollin (Eds.), *The well-being of farm animals: Challenges and Solutions* (pp. 85–101). Blackwell Publishing. https://doi.org/10.1002/9780470344859.ch5

Duncan, I. J. H. (2006). The changing concept of animal sentience. *Applied Animal Behaviour Science*, *100*(1), 11–19. https://doi.org/10.1016/j.applanim.2006.04.011

Dutton, D. M. (2008). Subjective assessment of chimpanzee (*Pan troglodytes*) personality: reliability and stability of trait ratings. *Primates*, *49*(4), 253–259. https://doi.org/10.1007/s10329-008-0094-1

Dutton, M. B., Pierre, P. J., Bailoo, J., Warkins, E., Michel, G. F., & Bennett, A. J. (2018). A model quantitative assessment tool for nonhuman primate environmental enrichment plans. *bioRxiv*, Article 341206. https://doi.org/10.1101/341206

European Association of Zoos and Aquaria. (2021). *TAG Reports 2021*. https://www.eaza.net/assets/Uploads/Annual-report/2021-TAGAR-web-VF.pdf

Ebel, S. J., Schmelz, M., Herrmann, E., & Call, J. (2019). Innovative problem solving in great apes: the role of visual feedback in the floating peanut task. *Animal cognition*, *22*(5), 791–805. https://doi.org/10.1007/s10071-019-01275-0

Ebenau, A., von Borell, C., Penke, L., Ostner, J., & Schülke, O. (2020). Integrative personality assessment in wild Assamese macaques (*Macaca assamensis*). *Journal of Comparative Psychology*, *134*(1), 27–41. https://doi.org/10.1037/com0000190

Eckardt, W., Steklis, D. H., Steklis, N. G., Fletcher, A. W., Stoinski, T. S., & Weiss, A. (2015). Personality dimensions and their behavioral correlates in wild Virunga mountain gorillas (*Gorilla beringei beringei*). *Journal of Comparative Psychology*, *129*(1), 26–41. https://doi.org/10.1037/a0038370

Egelkamp, C. L., & Ross, S. R. (2019). A review of zoo-based cognitive research using touchscreen interfaces. *Zoo Biology*, *38*(2), 220–235. https://doi.org/10.1002/zoo.21458

Elder, C. M., & Menzel, C. R. (2001). Dissociation of cortisol and behavioral indicators of stress in an orangutan (*Pongo pygmaeus*) during a computerized task. *Primates*, *42*(4), 345–357. https://doi.org/10.1007/BF02629625

Ergüneş, H. (2018). The review of five empirical studies: To what extent contemporary findings provide biological evidence for Eysenck's PEN Model? *Koç University Undergraduate Psychology Journal*(4), 18–24. https://kuupj.ku.edu.tr/downloads/KUUPJ_4.pdf

Erwin, J., Maple, T. L., & Mitchell, G. (1979). *Captivity and behavior: Primates in breeding colonies, laboratories, and zoos*. Van Nostrand Reinhold Company.

Eysenck, H. J. (1941). Personality factors and preference judgments. *Nature*, *148*(3751), 346–346. https://doi.org/10.1038/148346a0

Eysenck, H. J. (1944). Types of personality: A factorial study of seven hundred neurotics. *Journal of Mental Science*, *90*(381), 851–861. https://doi.org/10.1192/bjp.90.381.851

Eysenck, H. J. (1947). *Dimensions of personality*. Kegan Paul.

Eysenck, H. J. (1952). *The scientific study of personality*. Macmillan. https://doi.org/10.1111/j.2044-8317.1953.tb00132.x

Eysenck, H. J. (1963). Biological basis of personality. *Nature*, *199*, 1031–1034. https://doi.org/10.1038/1991031a0

Eysenck, H. J. (1967). *The biological basis of personality*. Thomas.

Eysenck, H. J. (1995). Creativity as a product of intelligence and personality. In D. H. Saklofske & M. Zeidner (Eds.), *International handbook of personality and intelligence* (pp. 231–247). Springer New York.

Eysenck, H. J., & Eysenck, S. B. G. (1964). *Manual of the Eysenck Personality Inventory*. University of London Press.

Eysenck, H. J., & Eysenck, S. B. G. (1976). *Psychoticism as a dimension of personality*. Hodder &. Stoughton.

Eysenck, H. J., & Furnham, A. (1993). Personality and the Barron-Welsh art scale. *Perceptual and motor skills*, *76*(3), 837–838. https://doi.org/10.2466/pms.1993.76.3.837

Eysenck, S. B. G., Eysenck, H. J., & Barrett, P. (1985). A revised version of the psychoticism scale. *Personality and Individual Differences*, *6*(1), 21–29. https://doi.org/10.1016/0191-8869(85)90026-1

Fagot, J., & Bonté, E. (2010). Automated testing of cognitive performance in monkeys: Use of a battery of computerized test systems by a troop of semi-free-ranging baboons (*Papio papio*). *Behavior Research Methods*, *42*(2), 507–516. https://doi.org/10.3758/BRM.42.2.507

Fagot, J., & Paleressompoulle, D. (2009). Automatic testing of cognitive performance in baboons maintained in social groups. *Behavior Research Methods*, *41*(2), 396–404. https://doi.org/10.3758/BRM.41.2.396

Fairbanks, L. A., Jorgensen, M. J., Huff, A., Blau, K., Hung, Y. Y., & Mann, J. J. (2004). Adolescent impulsivity predicts adult dominance attainment in male vervet monkeys. *American Journal of Primatology*, *64*(1), 1–17. https://doi.org/10.1002/ajp.20057

Farmer, K. H. (2002). Pan-African sanctuary alliance: status and range of activities for great ape conservation. *American Journal of Primatology*, *58*(3), 117–132. https://doi.org/10.1002/ajp.10054

Ferdowsian, H. R., Durham, D. L., Kimwele, C., Kranendonk, G., Otali, E., Akugizibwe, T., Mulcahy, J. B., Ajarova, L., & Johnson, C. M. (2011). Signs of mood and anxiety disorders in chimpanzees. *PLOS ONE*, *6*(6), Article e19855. https://doi.org/10.1371/journal.pone.0019855

Fernández-Lázaro, G., Latorre, R., Alonso-García, E., & Barja Núñez, I. (2019). Nonhuman primate welfare: Can there be a relationship between personality, lateralization and physiological indicators? *Behavioural processes*, *166*, Article 103897. https://doi.org/10.1016/j.beproc.2019.103897

Fernández, E. J., & Martin, A. L. (2021). Animal training, environmental enrichment, and animal welfare: A history of behavior analysis in zoos. *Journal of Zoological and Botanical Gardens*, *2*(4), 531–543. https://doi.org/10.3390/jzbg2040038

Ferrando, P. J., & Lorenzo-Seva, U. (2017). Program FACTOR at 10: Origins, development and future directions. *Psicothema*, *29*(2), 236–240. https://doi.org/10.7334/psicothema2016.304

Ferrie, G., Farmer, K. H., Kuhar, C., Grand, A., Sherman, J., & Bettinger, T. (2014). The social, economic, and environmental contributions of Pan African Sanctuary Alliance primate sanctuaries in Africa. *Biodiversity and Conservation*, *23*(1), 187–201. https://doi.org/10.1007/s10531-013-0592-3

Fichtel, C., Henke-von der Malsburg, J., & Kappeler, P. M. (2023). Cognitive performance is linked to fitness in a wild primate. *Science Advances*, *9*(28), Article eadf9365. https://doi.org/10.1126/sciadv.adf9365

Field, A. (2009). *Discovering Statistics Using SPSS* (5th ed.). SAGE Publications.

Figueredo, A. J., Sefcek, J. A., Vasquez, G., Brumbach, B. H., King, J. E., & Jacobs, W. J. (2015). Evolutionary personality psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 851–877). John Wiley & Sons. https://doi.org/10.1002/9780470939376.ch30

Finkemeier, M.-A., Krause, A., Tuchscherer, A., Puppe, B., & Langbein, J. (2022). Personality traits affect learning performance in dwarf goats (*Capra hircus*). *Frontiers in Veterinary Science*, *9*, Article 916459. https://doi.org/10.3389/fvets.2022.916459

Fisken, F. A., Carlsen, F., Elder, M., de Jongh, T., Pereboom, J. J. M., Pohl, B., Rietkerk, F., Ross, S. R., & Taniguchi, A. (2018). Global population records and managed-programme updates for the great apes: short report. *International Zoo Yearbook*, *52*(1), 212–226. https://doi.org/10.1111/izy.12206

Føllesdal, H., & Soto, C. J. (2022). The Norwegian adaptation of the Big Five Inventory-2 [Original Research]. *Frontiers in Psychology*, *13*, Article 858920. https://doi.org/10.3389/fpsyg.2022.858920

Forss, S., Motes-Rodrigo, A., Hrubesch, C., & Tennie, C. (2020). Chimpanzees' (*Pan troglodytes*) problem-solving skills are influenced by housing facility and captive care duration. *PeerJ*, *8*, Article e10263. https://doi.org/10.7717/peerj.10263

Franks, B., Reiss, D., Cole, P., Friedrich, V., Thompson, N., & Higgins, E. T. (2013). Predicting how individuals approach enrichment: Regulatory focus in cotton-top tamarins (*Sanguinus oedipus*). *Zoo Biology*, *32*(4), 427–435. https://doi.org/10.1002/zoo.21075

Fraser, D. (2009). Assessing animal welfare: different philosophies, different scientific approaches. *Zoo Biology*, *28*(6), 507–518. https://doi.org/10.1002/zoo.20253

Fraser, O. N., Stahl, D., & Aureli, F. (2008). Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Sciences*, *105*(25), 8557–8562. https://doi.org/10.1073/pnas.0804141105

Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: a review and evaluation of past research. *American Journal of Primatology*, *72*(8), 653–671. https://doi.org/10.1002/ajp.20833

Freeman, H. D., Gosling, S. D., & Schapiro, S. J. (2011). Comparison of methods for assessing personality in nonhuman primates. In A. Weiss, J. E. King, & L. Murray (Eds.), *Personality and temperament in nonhuman primates.* (pp. 17–40). Springer Science + Business Media. https://doi.org/10.1007/978-1-4614-0176-6_2

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Fritz, R. G., Zimmermann, E., Meier, M., Mestre-Francés, N., Radespiel, U., & Schmidtke, D. (2020). Neurobiological substrates of animal personality and cognition in a nonhuman primate (*Microcebus murinus*). *Brain and Behavior*, *10*(9), Article e01752. https://doi.org/10.1002/brb3.1752

Fröhlich, M., Wittig, R. M., & Pika, S. (2016). Play-solicitation gestures in chimpanzees in the wild: flexible adjustment to social circumstances and individual matrices. *Royal Society Open Science*, *3*(8), Article 160278. https://doi.org/10.1098/rsos.160278

Fultz, A. (2017). A guide for modern sanctuaries with examples from a captive chimpanzee sanctuary. *Animal Studies Journal*, *6*(2), 9–29. https://ro.uow.edu.au/asj/vol6/iss2/3

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

Fureix, C., & Meagher, R. K. (2015). What can inactivity (in its various forms) reveal about affective states in non-human animals? A review. *Applied Animal Behaviour Science*, *171*, 8–24. https://doi.org/10.1016/j.applanim.2015.08.036

Great Ape Information Network. (2015). *Great Ape Information Network*. Retrieved 26/20/2023 from https://shigen.nig.ac.jp/gain/

Garai, C., Weiss, A., Arnaud, C., & Furuichi, T. (2016). Personality in wild bonobos (*Pan paniscus*). *American Journal of Primatology*, *78*(11), 1178–1189. https://doi.org/10.1002/ajp.22573

Garcia-Pelegrin, E., Clark, F., & Miller, R. (2022). Increasing animal cognition research in zoos. *Zoo Biology*, *41*(4), 281–291. https://doi.org/10.1002/zoo.21674

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

Gartner, M. C., & Powell, D. (2012). Personality assessment in snow leopards (*Uncia uncia*). *Zoo Biology*, *31*(2), 151–165. https://doi.org/10.1002/zoo.20385

Gerstner, K. F., & Pruetz, J. D. (2022). Wild chimpanzee welfare: A focus on nutrition, foraging and health to inform great ape welfare in the wild and in captivity. *Animals*, *12*(23), Article 3370. https://doi.org/10.3390/ani12233370

Gilby, I. C., & Machanda, Z. P. (2022). Advanced cognition in wild chimpanzees: Lessons from observational studies. *Current Opinion in Behavioral Sciences*, *46*, Article 101183. https://doi.org/10.1016/j.cobeha.2022.101183

Gilloux, I., Gurnell, J., & Shepherdson, D. (1992). An enrichment device for great apes. *Animal Welfare*, *1*(4), 279–289. https://doi.org/10.1017/S0962728600015220

Girard-Buttoz, C., Zaccarella, E., Bortolato, T., Friederici, A. D., Wittig, R. M., & Crockford, C. (2022). Chimpanzees produce diverse vocal sequences with ordered and recombinatorial properties. *Communications Biology*, *5*(1), Article 410. https://doi.org/10.1038/s42003-022-03350-8

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

Goldberg, L. R. (1990). An alternative "description of personality": The big-five factor structure. *Journal of Personality and Social Psychology*, *59*(6), 1216–1229. https://doi.org/10.1037/0022-3514.59.6.1216

Goldberg, L. R., & Digman, J. M. (1994). Revealing structure in the data: Principles of exploratory factor analysis. In S. Strack & M. Lorr (Eds.), *Differentiating normal and abnormal personality* (pp. 216–242). Springer Publishing Company.

Goldberg, L. R., & Rosolack, T. K. (1994). The Big Five factor structure as an integrative framework: An empirical comparison with Eysenck's P-E-N model. In J. C. F. Halverson, G. A. Kohnstamm, & R. P. Martin (Eds.), *The developing structure of temperament and personality from infancy to adulthood.* (pp. 7–35). Lawrence Erlbaum Associates, Inc. https://projects.ori.org/lrg/PDFs_papers/BigFive-PEN.pdf

Goldhammer, F., Steinwascher, M. A., Kroehne, U., & Naumann, J. (2017). Modelling individual response time effects between and within experimental speed conditions: A GLMM approach for speeded tests. *British Journal of Mathematical and Statistical Psychology*, *70*(2), 238–256. https://doi.org/10.1111/bmsp.12099

Goldsborough, Z., Sterck, E. H. M., de Waal, F. B. M., & Webb, C. E. (2023). Individual variation in chimpanzee (*Pan troglodytes*) repertoires of abnormal behaviour. *Animal Welfare*, *31*(1), 125–135. https://doi.org/10.7120/09627286.31.1.011

Goldsborough, Z., van Leeuwen, E. J. C., Kolff, K. W. T., de Waal, F. B. M., & Webb, C. E. (2020). Do chimpanzees (*Pan troglodytes*) console a bereaved mother? *Primates*, *61*(1), 93–102. https://doi.org/10.1007/s10329-019-00752-x

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

Gorsuch, R. L. (1983). *Factor Analysis*. Psychology Press. https://doi.org/10.4324/9780203781098

Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, *127*(1), 45–86. https://doi.org/10.1037/0033-2909.127.1.45

Gosling, S. D., & John, O. P. (1999). Personality Dimensions in Nonhuman Animals:A Cross-Species Review. *Current Directions in Psychological Science*, *8*(3), 69–75. https://doi.org/10.1111/1467-8721.00017

Gosling, S. D., John, O. P., Craik, K. H., & Robins, R. W. (1998). Do people know how they behave? Self-reported act frequencies compared with on-line codings by observers. *Journal of Personality and Social Psychology*, *74*(5), 1337–1349. https://doi.org/10.1037/0022-3514.74.5.1337

Gosling, S. D., Lilienfeld, S. O., & Marino, L. (2003a). Personality. In D. Maestripieri (Ed.), *Primate psychology* (pp. 254–288). Harvard University Press.

Gosling, S. D., Rentfrow, P. J., & Swann, W. B. (2003b). A very brief measure of the Big-Five personality domains. *Journal of Research in Personality*, *37*(6), 504–528. https://doi.org/10.1016/S0092-6566(03)00046-1

Goswami, S., Tyagi, P. C., Malik, P. K., Pandit, S. J., Kadivar, R. F., Fitzpatrick, M., & Mondol, S. (2020). Effects of personality and rearing-history on the welfare of captive

Asiatic lions (*Panthera leo persica*). *PeerJ*, *8*, Article e8425. https://doi.org/10.7717/peerj.8425

Gottlieb, D. H., Del Rosso, L., Sheikhi, F., Gottlieb, A., McCowan, B., & Capitanio, J. P. (2018). Personality, environmental stressors, and diarrhea in Rhesus macaques: An interactionist perspective. *American Journal of Primatology*, *80*(12), Article e22908. https://doi.org/10.1002/ajp.22908

Gottlieb, D. H., Ghirardo, S., Minier, D. E., Sharpe, N., Tatum, L., & McCowan, B. (2011). Efficacy of 3 types of foraging enrichment for rhesus macaques (*Macaca mulatta*). *Journal of the American Association for Laboratory Animal Science*, *50*(6), 888–894. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3228926/

Gouveia, V., de Carvalho Rodrigues Araújo, R., Oliveira, I., Gonçalves, M., Milfont, T., Lins de Holanda Coelho, G., Santos, W., Medeiros, E., Silva Soares, A., P. Monteiro, R., Andrade, J., Cavalcanti, T., Nascimento, B., & Gouveia, R. (2021). A short version of the Big Five Inventory (BFI-20): Evidence on construct validity. *Revista Interamericana de psicologia/Interamerican Journal of Psychology*, *55*(1), Article e1312. https://doi.org/10.30849/ripijp.v55i1.1312

Great Apes Survival Partnership & IUCN. (2018). *Report to the CITES Standing Committee on the Status of Great Apes*. United Nations Environment Programme Great Apes Survival Partnership and International Union for Conservation of Nature. https://doi.org/10.13140/RG.2.2.24454.22085/1

Graziano, W. G., & Ward, D. (1992). Probing the Big Five in adolescence: Personality and adjustment during a developmental transition. *Journal of Personality*, *60*(2), 425–439. https://doi.org/10.1111/j.1467-6494.1992.tb00979.x

Griffin, A. S., Guillette, L. M., & Healy, S. D. (2015). Cognition and personality: An analysis of an emerging field. *Trends in Ecology & Evolution*, *30*(4), 207–214. https://doi.org/10.1016/j.tree.2015.01.012

Gruber, T., Clay, Z., & Zuberbühler, K. (2010). A comparison of bonobo and chimpanzee tool use: Evidence for a female bias in the Pan lineage. *Animal Behaviour*, *80*(6), 1023–1033. https://doi.org/10.1016/j.anbehav.2010.09.005

Gruber, T., Muller, M. N., Strimling, P., Wrangham, R., & Zuberbühler, K. (2009). Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. *Current Biology*, *19*(21), 1806–1810. https://doi.org/10.1016/j.cub.2009.08.060

Gruen, L. (2021). *Ethics and Animals: An Introduction* (2nd ed.). Cambridge University Press.

Guenther, A., Brust, V., Dersen, M., & Trillmich, F. (2014). Learning and personality types are related in cavies (*Cavia aperea*). *Journal of Comparative Psychology*, *128*(1), 74–81. https://doi.org/10.1037/a0033678

Hagemann, D., Hewig, J., Walter, C., Schankin, A., Danner, D., & Naumann, E. (2009). Positive evidence for Eysenck's arousal hypothesis: A combined EEG and MRI study with multiple measurement occasions. *Personality and Individual Differences*, *47*(7), 717–721. https://doi.org/10.1016/j.paid.2009.06.009

Hanamura, S. (2015). Fission–fusion grouping. In K. Hosaka, K. Zamma, M. Nakamura, & N. Itoh (Eds.), *Mahale chimpanzees: 50 years of research* (pp. 106–118). Cambridge University Press. https://doi.org/10.1017/CBO9781107280533

Hanus, D., & Call, J. (2011). Chimpanzee problem-solving: contrasting the use of causal and arbitrary cues. *Animal cognition*, *14*(6), 871–878. https://doi.org/10.1007/s10071-011-0421-6

Hanus, D., Mendes, N., Tennie, C., & Call, J. (2011). Comparing the performances of apes (*Gorilla gorilla*, *Pan troglodytes*, *Pongo pygmaeus*) and human children *(Homo* *sapiens*) in the floating peanut task. *PLOS ONE*, *6*(6), Article e19555. https://doi.org/10.1371/journal.pone.0019555

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

Hayashi, M., & Takeshita, H. (2022). Hierarchical object combination and tool use in the great apes and human children. *Primates*, *63*(5), 429–441. https://doi.org/10.1007/s10329-022-01003-2

He, S., & Lee, W. (2022). Generalized linear mixed-effects models for studies using different sets of stimuli across conditions. *Frontiers in Psychology*, *13*, Article 955722. https://doi.org/10.3389/fpsyg.2022.955722

Heath, A. C., & Martin, N. G. (1990). Psychoticism as a dimension of personality: A multivariate genetic test of Eysenck and Eysenck's psychoticism construct. *Journal of Personality and Social Psychology*, *58*(1), 111–121. https://doi.org/10.1037//0022-3514.58.1.111

Heaven, P. C., Ciarrochi, J., Leeson, P., & Barkus, E. (2013). Agreeableness, conscientiousness, and psychoticism: Distinctive influences of three personality dimensions in adolescence. *British Journal of Psychology*, *104*(4), 481–494. https://doi.org/10.1111/bjop.12002

Hebb, D. (1949). Temperament in chimpanzees: I. Method of analysis. *Journal of Comparative and Physiological Psychology*, *42*(3), 192–206. https://doi.org/10.1037/h0056842

Heesen, R., Kim, Y., Kret, M., & Clay, Z. (2024). Perceptual integration of bodily and facial emotion cues in chimpanzees and humans. *PNAS Nexus*, *3*(2), 1–14. https://doi.org/10.1093/pnasnexus/pgae012

Hemsworth, P. H., Mellor, D. J., Cronin, G. M., & Tilbrook, A. J. (2015). Scientific assessment of animal welfare. *New Zealand Veterinary Journal*, *63*(1), 24–30. https://doi.org/10.1080/00480169.2014.966167

Herrelko, E. S., Vick, S. J., & Buchanan-Smith, H. M. (2012). Cognitive research in zoo-housed chimpanzees: Influence of personality and impact on welfare. *American Journal of Physical Anthropology*, *74*(9), 828–840. https://doi.org/10.1002/ajp.22036

Herrmann, E., & Call, J. (2012). Are there geniuses among the apes? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1603), 2753–2761. https://doi.org/10.1098/rstb.2012.0191

Herrmann, E., Call, J., Hernàndez-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, *317*(5843), 1360–1366. https://doi.org/10.1126/science.1146282

Herrmann, E., Hernández-Lloreda, M. V., Call, J., Hare, B., & Tomasello, M. (2010). The structure of individual differences in the cognitive abilities of children and chimpanzees. *Psychological Science*, *21*(1), 102–110. https://doi.org/10.1177/0956797609356511

Highfill, L., Hanbury, D., Kristiansen, R., Kuczaj, S., & Watson, S. (2010). Rating vs. coding in animal personality research. *Zoo Biology*, *29*(4), 509–516. https://doi.org/10.1002/zoo.20279

Highfill, L. E., & Kuczaj, S. A. (2007). Do bottlenose dolphins (*Tursiops truncatus*) have distinct and stable personalities? *Aquatic mammals*, *33*(3), 380–389. https://doi.org/10.1578/AM.33.3.2007.380

Higley, J. D., Suomi, S. J., & Chaffin, A. C. (2011). Impulsivity and aggression as personality traits in nonhuman primates. In A. Weiss, J. E. King, & L. Murray (Eds.), *Personality* *and temperament in nonhuman primates* (pp. 257–283). Springer New York. https://doi.org/10.1007/978-1-4614-0176-6_10

Hilbert, S., & Bühner, M. (2020). Principal Components Analysis. In V. Zeigler-Hill & T. K. Shackelford (Eds.), *Encyclopedia of Personality and Individual Differences* (pp. 4030–4034). Springer International Publishing. https://doi.org/10.1007/978-3-319-24612-3_1340

Hill, S. P., & Broom, D. M. (2009). Measuring zoo animal welfare: theory and practice. *Zoo Biology*, *28*(6), 531–544. https://doi.org/10.1002/zoo.20276

Hirata, S. (2009). Chimpanzee social intelligence: Selfishness, altruism, and the mother–infant bond. *Primates*, *50*(1), 3–11. https://doi.org/10.1007/s10329-008-0122-1

Hirata, S., & Fuwa, K. (2007). Chimpanzees *(Pan troglodytes*) learn to act with other individuals in a cooperative task. *Primates*, *48*(1), 13–21. https://doi.org/10.1007/s10329-006-0022-1

Hirata, S., Morimura, N., Watanuki, K., & Ross, S. R. (2020). The establishment of sanctuaries for former laboratory chimpanzees: Challenges, successes, and cross-cultural context. In L. M. Hopper & S. R. Ross (Eds.), *Chimpanzees in context* (pp. 208–230). University of Chicago Press. https://doi.org/10.7208/9780226728032-012

Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLOS Biology*, *12*(9), Article e1001960. https://doi.org/10.1371/journal.pbio.1001960

Hofmann, M. J., Schneider, S., & Mokros, A. (2021). Fearless but anxious? A systematic review on the utility of fear and anxiety levels to classify subtypes of psychopathy. *Behavioral Sciences & the Law*, *39*(5), 512–540. https://doi.org/10.1002/bsl.2544

Honess, P. E., & Marin, C. M. (2006a). Behavioural and physiological aspects of stress and aggression in nonhuman primates. *Neuroscience & Biobehavioral Reviews*, *30*(3), 390–412. https://doi.org/10.1016/j.neubiorev.2005.04.003

Honess, P. E., & Marin, C. M. (2006b). Enrichment and aggression in primates. *Neuroscience & Biobehavioral Reviews*, *30*(3), 413–436. https://doi.org/10.1016/j.neubiorev.2005.05.002

Hopkins, William D., Russell, Jamie L., & Schaeffer, J. (2014). Chimpanzee intelligence is heritable. *Current Biology*, *24*(14), 1649–1652. https://doi.org/10.1016/j.cub.2014.05.076

Hopkins, W. D., & Sherwood, C. C. (2022). Genetic and environmental influences on chimpanzee brain and cognition. In B. L. Schwartz & M. J. Beran (Eds.), *Primate cognitive studies* (pp. 29–56). Cambridge University Press. https://doi.org/10.1017/9781108955836.003

Hopper, L. M. (2017). Cognitive research in zoos. *Current Opinion in Behavioral Sciences*, *16*, 100–110. https://doi.org/10.1016/j.cobeha.2017.04.006

Hopper, L. M., & Cronin, K. A. (2018). A multi-institutional assessment of a short-form personality questionnaire for use with macaques. *Zoo Biology*, *37*(5), 281–289. https://doi.org/10.1002/zoo.21439

Hopper, L. M., Freeman, H. D., & Ross, S. R. (2016). Reconsidering coprophagy as an indicator of negative welfare for captive chimpanzees. *Applied Animal Behaviour Science*, *176*, 112–119. https://doi.org/10.1016/j.applanim.2016.01.002

Hopper, L. M., Price, S. A., Freeman, H. D., Lambeth, S. P., Schapiro, S. J., & Kendal, R. L. (2014). Influence of personality, age, sex, and estrous state on chimpanzee problem-solving success. *Animal cognition*, *17*(4), 835–847. https://doi.org/10.1007/s10071-013-0715-y

Hopper, L. M., Tennie, C., Ross, S. R., & Lonsdorf, E. V. (2015). Chimpanzees create and modify probe tools functionally: A study with zoo-housed chimpanzees. *American Journal of Primatology*, *77*(2), 162–170. https://doi.org/10.1002/ajp.22319

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

Hoy, J. M., Murray, P. J., & Tribe, A. (2010). Thirty years later: Enrichment practices for captive mammals. *Zoo Biology*, *29*(3), 303–316. https://doi.org/10.1002/zoo.20254

Hughes, B. O., & Duncan, I. J. H. (1988). The notion of ethological 'need', models of motivation and animal welfare. *Animal Behaviour*, *36*(6), 1696–1707. https://doi.org/10.1016/S0003-3472(88)80110-6

Humle, T., Maisels, F., Oates, J. F., Plumptre, A., & Williamson, E. A. (2016). *Pan troglodytes. The IUCN Red List of Threatened Species 2016*. https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T15933A17964454.en

Hunt, G. R., Gray, R. D., & Taylor, A. H. (2013). Why is tool use rare in animals? In C. Boesch, C. M. Sanz, & J. Call (Eds.), *Tool use in animals: Cognition and ecology* (pp. 89–118). Cambridge University Press. https://doi.org/10.1017/CBO9780511894800.007

Hunt, K. D. (2020). *Chimpanzee: Lessons from our sister species*. Cambridge University Press. https://doi.org/10.1017/9781316339916

Hurtz, G. M., & Donovan, J. J. (2000). Personality and job performance: The Big Five revisited. *Journal of Applied Psychology*, *85*(6), 869–879. https://doi.org/10.1037/0021-9010.85.6.869

Inoue-Murayama, M., Yokoyama, C., Yamanashi, Y., & Weiss, A. (2018). Common marmoset (*Callithrix jacchus*) personality, subjective well-being, hair cortisol level and AVPR1a, OPRM1, and DAT genotypes. *8*(1), Article 10255. https://doi.org/10.1038/s41598-018-28112-7

Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *111*(2), 159–173. https://doi.org/10.1037/0735-7036.111.2.159

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

Itakura, S. (1993). Emotional behavior during the learning of a contingency task in a chimpanzee. *Perceptual and motor skills*, *76*(2), 563–566. https://doi.org/10.2466/pms.1993.76.2.563

Iwanicki, S., & Lehmann, J. (2015). Behavioral and trait rating assessments of personality in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology*, *129*(3), 205–217. https://doi.org/10.1037/a0039318

Izard, C. E. (2010). The many meanings/aspects of emotion: definitions, functions, activation, and regulation. *Emotion Review*, *2*(4), 363–370. https://doi.org/10.1177/1754073910374661

Izzo, G. N., Bashaw, M. J., & Campbell, J. B. (2011). Enrichment and individual differences affect welfare indicators in squirrel monkeys (*Saimiri sciureus*). *Journal of Comparative Psychology*, *125*(3), 347. https://doi.org/10.1037/a0024294

Jang, K. L., Livesley, W. J., & Vernon, P. A. (1996). Heritability of the big five personality dimensions and their facets: a twin study. *Journal of Personality*, *64*(3), 577–591. https://doi.org/10.1111/j.1467-6494.1996.tb00522.x

Jacobson, S. L., Kwiatt, A. C., Ross, S. R., & Cronin, K. A. (2019). The effects of cognitive testing on the welfare of zoo-housed Japanese macaques (*Macaca fuscata*). *Applied*

Animal Behaviour Science, *212*, 90–97. https://doi.org/10.1016/j.applanim.2018.12.014

Jacobson, S. L., Ross, S. R., & Bloomsmith, M. A. (2016). Characterizing abnormal behavior in a large population of zoo-housed chimpanzees: prevalence and potential influencing factors. *PeerJ*, *4*, Article e2225. https://doi.org/10.7717/peerj.2225

Janmaat, K. R., Ban, S. D., & Boesch, C. (2013). Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. *Animal Behaviour*, *86*(6), 1183–1205. https://doi.org/10.1016/j.anbehav.2013.09.021

Janssens, M. (2021). Animal business: An ethical exploration of corporate responsibility towards animals. *Food Ethics*, *7*(1), Article 2. https://doi.org/10.1007/s41055-021-00094-9

Jensen, G. D. (1963). Preference for bar pressing over “freeloading” as a function of number of rewarded presses. *Journal of Experimental Psychology, 65*(5), 451–454. https://doi.org/10.1037/h0049174

Jin, J., Yanjie, S. U., Tao, Y., Guo, S., & Zeying, Y. U. (2013). Personality as a predictor of general health in captive golden snub-nosed monkeys (*Rhinopithecus roxellana*). *American Journal of Primatology*, *75*(6), 524–533. https://doi.org/10.1002/ajp.22127

Jones, C., & Sabater Pi, J. (1969). Sticks used by chimpanzees in Rio Muni, West Africa. *Nature*, *223*(5201), 100–101. https://doi.org/10.1038/223100a0

Jones, N. A. R., Webster, M., Newport, C., Templeton, C. N., Schuster, S., & Rendell, L. (2020). Cognitive styles: Speed–accuracy trade-offs underlie individual differences in archerfish. *Animal Behaviour*, *160*(1), 1–14. https://doi.org/10.1016/j.anbehav.2019.11.019

Judge, T. A., & Zapata, C. P. (2015). The person–situation debate revisited: Effect of situation strength and trait activation on the validity of the Big Five personality traits in predicting job performance. *Academy of Management Journal*, *58*(4), 1149–1179. http://www.jstor.org/stable/43589388

Jung, S. (2013). Exploratory factor analysis with small sample sizes: A comparison of three approaches. *Behavioural processes*, *97*, 90–95. https://doi.org/10.1016/j.beproc.2012.11.016

Jung, S., & Lee, S. (2011). Exploratory factor analysis for small samples. *Behavioral Research Methods*, *43*(3), 701–709. https://doi.org/10.3758/s13428-011-0077-9

Jung, S., Seo, D. G., & Park, J. (2020). Regularized exploratory bifactor analysis with small sample sizes. *Frontiers in Psychology*, *11*, Article 507. https://doi.org/10.3389/fpsyg.2020.00507

Kagan, R., Carter, S., & Allard, S. (2015). A universal animal welfare framework for zoos. *Journal of Applied Animal Welfare Science*, *18*(sup1), S1–S10. https://doi.org/10.1080/10888705.2015.1075830

Kalan, A. K., Kulik, L., Arandjelovic, M., Boesch, C., Haas, F., Dieguez, P., Barratt, C. D., Abwe, E. E., Agbor, A., Angedakin, S., Aubert, F., Ayimisin, E. A., Bailey, E., Bessone, M., Brazzola, G., Buh, V. E., Chancellor, R., Cohen, H., Coupland, C., ... Kühl, H.S. (2020). Environmental variability supports chimpanzee behavioural diversity. *Nature Communications*, *11*(1), 4451. https://doi.org/10.1038/s41467-020-18176-3

Kalcher-Sommersguter, E., Preuschoft, S., Franz-Schaider, C., Hemelrijk, C. K., Crailsheim, K., & Massen, J. J. M. (2015). Early maternal loss affects social integration of chimpanzees throughout their lifetime. *Scientific Reports*, *5*(1), Article 16439. https://doi.org/10.1038/srep16439

Khatibi, M., & Khormaei, F. (2016). Biological basis of personality: A brief review. *Journal of Life Science and Biomedicine*, *6*(2), 33–36.

Kieffer, K. M. (1998, November 4-6). *Orthogonal versus oblique factor rotation: A review of the literature regarding the pros and cons* [Paper presentation]. Annual Meeting of the Mid-South Educational Research Association, New Orleans, LA, United States. https://eric.ed.gov/?id=ED427031

Kiley-Worthington, M. (1989). Ecological, ethological, and ethically sound environments for animals: Toward symbiosis. *Journal of Agricultural Ethics*, *2*(4), 323–347. https://doi.org/10.1007/BF01826810

King, J., & Weiss, A. (2011). Personality from the perspective of a primatologist. In A. Weiss, J. E. King, & L. Murray (Eds.), *Developments in primatology: Progress and prospects* (pp. 77–99). Springer. https://doi.org/10.1007/978-1-4614-0176-6_4

King, J. E., & Figueredo, A. J. (1997). The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality*, *31*(2), 257–271. https://doi.org/10.1006/jrpe.1997.2179

King, J. E., Weiss, A., & Farmer, K. H. (2005). A chimpanzee (*Pan troglodytes*) analogue of cross-national generalization of personality structure: Zoological parks and an African sanctuary. *Journal of Personality*, *73*(2), 389–410. https://doi.org/10.1111/j.1467-6494.2005.00313.x

King, J. E., Weiss, A., & Sisco, M. M. (2008). Aping humans: age and sex effects in chimpanzee (*Pan troglodytes*) and human (*Homo sapiens*) personality. *Journal of Comparative Psychology*, *122*(4), 418–427. https://doi.org/10.1037/a0013125

Kleespies, M. W., Feucht, V., Becker, M., & Dierkes, P. W. (2022). Environmental education in zoos—Exploring the impact of guided zoo tours on connection to nature and attitudes towards species conservation. *Journal of Zoological and Botanical Gardens*, *3*(1), 56–68. https://doi.org/10.3390/jzbg3010005

Kline, P. (1987). Factor analysis and personality theory. *European Journal of Personality*, *1*(1), 21–36. https://doi.org/10.1002/per.2410010105

Kline, P. (2014). *An easy guide to factor analysis*. Routledge. https://doi.org/10.4324/9781315788135

Konečná, M., Lhota, S., Weiss, A., Urbánek, T., Adamová, T., & Pluháček, J. (2008). Personality in free-ranging Hanuman langur (*Semnopithecus entellus*) males: Subjective ratings and recorded behavior. *Journal of Comparative Psychology*, *122*(4), 379–389. https://doi.org/10.1037/a0012625

Konečná, M., Weiss, A., Lhota, S., & Wallner, B. (2012). Personality in Barbary macaques (*Macaca sylvanus*): Temporal stability and social rank. *Journal of Research in Personality*, *46*(5), 581–590. https://doi.org/10.1016/j.jrp.2012.06.004

Koolhaas, J. M., de Boer, S. F., Coppens, C. M., & Buwalda, B. (2010). Neuroendocrinology of coping styles: towards understanding the biology of individual variation. *Frontiers in Neuroendocrinology*, *31*(3), 307–321. https://doi.org/10.1016/j.yfrne.2010.04.001

Koolhaas, J. M., Korte, S. M., de Boer, S. F., van der Vegt, B. J., van Reenen, C. G., Hopster, H., de Jong, I. C., Ruis, M. A., & Blokhuis, H. J. (1999). Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews*, *23*(7), 925–935. https://doi.org/10.1016/s0149-7634(99)00026-3

Koops, K., Schöning, C., Isaji, M., & Hashimoto, C. (2015). Cultural differences in ant-dipping tool length between neighbouring chimpanzee communities at Kalinzu, Uganda. *Scientific Reports*, *5*, Article 12456. https://doi.org/10.1038/srep12456

Koski, S. E. (2011). Social personality traits in chimpanzees: temporal stability and structure of behaviourally assessed personality traits in three captive populations. *Behavioral Ecology and Sociobiology*, *65*(11), 2161–2174. https://doi.org/10.1007/s00265-011-1224-0

Koski, S. E. (2014). Broader horizons for animal personality research. *Frontiers in Ecology and Evolution*, *2*, Article 70. https://doi.org/10.3389/fevo.2014.00070

Koski, S. E., & Sterck, E. H. M. (2010). Empathic chimpanzees: A proposal of the levels of emotional and cognitive processing in chimpanzee empathy. *European Journal of Developmental Psychology*, *7*(1), 38–66. https://doi.org/10.1080/17405620902986991

Kralj-Fišer, S., & Schuett, W. (2014). Studying personality variation in invertebrates: Why bother? *Animal Behaviour*, *91*, 41–52. https://doi.org/10.1016/j.anbehav.2014.02.016

Kret, M. E., Prochazkova, E., Sterck, E. H., & Clay, Z. (2020). Emotional expressions in human and non-human great apes. *Neuroscience & Biobehavioral Reviews*, *115*, 378–395. https://doi.org/10.1016/j.neubiorev.2020.01.027

Krishnadas, R., Palaniyappan, L., Lang, J., McLean, J., & Cavanagh, J. (2014). Psychoticism and salience network morphology. *Personality and Individual Differences*, *57*, 37–42. https://doi.org/10.1016/j.paid.2013.09.016

Kubak, F. A., & Salekin, R. T. (2009). Psychopathy and anxiety in children and adolescents: New insights on developmental pathways to offending. *Journal of Psychopathology and Behavioral Assessment*, *31*(4), 271–284. https://doi.org/10.1007/s10862-009-9144-2

Kurtycz, L. M., Wagner, K. E., & Ross, S. R. (2014). The choice to access outdoor areas affects the behavior of great apes. *Journal of Applied Animal Welfare Science*, *17*(3), 185–197. https://doi.org/10.1080/10888705.2014.896213

Kutsukake, N., & Castles, D. L. (2001). Reconciliation and variation in post-conflict stress in Japanese macaques (*Macaca fuscata fuscata*): Testing the integrated hypothesis. *Animal cognition*, *4*(3–4), 259–268. https://doi.org/10.1007/s10071-001-0119-2

Lages, Y. V., & McNaughton, N. (2022). Non-human contributions to personality neuroscience – from fish through primates. An introduction to the special issue. *Personality Neuroscience*, *5*, Article e11. https://doi.org/10.1017/pen.2022.4

Laméris, D. W., Verspeek, J., Depoortere, A., Plessers, L., & Salas, M. (2021). Effects of enclosure and environmental enrichment on the behaviour of ring-tailed lemurs (*Lemur catta*). *Journal of Zoological and Botanical Gardens*, *2*(2), 164–173. https://doi.org/10.3390/jzbg2020012

Laméris, D. W., Verspeek, J., Salas, M., Staes, N., Torfs, J. R. R., Eens, M., & Stevens, J. M. G. (2022). Evaluating self-directed behaviours and their association with emotional arousal across two cognitive tasks in bonobos (*Pan paniscus*). *Animals*, *12*(21), Article 3002. https://doi.org/10.3390/ani12213002

Latzman, R. D., Boysen, S. T., & Schapiro, S. J. (2018). Neuroanatomical correlates of hierarchical personality traits in chimpanzees: Associations with limbic structures. *Personality Neuroscience*, *1*, Article e4. https://doi.org/10.1017/pen.2018.1

Latzman, R. D., Drislane, L. E., Hecht, L. K., Brislin, S. J., Patrick, C. J., Lilienfeld, S. O., Freeman, H. J., Schapiro, S. J., & Hopkins, W. D. (2016). A chimpanzee (*Pan troglodytes*) model of triarchic psychopathy constructs: Development and initial validation. *Clinical Psychological Science*, *4*(1), 50–66. https://doi.org/10.1177/2167702615568989

Latzman, R. D., Hecht, L. K., Freeman, H. D., Schapiro, S. J., & Hopkins, W. D. (2015). Neuroanatomical correlates of personality in chimpanzees (*Pan troglodytes*): Associations between personality and frontal cortex. *Neuroimage*, *123*, 63–71. https://doi.org/10.1016/j.neuroimage.2015.08.041

Latzman, R. D., Schapiro, S. J., & Hopkins, W. D. (2017). Triarchic psychopathy dimensions in chimpanzees (*Pan troglodytes*): Investigating associations with genetic variation in the vasopressin receptor 1A gene. *Frontiers in Neuroscience*, *11*, Article 407. https://doi.org/10.3389/fnins.2017.00407

Learmonth, M. J. (2019). Dilemmas for natural living concepts of zoo animal welfare. *Animals*, *9*(6), 318. https://doi.org/10.3390/ani9060318

Leavens, D., Aureli, F., & Hopkins, W. (2004). Behavioral evidence for the cutaneous expression of emotion in a chimpanzee (*Pan troglodytes*). *Behaviour*, *141*, 979–997. https://doi.org/10.1163/1568539042360189

Leavens, D., Aureli, F., Hopkins, W. D., & Hyatt, C. W. (2001). Effects of cognitive challenge on self-directed behaviors by chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *55*(1), 1–14. https://doi.org/10.1002/ajp.1034

Lee, K., & Ashton, M. C. (2007). Factor analysis in personality research. In R. W. Robins, R. C. Fraley, & R. F. Krueger (Eds.), *Handbook of research methods in personality psychology* (pp. 424–443). Guilford Publications. https://www.guilford.com/excerpts/robins.pdf?t=1

Leeds, A., & Lukas, K. (2018). Experimentally evaluating the function of self-directed behaviour in two adult mandrills (*Mandrillus sphinx*). *Animal Welfare*, *27*(1), 81–86. https://doi.org/10.7120/09627286.27.1.081

Lenth, R. (2020). emmeans: estimated marginal Means, aka least-squares means. R package version 1.4.8. https://CRAN.R-project.org/package=emmeans

Lewis, A., Berntsen, D., & Call, J. (2019). Long-term memory of past events in great apes. *Current Directions in Psychological Science*, *28*(2), 117–123. https://doi.org/10.1177/0963721418812781

Li, J., Tian, M., Fang, H., Xu, M., Li, H., & Liu, J. (2010). Extraversion predicts individual differences in face recognition. *Communicative & Integrative Biology*, *3*(4), 295–298. https://doi.org/10.4161/cib.3.4.12093

Lilienfeld, S. O., Gershon, J., Duke, M., Marino, L., & de Waal, F. B. M. (1999). A preliminary investigation of the construct of psychopathic personality (psychopathy) in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *113*(4), 365–375. https://doi.org/10.1037/0735-7036.113.4.365

Locurto, C. (2007). Individual differences and animal personality. *Comparative Cognition & Behavior Reviews*, *2*(1), 67–78.

Loehlin, J., Medland, S., Montgomery, G., & Martin, N. (2005). Eysenck's Psychoticism and the X-linked androgen receptor gene CAG polymorphism in additional Australian samples. *Personality and Individual Differences*, *39*(3), 661–667. https://doi.org/10.1016/j.paid.2005.02.016

Lonsdorf, E. V. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour*, *70*(3), 673–683. https://doi.org/10.1016/j.anbehav.2004.12.014

Lonsdorf, E. V. (2006). What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal cognition*, *9*(1), 36–46. https://doi.org/10.1007/s10071-005-0002-7

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

Lonsdorf, E. V., Eberly, L. E., & Pusey, A. E. (2004). Sex differences in learning in chimpanzees. *Nature*, *428*(6984), 715–716. https://doi.org/10.1038/428715a

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

Lopresti-Goodman, S. M., Kameka, M., & Dube, A. (2012). Stereotypical behaviors in chimpanzees rescued from the african bushmeat and pet trade. *Behavioral Sciences*, *3*(1), 1–20. https://doi.org/10.3390/bs3010001

Lopresti-Goodman, S. M., & Villatoro-Sorto, B. (2023). The benefits and challenges of conducting primate research in different settings. *Animals*, *13*(1), Article 133. https://doi.org/10.3390/ani13010133

Lorenz, K. (1935). Der Kumpan in der Umwelt des Vogels. Der Artgenosse als auslösendes Moment sozialer Verhaltungsweisen [The companion in the bird's world. The fellow-member of the species as releasing factor of social behavior]. *Journal für Ornithologie. Beiblatt. (Leipzig)*, *83*, 137–213. https://doi.org/10.1007/BF01905355

Lorenzo-Seva, U., & Ferrando, P. J. (2006). FACTOR: A computer program to fit the exploratory factor analysis model. *Behavior Research Methods*, *38*(1), 88–91. https://doi.org/10.3758/BF03192753

Lorenzo-Seva, U., & Ferrando, P. J. (2013). Factor 9.2: A comprehensive program for fitting exploratory and semiconfirmatory factor analysis and IRT models. *Applied Psychological Measurement*, *37*, 497–498. https://doi.org/10.1177/0146621613487794

Lukas, K. E., Hoff, M. P., & Maple, T. L. (2003). Gorilla behavior in response to systematic alternation between zoo enclosures. *Applied Animal Behaviour Science*, *81*(4), 367–386. https://doi.org/10.1016/S0168-1591(02)00237-X

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

Lutz, C. K., & Coleman, K. (2022). Nonhuman primate abnormal behavior: Etiology, assessment, and treatment. *American Journal of Primatology*, *84*(6), Article e23380. https://doi.org/10.1002/ajp.23380

Lutz, C. K., & Novak, M. A. (2005). Environmental enrichment for nonhuman primates: Theory and application. *ILAR journal*, *46*(2), 178–191. https://doi.org/10.1093/ilar.46.2.178

Luu, S., & ElBassiouny, A. (2020). Factor analysis in personality research. In B. J. Carducci, C. S. Nave, J. S. Mio, & R. E. Riggio (Eds.), *The wiley encyclopedia of personality and individual differences* (Vol. 2, pp. 109–111). John Wiley & Sons Ltd. https://doi.org/10.1002/9781119547167.ch88

Lycett, S. J., Collard, M., & McGrew, W. C. (2010). Are behavioral differences among wild chimpanzee communities genetic or cultural? An assessment using tool-use data and phylogenetic methods. *American Journal of Physical Anthropology*, *142*(3), 461–467. https://doi.org/10.1002/ajpa.21249

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

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

Macdonald, S., & Ritvo, S. (2016). Comparative cognition outside the laboratory. *Comparative Cognition & Behavior Reviews*, *11*(1), 49–61. https://doi.org/10.3819/ccbr.2016.110003

Maestripieri, D. (2018). Maternal influences on primate social development. *Behavioral Ecology and Sociobiology*, *72*(8), Article 130. https://doi.org/10.1007/s00265-018-2547-x

Maestripieri, D., Schino, G., Aureli, F., & Troisi, A. (1992). A modest proposal: Displacement activities as an indicator of emotions in primates. *Animal Behaviour*, *44*(5), 967–979. https://doi.org/10.1016/S0003-3472(05)80592-5

Maki, S., Alford, P. L., Bloomsmith, M. A., & Franklin, J. (1989). Food puzzle device simulating termite fishing for captive chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *Suppl 1*, 71–78.

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

Malezieux, M., Klein, A. S., & Gogolla, N. (2023). Neural circuits for emotion. *Annual Review of Neuroscience*, *46*, 211–231. https://doi.org/10.1146/annurev-neuro-111020-103314

Mammadov, S. (2022). Big Five personality traits and academic performance: A meta-analysis. *Journal of Personality*, *90*(2), 222–255. https://doi.org/10.1111/jopy.12663

ManyPrimates, Altschul, D. M., Beran, M. J., Bohn, M., Call, J., DeTroy, S., Duguid, S. J., Egelkamp, C. L., Fichtel, C., Fischer, J., Flessert, M., Hanus, D., Haun, D. B. M., Haux, L. M., Hernandez-Aguilar, R. A., Herrmann, E., Hopper, L. M., Joly, M., Kano, F., … Watzek, J. (2019a). Establishing an infrastructure for collaboration in primate cognition research. *PLOS ONE*, *14*(10), Article e0223675. https://doi.org/10.1371/journal.pone.0223675

ManyPrimates, Altschul, D. M., Beran, M. J., Bohn, M., Caspar, K. R., Fichtel, C., Försterling, M., Grebe, N. M., Hernandez-Aguilar, R. A., Kwok, S. C., Llorente, M., Motes-Rodrigo, A., Proctor, D., Sánchez-Amaro, A., Simpson, E. A., Szabelska, A., Taylor, D., van der Meshct, J., Völter, C. J., & Watzek, J. (2019b). Collaborative open science as a way to reproducibility and new insights in primate cognition research. *Japanese Psychological Review*, *62*(3), 205–220. https://doi.org/10.24602/sjpr.62.3_205

Maple, T. L., & Bloomsmith, M. A. (2018). Introduction: The science and practice of optimal animal welfare. *Behavioural processes*, *156*, 1–2. https://doi.org/10.1016/j.beproc.2017.09.012

Maple, T. L., & Perdue, B. M. (2013). Environmental enrichment. In *Zoo animal welfare* (pp. 95–117). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-35955-2_6

Marciano, Z. (2019). *Relationships between personality type and cognitive ability in marmoset monkeys (Callithrix jacchus)* [Master's Thesis, University of Massachusetts Amherst]. ScholarWorks@UMass Amherst repository. https://scholarworks.umass.edu/masters_theses_2/845

Martin-Ordas, G., Schumacher, L., & Call, J. (2012). Sequential tool use in great apes. *PLOS ONE*, *7*(12), Article e52074. https://doi.org/10.1371/journal.pone.0052074

Martin, J. E. (2023). Early life experiences: Activity levels and abnormal behaviours in resocialised chimpanzees. *Animal Welfare*, *11*(4), 419–436. https://doi.org/10.1017/S0962728600025148

Martin, P., & Bateson, P. (2007). Recording methods. In P. Martin & P. Bateson (Eds.), *Measuring behaviour: An introductory guide* (pp. 84–100). Cambridge University Press. https://doi.org/10.1017/CBO9781139168342.009

Masilkova, M., Weiss, A., & Konečná, M. (2018). How long does it take? Reliable personality assessment based on common behaviour in cotton-top tamarins (*Saguinus oedipus*). *Behavioural processes*, *157*, 59–67. https://doi.org/10.1016/j.beproc.2018.08.009

Mason, G., Clubb, R., Latham, N., & Vickery, S. (2007). Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science*, *102*(3), 163–188. https://doi.org/10.1016/j.applanim.2006.05.041

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

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

Matsuzawa, T. (2016). SAGA and GAIN for great apes. *Primates*, *57*(1), 1–2. https://doi.org/10.1007/s10329-015-0504-0

Matsuzawa, T., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R., & Yamakoshi, G. (2001). Emergence of culture in wild chimpanzees: Education by master-apprenticeship. In T. Matsuzawa (Ed.), *Primate origins of human cognition and behavior* (pp. 557–574). Springer Japan. https://doi.org/10.1007/978-4-431-09423-4_28

Matthews, G. (1999). Personality and skill: A cognitive-adaptive framework. In *Learning and individual differences: Process, trait, and content determinants.* (pp. 251–273). American Psychological Association. https://doi.org/10.1037/10315-011

Matzel, L. D., Han, Y. R., Grossman, H., Karnik, M. S., Patel, D., Scott, N., Specht, S. M., & Gandhi, C. C. (2003). Individual differences in the expression of a "general" learning ability in mice. *Journal of Neuroscience*, *23*(16), 6423–6433. https://doi.org/10.1523/jneurosci.23-16-06423.2003

McCrae, R. R., & Costa, P. T. (1985). Comparison of EPI and psychoticism scales with measures of the five-factor model of personality. *Personality and Individual Differences*, *6*(5), 587–597. https://doi.org/10.1016/0191-8869(85)90008-X

McEwen, E. S., Warren, E., Tenpas, S., Jones, B., Durdevic, K., Rapport Munro, E., & Call, J. (2022). Primate cognition in zoos: Reviewing the impact of zoo-based research over 15 years. *American Journal of Primatology*, *84*(10), Article e23369. https://doi.org/10.1002/ajp.23369

McGowan, R.T.S., Robbins, C.T., Alldredge, J.R., & Newberry, R.C. (2010). Contrafreeloading in grizzly bears: implications for captive foraging enrichment. *Zoo Biology*, *29*(4), 484–502. https://doi.org/10.1002/zoo.20282

McGrew, W. (1979). Evolutionary implications of sex differences in chimpanzee predation and tool use. In (Vol. 5, pp. 441–463).

McGrew, W. C., & McGrew, W. C. (1992). *Chimpanzee material culture: implications for human evolution*. Cambridge University Press. https://doi.org/10.1017/CBO9780511565519

McMillan, F. D., & Yeates, J. W. (2020). The problems with well-being terminology. In F. D. McMillan (Ed.), *Mental health and well-being in animals* (2nd ed., pp. 8–20). CABI International. https://doi.org/10.1079/9781786393401.0008

Meehan, C. L., & Mench, J. A. (2007). The challenge of challenge: Can problem solving opportunities enhance animal welfare? *Applied Animal Behaviour Science*, *102*(3–4), 246–261. https://doi.org/10.1016/j.applanim.2006.05.031

Melis, A. P., & Rossano, F. (2022). When and how do non-human great apes communicate to support cooperation? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *377*(1859), Article 20210109. https://doi.org/10.1098/rstb.2021.0109

Melis, A. P., Warneken, F., Jensen, K., Schneider, A. C., Call, J., & Tomasello, M. (2011). Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the Royal Society B*, *278*(1710), 1405–1413. https://doi.org/10.1098/rspb.2010.1735

Mellor, D. J. (2015a). Enhancing animal welfare by creating opportunities for positive affective engagement. *New Zealand Veterinary Journal*, *63*(1), 3–8. https://doi.org/10.1080/00480169.2014.926799

Mellor, D. J. (2015b). Positive animal welfare states and encouraging environment-focused and animal-to-animal interactive behaviours. *New Zealand Veterinary Journal*, *63*(1), 9–16. https://doi.org/10.1080/00480169.2014.926800

Mellor, D. J. (2016). Updating animal welfare thinking: Moving beyond the "five freedoms" towards "a life worth living". *Animals*, *6*(3), Article 21. https://doi.org/10.3390/ani6030021

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

Mellor, D. J., Hunt, S., & Gusset, M. (2015). *Caring for wildlife: The World Zoo and Aquarium animal welfare strategy* (978-2-8399-1695-0). https://www.waza.org/wp-content/uploads/2019/03/WAZA-Animal-Welfare-Strategy-2015_Landscape.pdf

Menzies, A. K., Timonin, M. E., McGuire, L. P., & Willis, C. K. R. (2013). Personality variation in little brown bats. *PLOS ONE*, *8*(11), Article e80230. https://doi.org/10.1371/journal.pone.0080230

Meyer, J. S., & Hamel, A. F. (2014). Models of stress in nonhuman primates and their relevance for human psychopathology and endocrine dysfunction. *ILAR journal*, *55*(2), 347–360. https://doi.org/10.1093/ilar/ilu023

Michalski, R. L., & Shackelford, T. K. (2010). Evolutionary personality psychology: Reconciling human nature and individual differences. *Personality and Individual Differences*, *48*, 509–516. https://doi.org/10.1016/j.paid.2009.10.027

Micheletti, K., Ndiaye, P., Aguado, W., & Pruetz, J. (2022). Indirect evidence of tool-assisted hunting in the Bantan chimpanzee (*Pan troglodytes verus*) community in southeastern Senegal savanna-woodlands. *Pan Africa News*, *28*(2), 14–16. https://doi.org/10.5134/274453

Mine, J. G., Slocombe, K. E., Willems, E. P., Gilby, I. C., Yu, M., Thompson, M. E., Muller, M. N., Wrangham, R. W., Townsend, S. W., & Machanda, Z. P. (2022). Vocal signals facilitate cooperative hunting in wild chimpanzees. *Science Advances*, *8*(30), Article eabo5553. https://doi.org/10.1126/sciadv.abo5553

Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, *77*(3), 633–640. https://doi.org/10.1016/j.anbehav.2008.11.021

Mitchell, R. L. C., & Kumari, V. (2016). Hans Eysenck's interface between the brain and personality: Modern evidence on the cognitive neuroscience of personality. *Personality and Individual Differences*, *103*, 74–81. https://doi.org/10.1016/j.paid.2016.04.009

Morgan, K. N., & Tromborg, C. T. (2007). Sources of stress in captivity. *Applied Animal Behaviour Science*, *102*(3–4), 262–302. https://doi.org/10.1016/j.applanim.2006.05.032

Morimura, N. (2003). A note on enrichment for spontaneous tool use by chimpanzees (*Pan troglodytes*). *Applied Animal Behaviour Science*, *82*(3), 241–247. https://doi.org/10.1016/S0168-1591(03)00058-3

Morimura, N. (2006). Cognitive enrichment in chimpanzees: An approach of welfare entailing an animal’s entire resources. In T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds.), *Cognitive development in chimpanzees* (pp. 368–391). Springer Tokyo. https://doi.org/10.1007/4-431-30248-4_23

Morimura, N., Hirata, S., & Matsuzawa, T. (2023). Challenging cognitive enrichment: Examples from caring for the chimpanzees in the Kumamoto sanctuary, Japan and Bossou, Guinea. In L. M. Robinson & A. Weiss (Eds.), *Nonhuman primate welfare: From history, science, and ethics to practice* (pp. 501–528). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_21

Morton, B. F., Lee, P. C., & Buchanan-Smith, H. M. (2013a). Taking personality selection bias seriously in animal cognition research: a case study in capuchin monkeys (*Sapajus apella*). *Animal cognition*, *16*(4), 677–684. https://doi.org/10.1007/s10071-013-0603-5

Morton, B. F., Lee, P. C., Buchanan-Smith, H. M., Brosnan, S. F., Thierry, B., Paukner, A., de Waal, F. B. M., Widness, J., Essler, J. L., & Weiss, A. (2013b). Personality structure in brown capuchin monkeys (*Sapajus apella*): Comparisons with chimpanzees (*Pan troglodytes*), orangutans (*Pongo spp.*), and rhesus macaques (*Macaca mulatta*). *Journal of Comparative Psychology*, *127*(3), 282–298. https://doi.org/10.1037/a0031723

Moscatelli, A., Mezzetti, M., & Lacquaniti, F. (2012). Modeling psychophysical data at the population-level: the generalized linear mixed model. *Journal of Vision*, *12*(11), 26–26. https://doi.org/10.1167/12.11.26

Motes-Rodrigo, A., & Tennie, C. (2022). Captive great apes tend to innovate simple tool behaviors quickly. *American Journal of Primatology*, *84*(10), Article e23311. https://doi.org/10.1002/ajp.23311

Mount, M. K., Barrick, M. R., & Strauss, J. P. (1999). The joint relationship of conscientiousness and ability with performance: Test of the interaction hypothesis. *Journal of Management*, *25*(5), 707–721. https://doi.org/10.1016/S0149-2063(99)00022-7

Mulcahy, N. J., & Call, J. (2006). Apes save tools for future use. *Science*, *312*(5776), 1038–1040. https://doi.org/10.1126/science.1125456

Muller, M. N., & Mitani, J. C. (2005). Conflict and cooperation in wild chimpanzees. In P. J. B. Slater, C. T. Snowdon, T. J. Roper, H. J. Brockmann, & M. Naguib (Eds.), *Advances in the study of behavior* (Vol. 35, pp. 275–331). Academic Press. https://doi.org/10.1016/S0065-3454(05)35007-8

Murray, L. (2011). Predicting primate behavior from personality ratings. In A. Weiss, J. E. King, & L. Murray (Eds.), *Personality and temperament in nonhuman primates* (pp. 129–167). Springer New York. https://doi.org/10.1007/978-1-4614-0176-6_6

Murray, L., Goddard, J., & Gordon, D. (2023). Facial expression of TIPI personality and CHMP-Tri psychopathy traits in chimpanzees (*Pan troglodytes*). *Human Nature*, *34*, 513–528. https://doi.org/10.1007/s12110-023-09462-2

Musgrave, S., & Lonsdorf, E. (2021). The ontogeny of termite gathering among chimpanzees in the Goualougo Triangle, Republic of Congo. *174*(2), 187–200. https://doi.org/10.1002/ajpa.24125

Musgrave, S., Lonsdorf, E., Morgan, D., Prestipino, M., Bernstein-Kurtycz, L., Mundry, R., & Sanz, C. (2020). Teaching varies with task complexity in wild chimpanzees. *Proceedings of the National Academy of Sciences*, *117*(2), 969–976. https://doi.org/doi:10.1073/pnas.1907476116

Nagell, K., Olguin, R. S., & Tomasello, M. (1993). Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Journal of Comparative Psychology*, *107*(2), 174. https://doi.org/10.1037/0735-7036.107.2.174

Nakamura, M., Hayaki, H., Hosaka, K., Itoh, N., & Zamma, K. (2014). Brief communication: Orphaned male chimpanzees die young even after weaning. *American Journal of Physical Anthropology*, *153*(1), 139–143. https://doi.org/10.1002/ajpa.22411

Nash, R., Johnston, H., Robbins, A., & Descovich, K. (2021). The effect of enrichment filling and engagement time on regurgitation and reingestion behaviour in three zoo-housed orangutans. *Journal of Zoological and Botanical Gardens*, *2*(1), 10–20. https://doi.org/10.3390/jzbg2010002

Nash, V., & Chamove, A. (1981). Personality and dominance behaviour in stumptailed macaques. In A.B. Chiarelli & R. Corruccini (Eds.), *Primate Behavior and Sociobiology. Proceedings in Life Sciences* (88–92). Springer. https://doi.org/10.1007/978-3-642-68254-4_12

Nash, V. J. (1982). Tool use by captive chimpanzees at an artificial termite mound. *Zoo Biology*, *1*(3), 211–221. https://doi.org/10.1002/zoo.1430010305

Naylor, W., & Parsons, E. (2019). An international online survey on public attitudes towards the keeping of whales and dolphins in captivity. *Tourism in Marine Environments*, *14*(3), 133–142. https://doi.org/10.3727/154427319X15627970573318

Neadle, D., Bandini, E., & Tennie, C. (2020). Testing the individual and social learning abilities of task-naïve captive chimpanzees (*Pan troglodytes sp.*) in a nut-cracking task. *PeerJ*, *8*, Article e8734. https://doi.org/10.7717/peerj.8734

Neal, S. J., & Caine, N. G. (2016). Scratching under positive and negative arousal in common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, *78*(2), 216–226. https://doi.org/10.1002/ajp.22498

Neal Webb, S. J., Hau, J., & Schapiro, S. J. (2019). Does group size matter? Captive chimpanzee (*Pan troglodytes*) behavior as a function of group size and composition. *American Journal of Primatology*, *81*(1), Article e22947. https://doi.org/10.1002/ajp.22947

Neal Webb, S. J., & Schapiro, S. J. (2023). Locomotion as a measure of well-being in captive chimpanzees (*Pan troglodytes*). *Animals*, *13*(5), Article 803. https://doi.org/10.3390/ani13050803

Nettle, D., & Penke, L. (2010). Personality: Bridging the literatures from human psychology and behavioural ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 4043–4050. https://doi.org/10.1098/rstb.2010.0061

Neumann, I. D., Veenema, A. H., & Beiderbeck, D. I. (2010). Aggression and anxiety: Social context and neurobiological links. *Frontiers in Behavioral Neuroscience*, *4*, Article 12. https://doi.org/10.3389/fnbeh.2010.00012

Newberry, R. C. (1995). Environmental enrichment: increasing the biological relevance of captive environments. *Applied Animal Behaviour Science*, *44*(2–4), 229–243. https://doi.org/10.1016/0168-1591(95)00616-Z

Newton-Fisher, N. E. (2006). Female coalitions against male aggression in wild chimpanzees of the Budongo Forest. *International Journal of Primatology*, *27*(6), 1589–1599. https://doi.org/10.1007/s10764-006-9087-3

Nishida, T., Zamma, K., Matsusaka, T., Inaba, A., & McGrew, W. C. (2010). Catalogue. In *Chimpanzee behavior in the wild: An audio-visual encyclopedia* (pp. 15–24). Springer Japan. https://doi.org/10.1007/978-4-431-53895-0_5

Noë, R., Waal, F., & van Hooff, J. (1980). Types of dominance in a chimpanzee colony. *Folia primatologica*, *34*, 90–110. https://doi.org/10.1159/000155949

Noftle, E. E., & Robins, R. W. (2007). Personality predictors of academic outcomes: Big five correlates of GPA and SAT scores. *Journal of Personality and Social Psychology*, *93*(1), 116–130. https://doi.org/10.1037/0022-3514.93.1.116

Norman, M., Rowden, L. J., & Cowlishaw, G. (2021). Potential applications of personality assessments to the management of non-human primates: A review of 10 years of study. *PeerJ*, *9*, Article e12044. https://doi.org/10.7717/peerj.12044

Novak, M. A., Hamel, A. F., Kelly, B. J., Dettmer, A. M., & Meyer, J. S. (2013). Stress, the HPA axis, and nonhuman primate well-being: A review. *Applied Animal Behaviour Science*, *143*(2–4), 135–149. https://doi.org/10.1016/j.applanim.2012.10.012

Novak, M. A., & Suomi, S. J. (1988). Psychological well-being of primates in captivity. *American Psychologist*, *43*(10), 765–773. https://doi.org/10.1037//0003-066x.43.10.765

Nunes, A., Limpo, T., Lima, C. F., & Castro, S. L. (2018). Short scales for the assessment of personality traits: Development and validation of the Portuguese Ten-Item Personality Inventory (TIPI). *Frontiers in Psychology*, *9*, Article 461. https://doi.org/10.3389/fpsyg.2018.00461

Nygren, N. V., & Ojalammi, S. (2018). Conservation education in zoos: A literature review. *TRACE∴ Journal for Human-Animal Studies*, *4*, 62–76. https://doi.org/10.23984/fjhas.66540

Oates, J. F. (2006). Is the chimpanzee, *Pan troglodytes*, an endangered species? It depends on what "endangered" means. *Primates*, *47*(1), 102–112. https://doi.org/10.1007/s10329-005-0149-5

Ogura T. (2011). Contrafreeloading and the value of control over visual stimuli in Japanese macaques (*Macaca fuscata*). *Animal Cognition*, *14*(3), 427–431. https://doi.org/10.1007/s10071-010-0377-y

Ormel, J., Bastiaansen, A., Riese, H., Bos, E. H., Servaas, M., Ellenbogen, M., Rosmalen, J. G., & Aleman, A. (2013). The biological and psychological basis of neuroticism:

current status and future directions. *Neuroscience and Biobehavioral Reviews*, *37*(1), 59–72. https://doi.org/10.1016/j.neubiorev.2012.09.004

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

Osvath, M. (2009). Spontaneous planning for future stone throwing by a male chimpanzee. *Current Biology*, *19*(5), R190–R191. https://doi.org/10.1016/j.cub.2009.01.010

Ottoni, E. B., & Izar, P. (2008). Capuchin monkey tool use: Overview and implications. *Evolutionary Anthropology: Issues, News, and Reviews*, *17*(4), 171–178. https://doi.org/10.1002/evan.20185

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

Pal, A., & Sinha, A. (2022). Beyond food for thought: Tool use and manufacture by wild nonhuman primates in nonforaging contexts. *Current Opinion in Behavioral Sciences*, *47*, Article 101201. https://doi.org/10.1016/j.cobeha.2022.101201

Panksepp, J. (2005). Affective consciousness: Core emotional feelings in animals and humans. *Consciousness and cognition*, *14*(1), 30–80. https://doi.org/10.1016/j.concog.2004.10.004

Panksepp, J. (2011). Cross-species affective neuroscience decoding of the primal affective experiences of humans and related animals. *PLOS ONE*, *6*(9), Article e21236. https://doi.org/10.1371/journal.pone.0021236

Paquette, D., & Prescott, J. (1988). Use of novel objects to enhance environments of captive chimpanzees. *Zoo Biology*, *7*(1), 15–23. https://doi.org/10.1002/zoo.1430070103

PASA. (2021). *Primates in peril: The impact of climate change on african primates. 2021 census report*. https://pasa.org/wp-content/uploads/2022/02/PASA-CLIMATE-CRISIS-REPORT.pdf

Patrick, C. J., Fowles, D. C., & Krueger, R. F. (2009). Triarchic conceptualization of psychopathy: Developmental origins of disinhibition, boldness, and meanness. *Developmental Psychopathology*, *21*(3), 913–938. https://doi.org/10.1017/S0954579409000492

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

Paul, E. S., & Mendl, M. T. (2018). Animal emotion: descriptive and prescriptive definitions and their implications for a comparative perspective. *Applied Animal Behaviour Science*, *205*, 202–209. https://doi.org/10.1016/j.applanim.2018.01.008

Pavlov, I. P. (1906). The scientific investigation of the psychical faculties or processes in the higher animals. *Science*, *24*(620), 613–619. https://doi.org/10.1126/science.24.620.613

Pavlov, I. P. (1941). *Lectures on conditioned reflexes. Conditioned reflexes and psychiatry* (Vol. 2). International Publishers.

Pederson, A. K., King, J. E., & Landau, V. I. (2005). Chimpanzee (*Pan troglodytes*) personality predicts behavior. *Journal of Research in Personality*, *39*(5), 534–549. https://doi.org/10.1016/j.jrp.2004.07.002

Perdue, B. M., Clay, A. W., Gaalema, D. E., Maple, T. L., & Stoinski, T. S. (2012). Technology at the zoo: The influence of a touchscreen computer on orangutans and zoo visitors. *Zoo Biology*, *31*(1), 27–39. https://doi.org/10.1002/zoo.20378

Perdue, B. M., Sherwen, S. L., & Maple, T. L. (2020). The science and practice of captive animal welfare. *Frontiers in Psychology*, *11*, Article 1851. https://doi.org/10.3389/fpsyg.2020.01851

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

Poole, T. B. (1988). Behaviour, housing and welfare of non-human primates. In A. C. Beynen & H. A. Solleveld (Eds.), *New developments in biosciences: Their implications for laboratory animal science:* (pp. 231–237). Springer Netherlands. https://doi.org/10.1007/978-94-009-3281-4_38

Powell, D. M., & Gartner, M. C. (2011). Applications of personality to the management and conservation of nonhuman animals. In M. Inoue-Murayama, S. Kawamura, & A. Weiss (Eds.), *From genes to animal behavior: Social structures, personalities, communication by color* (pp. 185–199). Springer. https://doi.org/10.1007/978-4-431-53892-9_8

Pruetz, J. D., Bertolani, P., Ontl, K. B., Lindshield, S., Shelley, M., & Wessling, E. G. (2015). New evidence on the tool-assisted hunting exhibited by chimpanzees (*Pan troglodytes verus*) in a savannah habitat at Fongoli, Sénégal. *Royal Society Open Science*, *2*(4), 140507. https://doi.org/10.1098/rsos.140507

Pruetz, J. D., Bogart, S. L., & Lindshield, S. (2020). Extractive foraging in an extreme environment: Tool and proto-tool use by chimpanzees at Fongoli, Senegal. In L. M. Hopper & S. R. Ross (Eds.), *Chimpanzees in context* (pp. 391–409). University of Chicago Press. https://doi.org/10.7208/9780226728032-020

Pruetz, J. D., & McGrew, W. C. (2001). What does a chimpanzee need? Using natural behavior to guide the care and management of captive populations. In L. Brent (Ed.), *Care and management of captive chimpanzees* (pp. 17–37). The American Society of Primatologists.

Pullin, A. N., Pairis-Garcia, M. D., Campbell, B. J., Campler, M. R., & Proudfoot, K. L. (2017). Technical note: Instantaneous sampling intervals validated from continuous video observation for behavioral recording of feedlot lambs. *Journal of Animal Science*, *95*(11), 4703–4707. https://doi.org/10.2527/jas2017.1835

Quintavalle Pastorino, G., Preziosi, R., Faustini, M., Curone, G., Albertini, M., Nicoll, D., Moffat, L., Pizzi, R., & Mazzola, S. (2019). Comparative personality traits assessment of three species of communally housed captive penguins. *Animals*, *9*(6), Article 376. https://doi.org/10.3390/ani9060376

Rawlings, B., Flynn, E., Freeman, H., Reamer, L., Schapiro, S. J., Lambeth, S., & Kendal, R. L. (2020). Sex differences in longitudinal personality stability in chimpanzees. *Evolutionary Human Sciences*, *2*, e46, Article e46. https://doi.org/10.1017/ehs.2020.45

Réale, D., Dingemanse, N. J., Kazem, A. J. N., & Wright, J. (2010). Evolutionary and ecological approaches to the study of personality. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*(1560), 3937–3946. https://doi.org/10.1098/rstb.2010.0222

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*(2), 291–318. https://doi.org/10.1111/j.1469-185x.2007.00010.x

Reamer, L. A., Haller, R. L., Thiele, E. J., Freeman, H. D., Lambeth, S. P., & Schapiro, S. J. (2014). Factors affecting initial training success of blood glucose testing in captive chimpanzees (*Pan troglodytes*). *Zoo Biology*, *33*(3), 212–220. https://doi.org/10.1002/zoo.21123

Reber, S. A., Oh, J., Janisch, J., Stevenson, C., Foggett, S., & Wilkinson, A. (2021). Early life differences in behavioral predispositions in two Alligatoridae species. *Animal cognition*, *24*(4), 753–764. https://doi.org/10.1007/s10071-020-01461-5

Reddy, R. B., & Sandel, A. A. (2020). Social relationships between chimpanzee sons and mothers endure but change during adolescence and adulthood. *Behavioral Ecology and Sociobiology*, *74*(12), Article 150. https://doi.org/10.1007/s00265-020-02937-7

Regulation 1/2005. *Council Regulation (EC) No 1/2005 of 22 December 2004 on the protection of animals during transport and related operations and amending Directives 64/432/EEC and 93/119/EC and Regulation (EC) No 1255/97.* http://data.europa.eu/eli/reg/2005/1/oj

Reinhardt, V. (1994). Caged rhesus macaques voluntarily work for ordinary food. *Primates*, *35*, 95–98. https://doi.org/10.1007/BF02381490

Remis, M. J. (2002). Food preferences among captive western gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*). *International Journal of Primatology*, *23*(2), 231–249. https://doi.org/10.1023/A:1013837426426

Reynolds, J., McClelland, A., & Furnham, A. (2014). An investigation of cognitive test performance across conditions of silence, background noise and music as a function of neuroticism. *Anxiety, Stress, & Coping*, *27*(4), 410–421.

Reynolds, V. (2005). *The chimpanzees of the Budongo forest: Ecology, behaviour and conservation*. OUP Oxford. https://doi.org/10.1093/acprof:oso/9780198515463.001.0001

Riba, D. (2016). *Mecanismos cognitivos de aprendizaje social en chimpancés (Pan troglodytes): Evaluación experimental a través de múltiples tareas* [Doctoral dissertation, Universitat Rovira i Virgili]. Repositori de la Universitat Rovira i Virgili. http://hdl.handle.net/20.500.11797/TDX2440

Robinson, L. M., Altschul, D., Wallace, E. K., Úbeda, Y., Llorente, M., Machanda, Z., Slocombe, K. E., Leach, M. C., Waran, N. K., & Weiss, A. (2017). Chimpanzees with positive welfare are happier, extraverted, and emotionally stable. *Applied Animal Behaviour Science*, *191*, 90–97. https://doi.org/10.1016/j.applanim.2017.02.008

Robinson, L. M., Coleman, K., Capitanio, J. P., Gottlieb, D. H., Handel, I. G., Adams, M. J., Leach, M. C., Waran, N. K., & Weiss, A. (2018). Rhesus macaque personality, dominance, behavior, and health. *American Journal of Primatology*, *80*(2), Article e22739. https://doi.org/10.1002/ajp.22739

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

Roe, K., McConney, A., & Mansfield, C. F. (2014). The role of zoos in modern society—A comparison of zoos' reported priorities and what visitors believe they should be. *Anthrozoös*, *27*(4), 529–541. https://doi.org/10.2752/089279314X14072268687808

Rolls, E.T. (2007). *Emotion Explained*. Oxford University Press.

Romero, E., Villar, P., Gómez-Fraguela, J. A., & López-Romero, L. (2012). Measuring personality traits with ultra-short scales: A study of the Ten Item Personality Inventory (TIPI) in a Spanish sample. *Personality and Individual Differences*, *53*(3), 289–293. https://doi.org/10.1016/j.paid.2012.03.035

Romero, T., Colmenares, F., & Aureli, F. (2009). Testing the function of reconciliation and third-party affiliation for aggressors in hamadryas baboons (*Papio hamadryas hamadryas*). *American Journal of Primatology*, *71*(1), 60–69. https://doi.org/10.1002/ajp.20619

Rooney, M. B., & Sleeman, J. (1998). Effects of selected behavioral enrichment devices on behavior of Western Lowland Gorillas (*Gorilla gorilla gorilla*). *Journal of Applied Animal Welfare Science*, *1*(4), 339–351. https://doi.org/10.1207/s15327604jaws0104_2

Rosati, A. G., DiNicola, L. M., & Buckholtz, J. W. (2018). Chimpanzee cooperation is fast and independent from self-control. *Psychological Science*, *29*(11), 1832–1845. https://doi.org/10.1177/0956797618800042

Rose, P., & Riley, L. (2019). The use of Qualitative Behavioural Assessment to zoo welfare measurement and animal husbandry change. *Journal of Zoo and Aquarium Research*, *7*(4), 150–161. https://doi.org/10.19227/jzar.v7i4.423

Rose, P. E., Brereton, J. E., Rowden, L. J., de Figueiredo, R. L., & Riley, L. M. (2019). What's new from the zoo? An analysis of ten years of zoo-themed research output. *Palgrave Communications*, *5*(1), 128. https://doi.org/10.1057/s41599-019-0345-3

Rose, P. E., & Riley, L. M. (2021). Conducting behavioural research in the zoo: A guide to ten important methods, concepts and theories. *Journal of Zoological and Botanical Gardens*, *2*(3), 421–444. https://doi.org/10.3390/jzbg203003

Ross, M., Niemann, T., Wark, J., Heintz, M., Horrigan, A., Cronin, K., Shender, M., & Gillespie, K. (2016). Zoomonitor (Version 1) [Mobile application software]. Available from https://zoomonitor.org. In.

Ross, S. R. (2010). How cognitive studies help shape our obligation for the ethical care of chimpanzees In E. V. Lonsdorf, S. R. Ross, T. Matsuzawa, & J. Goodall (Eds.), *The mind of the chimpanzee: Ecological and experimental perspectives*

University of Chicago Press. https://doi.org/10.7208/9780226492810-026

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

Ross, S. R., & Leinwand, J. G. (2020). A review of research in primate sanctuaries. *Biology Letters*, *16*(4), Article 20200033. https://doi.org/10.1098/rsbl.2020.0033

Rothe, J. P. (2017). *The scientific analysis of personality*. Routledge. https://doi.org/10.4324/9781315134772

Routman, E. O., & Khalil, K. (2022). Beyond inspiration: Translating zoo and aquarium experiences into conservation behavior. *41*(5), 398–408. https://doi.org/10.1002/zoo.21716

Rrick, M. R., & Mount, M. K. (1991). The Big Five personality dimensions and job performance: A meta-analysis. *Personnel Psychology*, *44*(1), 1–26. https://doi.org/10.1111/j.1744-6570.1991.tb00688.x

Ruby, S., & Buchanan-Smith, H. M. (2015). The effects of individual cubicle research on the social interactions and individual behavior of brown capuchin monkeys (*Sapajus apella*). *American Journal of Primatology*, *77*(10), 1097–1108. https://doi.org/10.1002/ajp.22444

Ruch, W., Heintz, S., Gander, F., Hofmann, J., Platt, T., & Proyer, R. (2020). The long and winding road: A comprehensive analysis of 50 years of Eysenck instruments for the assessment of personality. *Personality and Individual Differences*, *169*, Article 110070. https://doi.org/10.1016/j.paid.2020.110070

Russell, D. W. (2002). In search of underlying dimensions: The use (and abuse) of factor analysis in Personality and Social Psychology Bulletin. *Personality and social psychology bulletin*, *28*(12), 1629–1646. https://doi.org/10.1177/014616702237645

Russell, J. L., Lyn, H., Schaeffer, J. A., & Hopkins, W. D. (2011). The role of socio-communicative rearing environments in the development of social and physical cognition in apes. *Developmental science*, *14*(6), 1459–1470. https://doi.org/10.1111/j.1467-7687.2011.01090.x

Saggino, A. (2000). The Big Three or the Big Five? A replication study. *Personality and Individual Differences*, *28*(5), 879–886. https://doi.org/10.1016/S0191-8869(99)00146-4

Sainsbury, D. (1986). *Farm animal welfare-cattle, pigs and poultry*. Collins.

Sambrook, T., & Buchanan-Smith, H. (1997). Control and complexity in novel object enrichment. *Animal Welfare*, *6*(3), 207–216. https://doi.org/10.1017/S0962728600019801

Sampaio, M. B., Schiel, N., & Souto, A. d. S. (2020). From exploitation to conservation: a historical analysis of zoos and their functions in human societies. *Ethnobiology and Conservation*, *9*. https://doi.org/10.15451/ec2020-01-9.02-1-32

Samuni, L., Crockford, C., & Wittig, R. M. (2021). Group-level cooperation in chimpanzees is shaped by strong social ties. *Nature Communications*, *12*(1), 539. https://doi.org/10.1038/s41467-020-20709-9

Samuni, L., Lemieux, D., Lamb, A., Galdino, D., & Surbeck, M. (2022). Tool use behavior in three wild bonobo communities at Kokolopori. *American Journal of Primatology*, *84*(1), Article e23342. https://doi.org/10.1002/ajp.23342

Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R. M., & Crockford, C. (2018). Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1888), Article 20181643. https://doi.org/10.1098/rspb.2018.1643

Samuni, L., Tkaczynski, P., Deschner, T., Löhrrich, T., Wittig, R. M., & Crockford, C. (2020). Maternal effects on offspring growth indicate post-weaning juvenile dependence in chimpanzees (*Pan troglodytes verus*). *Frontiers in Zoology*, *17*(1). https://doi.org/10.1186/s12983-019-0343-8

Sanchez-Roige, S., Gray, J. C., MacKillop, J., Chen, C. H., & Palmer, A. A. (2018). The genetics of human personality. *Genes, Brain and Behavior*, *17*(3), Article e12439. https://doi.org/10.1111/gbb.12439

Sánchez, M. M., Ladd, C. O., & Plotsky, P. M. (2001). Early adverse experience as a developmental risk factor for later psychopathology: evidence from rodent and primate models. *Dev Psychopathol*, *13*(3), 419–449. https://doi.org/10.1017/s0954579401003029

Sandvik, A. M., Hansen, A. L., Hystad, S. W., Johnsen, B. H., & Bartone, P. T. (2015). Psychopathy, anxiety, and resiliency – Psychological hardiness as a mediator of the psychopathy–anxiety relationship in a prison setting. *Personality and Individual Differences*, *72*, 30–34. https://doi.org/10.1016/j.paid.2014.08.009

Schaefer, S., & Steklis, H. (2014). Personality and subjective well-being in captive male western lowland gorillas living in bachelor groups. *American Journal of Primatology*, *76*(9), 879–889. https://doi.org/10.1002/ajp.22275

Schapiro, S. J., & Lambeth, S. P. (2007). Control, choice, and assessments of the value of behavioral management to nonhuman primates in captivity. *Journal of Applied Animal Welfare Science*, *10*(1), 39–47. https://doi.org/10.1080/10888700701277345

Schino, G., Rosati, L., Geminiani, S., & Aureli, F. (2007). Post-conflict anxiety in japanese macaques (*Macaca fuscata*): Aggressor's and victim's perspectives. *Ethology*, *113*(11), 1081–1088. https://doi.org/10.1111/j.1439-0310.2007.01407.x

Schmelz, M., Grueneisen, S., Kabalak, A., Jost, J., & Tomasello, M. (2017). Chimpanzees return favors at a personal cost. *Proceedings of the National Academy of Sciences*, *114*(28), 7462–7467. https://doi.org/10.1073/pnas.1700351114

Schmitt, V. (2018). Implementing new portable touchscreen-setups to enhance cognitive research and enrich zoo-housed animals. *bioRxiv*, Article 316042. https://doi.org/10.1101/316042

Schmitt, W. A., & Newman, J. P. (1999). Are all psychopathic individuals low-anxious? *Journal of Abnormal Psychology*, *108*(2), 353–358. https://doi.org/10.1037/0021-843X.108.2.353

Schöning, C., Ellis, D., Fowler, A., & Sommer, V. (2007). Army ant prey availability and consumption by chimpanzees (*Pan troglodytes vellerosus*) at Gashaka (Nigeria). *Journal of Zoology*, *271*(2), 125–133. https://doi.org/10.1111/j.1469-7998.2006.00177.x

Schubiger, M. N., Wüstholz, F. L., Wunder, A., & Burkart, J. M. (2015). High emotional reactivity toward an experimenter affects participation, but not performance, in cognitive tests with common marmosets (*Callithrix jacchus*). *Animal cognition*, *18*(3), 701–712. https://doi.org/10.1007/s10071-015-0837-5

Schwartz, B. L., & Beran, M. J. (2022). *Primate Cognitive Studies*. Cambridge University Press. https://books.google.es/books?id=WNd-EAAAQBAJ

Sellers, J. G., Mehl, M. R., & Josephs, R. A. (2007). Hormones and personality: Testosterone as a marker of individual differences. *Journal of Research in Personality*, *41*(1), 126–138. https://doi.org/10.1016/j.jrp.2006.02.004

Sha, J., Han, S., Marlena, D., & Kee, J. (2012). Effects of single-use and group-use enrichment on stereotypy and intragroup aggressive and affiliative behaviors of a social group of squirrel monkeys (*Saimiri sciureus*) at the Singapore Zoo. *Journal of Applied Animal Welfare Science*, *15*(4), 358–371. https://doi.org/10.1080/10888705.2012.709148

Sherwen, S. L., Hemsworth, L. M., Beausoleil, N. J., Embury, A., & Mellor, D. J. (2018). An animal welfare risk assessment process for zoos. *Animals*, *8*(8). https://doi.org/10.3390/ani8080130

Shigehisa, P. M., Shigehisa, T., & Symons, J. R. (1973). Effects of intensity of auditory stimulation of photopic visual sensitivity in relation to personality. *Japanese Psychological Research*, *15*(4), 164–172. https://doi.org/10.1111/j.2044-8295.1973.tb01344.x

Shrout, P. E., & Fleiss, J. L. (1979). Intraclass correlations: uses in assessing rater reliability. *Psychological Bulletin*, *86*(2), 420–428. https://doi.org/10.1037/0033-2909.86.2.420

Siegford, J. M. (2013). Multidisciplinary approaches and assessment techniques to better understand and enhance zoo nonhuman animal welfare. *Journal of Applied Animal Welfare Science*, *16*(4), 300–318. https://doi.org/10.1080/10888705.2013.827914

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *The Quarterly Review of Biology*, *79*(3), 241–277. https://doi.org/10.1086/422893

Sih, A., & Giudice, M. (2012). Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *367*(1603), 2762–2772. https://doi.org/10.1098/rstb.2012.0216

Silk, J. (2002). Using the'F'-word in primatology. *Behaviour*, *139*(2), 421–446. https://doi.org/10.1163/156853902760102735

Singmann, H., & Kellen, D. (2019). An introduction to mixed models for experimental psychology. In D. H. Spieler & E. Schumacher (Eds.), *New methods in cognitive psychology* (pp. 4–31). Routledge.

Šlipogor, V., Burkart, J. M., & Martin, J. S. (2020). Personality method validation in common marmosets (Callithrix jacchus): Getting the best of both worlds. *134*(1), 52–70. https://doi.org/10.1037/com0000188

Šlipogor, V., Graf, C., Massen, J. J. M., & Bugnyar, T. (2022). Personality and social environment predict cognitive performance in common marmosets (*Callithrix jacchus*). *Scientific Reports*, *12*(1), Article 6702. https://doi.org/10.1038/s41598-022-10296-8

Šlipogor, V., Massen, J. J., Schiel, N., Souto, A., & Bugnyar, T. (2021). Temporal consistency and ecological validity of personality structure in common marmosets (*Callithrix jacchus*): A unifying field and laboratory approach. *American Journal of Primatology*, *83*(2), e23229.

Slocombe, K. E., Lahiff, N. J., Wilke, C., & Townsend, S. W. (2022). Chimpanzee vocal communication: what we know from the wild. *Current Opinion in Behavioral Sciences*, *46*, Article 101171. https://doi.org/10.1016/j.cobeha.2022.101171

Slocombe, K. E., & Zuberbühler, K. (2006). Food-associated calls in chimpanzees: responses to food types or food preferences? *Animal Behaviour*, *72*(5), 989–999. https://doi.org/10.1016/j.anbehav.2006.01.030

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology*, *19*(2), 448–455. https://doi.org/10.1093/beheco/arm144

Smith, G.E, Bastos, A.M., Chodorow, M., Taylor, A.H., & Pepperberg I.M. (2022). Contrafreeloading in kea (*Nestor notabilis*) in comparison to Grey parrots (*Psittacus erithacus*). *Scientific Reports*, *12*, Article 17415. https://doi.org/10.1038/s41598-022-21370-6

Soliemanifar, O., Soleymanifar, A., & Afrisham, R. (2018). Relationship between personality and biological reactivity to stress: A review. *Psychiatry Investig*, *15*(12), 1100–1114. https://doi.org/10.30773/pi.2018.10.14.2

Speiran, S. I., Jeyaraj-Powell, T., Kauffman, L., & Rodrigues, M. A. (2023). Rescue, rehabilitation, and reintroduction. In T. McKinney, S. Waters, & M. A. Rodrigues (Eds.), *Primates in Anthropogenic Landscapes: Exploring Primate Behavioural Flexibility Across Human Contexts* (pp. 267–287). Springer International Publishing. https://doi.org/10.1007/978-3-031-11736-7_15

Spencer-Booth, Y., & Hinde, R. A. (1969). Tests of behavioural characteristics for rhesus monkeys. *Behaviour*, *33*(3/4), 179–211. http://www.jstor.org/stable/4533264

Špinka, M., & Wemelsfelder, F. (2011). Environmental challenge and animal agency. In M. C. Appleby, J. A. Mench, I. A. S. Olsson, & B. O. Hughes (Eds.), *Animal Welfare* (pp. 27–44). CABI. https://doi.org/10.1079/9781845936594.0027

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

Stroup, W. W. (2016). *Generalized Linear Mixed Models: Modern Concepts, Methods and Applications* (1st ed.). CRC Press. https://doi.org/10.1201/b13151

Suchak, M., Eppley, T. M., Campbell, M. W., Feldman, R. A., Quarles, L. F., & de Waal, F. B. M. (2016). How chimpanzees cooperate in a competitive world. *Proceedings of the National Academy of Sciences*, *113*(36), 10215–10220. https://doi.org/10.1073/pnas.1611826113

Suntsova, M. V., & Buzdin, A. A. (2020). Differences between human and chimpanzee genomes and their implications in gene expression, protein functions and biochemical properties of the two species. *BMC Genomics*, *21*(7), Article 535. https://doi.org/10.1186/s12864-020-06962-8

Suomi, S. J., Chaffin, A. C., & Higley, J. D. (2011). Reactivity and behavioral inhibition as personality traits in nonhuman primates. In A. Weiss, J. E. King, & L. Murray (Eds.), *Personality and temperament in nonhuman primates* (pp. 285–311). Springer New York. https://doi.org/10.1007/978-1-4614-0176-6_11

Surbeck, M., Girard-Buttoz, C., Boesch, C., Crockford, C., Fruth, B., Hohmann, G., Langergraber, K. E., Zuberbühler, K., Wittig, R. M., & Mundry, R. (2017). Sex-specific association patterns in bonobos and chimpanzees reflect species differences in cooperation. *Royal Society Open Science*, *4*(5), Article 161081. https://doi.org/10.1098/rsos.161081

Swaisgood, R. R., & Shepherdson, D. J. (2005). Scientific approaches to enrichment and stereotypies in zoo animals: What's been done and where should we go next? *Zoo Biology*, *24*(6), 499–518. https://doi.org/10.1002/zoo.20066

Symington, M. M. (1990). Fission-fusion social organization in *Ateles* and *Pan*. *International Journal of Primatology*, *11*(1), 47–61. https://doi.org/10.1007/BF02193695

Szymura, B., & Nęcka, E. (1998). Visual selective attention and personality: An experimental verification of three models of extra version. *Personality and Individual Differences*, *24*(5), 713–729. https://doi.org/10.1016/S0191-8869(97)00198-0

Szymura, B., Śmigasiewicz, K., & Corr, P. (2007). Psychoticism and attentional flexibility. *Personality and Individual Differences*, *43*(8), 2033–2046. https://doi.org/10.1016/j.paid.2007.06.023

Szymura, B., & Wodniecka, Z. (2003). What really bothers neurotics? In search for factors impairing attentional performance. *Personality and Individual Differences*, *34*(1), 109–126. https://doi.org/10.1016/S0191-8869(02)00034-X

Talbot, C. F., Reamer, L. A., Lambeth, S. P., Schapiro, S. J., & Brosnan, S. F. (2023). Meeting cognitive, behavioral, and social needs of primates in captivity. In L. M. Robinson &

A. Weiss (Eds.), *Nonhuman primate welfare: From history, science, and ethics to practice* (pp. 267–305). Springer International Publishing. https://doi.org/10.1007/978-3-030-82708-3_12

Tarou, L. R., Kuhar, C. W., Adcock, D., Bloomsmith, M., & Maple, T. (2004). Computer-assisted enrichment for zoo-housed orangutans (*Pongo pygmaeus*). *Animal Welfare*, *13*(4), 445–453. https://doi.org/10.1017/S0962728600028712

Taylor, R., White, B., Ferguson, S., & Binienda, Z. (1994). The use of foraging devices for environmental enrichment of individually housed rhesus monkeys in a laboratory colony. *Contemporary Topics in Llaboratory Animal Science*, *33*(6), 71–73.

Thornton, A., & Lukas, D. (2012). Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *367*(1603), 2773–2783. https://doi.org/10.1098/rstb.2012.0214

Toates, F. M. (1986). *Motivational systems*. Cambridge University Press.

Tomasello, M., & Call, J. (2004). The role of humans in the cognitive development of apes revisited. *Animal cognition*, *7*(4), 213–215. https://doi.org/10.1007/s10071-004-0227-x

Torigoe, T. (1985). Comparison of object manipulation among 74 species of non-human primates. *Primates*, *26*(2), 182–194. https://doi.org/10.1007/BF02382017

Tribe, A., & Booth, R. (2003). Assessing the role of zoos in wildlife conservation. *Human dimensions of wildlife*, *8*(1), 65–74. https://doi.org/10.1080/10871200390180163

Turakulov, R., Jorm, A. F., Jacomb, P., Tan, X., & Easteal, S. (2004). Association of dopamine-β-hydroxylase and androgen receptor gene polymorphisms with Eysenck's P and other personality traits. *Personality and Individual Differences*, *37*(1), 191–202. https://doi.org/10.1016/j.paid.2003.08.011

Turner, C. H., Davenport Jr, R. K., & Rogers, C. M. (1969). The effect of early deprivation on the social behavior of adolescent chimpanzees. *American Journal of Psychiatry*, *125*(11), 1531–1536. https://doi.org/10.1176/ajp.125.11.1531

Úbeda, Y., Fatjó, J., Rostán, C., Crailsheim, D., Gomara, A., Almunia, J., & Llorente, M. (2021). A preliminary investigation on the evaluation of psychopathologies in a group of ex-pet and ex-performer chimpanzees (*Pan troglodytes*): A rating approach based on the Diagnostic and Statistical Manual of Mental Disorders (DSM). *Journal of Veterinary Behavior*, *41*, 52–64. https://doi.org/10.1016/j.jveb.2020.08.006

Úbeda, Y., & Llorente, M. (2015). Personality in sanctuary-housed chimpanzees: A comparative approach of psychobiological and penta-factorial human models. *Evolutionary Psychology*, *13*(1), 182–196. https://doi.org/10.1177/147470491501300111

Úbeda, Y., Ortín, S., St Leger, J., Llorente, M., & Almunia, J. (2019). Personality in captive killer whales (*Orcinus orca*): A rating approach based on the five-factor model. *Journal of Comparative Psychology*, *133*(2), 252–261. https://doi.org/10.1037/com0000146

Uher, J., & Asendorpf, J. B. (2008). Personality assessment in the Great Apes: Comparing ecologically valid behavior measures, behavior ratings, and adjective ratings. *Journal of Research in Personality*, *42*(4), 821–838. https://doi.org/10.1016/j.jrp.2007.10.004

Uher, J., & Visalberghi, E. (2016). Observations versus assessments of personality: A five-method multi-species study reveals numerous biases in ratings and methodological limitations of standardised assessments. *Journal of Research in Personality*, *61*, 61–79. https://doi.org/10.1016/j.jrp.2016.02.003

van der Marel, A., O'Connell, C. L., Prasher, S., Carminito, C., Francis, X., & Hobson, E. A. (2022). A comparison of low-cost behavioral observation software applications for handheld computers and recommendations for use. *Ethology*, *128*(3), 275–284. https://doi.org/10.1111/eth.13251

van Leeuwen, E. J. C., Mulenga, I., Bodamer, M., & Cronin, K. (2016). Chimpanzees' responses to the dead body of a 9-year-old group member. *American Journal of Primatology*, *78*(9), 914–922. https://doi.org/10.1002/ajp.22560

van Oers, K., & Naguib, M. (2013). Avian personality. In C. Carere & D. Maestripieri (Eds.), *Animal personalities: Behavior, physiology, and evolution* (pp. 66–95). University of Chicago Press. https://doi.org/10.7208/chicago/9780226922065.003.0004

Vasconcellos, A.D., Adania, C.H., & Ades, C. (2012). Contrafreeloading in maned wolves: Implications for their management and welfare. *Applied Animal Behaviour Science*, *140*(Suppl 1), 85–91. https://doi.org/10.1016/j.applanim.2012.04.012

Vazire, S., Gosling, S. D., Dickey, A. S., & Schapiro, S. J. (2007). Measuring personality in nonhuman animals. In R. W. Robins, R. C. Fraley, & R. F. Krueger (Eds.), *Handbook of research methods in personality psychology* (pp. 190–206). Guilford Press.

Veasey, J. S. (2017). In pursuit of peak animal welfare; the need to prioritize the meaningful over the measurable. *Zoo Biology*, *36*(6), 413–425. https://doi.org/10.1002/zoo.21390

Veasey, J. S., Waran, N. K., & Young, R. J. (1996). On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator. *Animal Welfare*, *5*(1), 13–24. https://doi.org/10.1017/S0962728600018297

Verspeek, J., Behringer, V., Laméris, D. W., Murtagh, R., Salas, M., Staes, N., Deschner, T., & Stevens, J. M. G. (2021). Time-lag of urinary and salivary cortisol response after a psychological stressor in bonobos *(Pan paniscus*). *Scientific Reports*, *11*(1), Article 7905. https://doi.org/10.1038/s41598-021-87163-5

Verspeek, J., & Staes, N. (2019). Bonobo personality predicts friendship. *Scientific Reports*, *9*(1), 19245, Article 19245. https://doi.org/10.1038/s41598-019-55884-3

Voinov, P. V., Call, J., Knoblich, G., Oshkina, M., & Allritz, M. (2020). Chimpanzee coordination and potential communication in a two-touchscreen turn-taking game. *Scientific Reports*, *10*(1), Article 3400. https://doi.org/10.1038/s41598-020-60307-9

Völter, C. J., & Call, J. (2014). Younger apes and human children plan their moves in a maze task. *Cognition*, *130*(2), 186–203. https://doi.org/10.1016/j.cognition.2013.10.007

Völter, C. J., Sentís, I., & Call, J. (2016). Great apes and children infer causal relations from patterns of variation and covariation. *Cognition*, *155*, 30–43. https://doi.org/10.1016/j.cognition.2016.06.009

von Stumm, S., Hell, B., & Chamorro-Premuzic, T. (2011). The hungry mind: Intellectual curiosity is the third pillar of academic performance. *Perspectives on Psychological science*, *6*(6), 574–588. https://doi.org/10.1177/1745691611421204

Vonk, J., & Povinelli, D. (2011). Individual differences in long-term cognitive testing in a group of captive chimpanzees. *International Journal of Comparative Psychology*, *24*(1), 137–167. https://doi.org/10.46867/IJCP.2011.24.01.01

Wagner, K. E., Hopper, L. M., & Ross, S. R. (2016). Asymmetries in the production of self-directed behavior by chimpanzees and gorillas during a computerized cognitive test. *Animal cognition*, *19*(2), 343–350. https://doi.org/10.1007/s10071-015-0937-2

Walsh, S., Bramblett, C. A., & Alford, P. L. (1982). A vocabulary of abnormal behaviors in restrictively reared chimpanzees. *American Journal of Primatology*, *3*(1-4), 315–319. https://doi.org/10.1002/ajp.1350030131

Ward, S. J., Sherwen, S., & Clark, F. E. (2018). Advances in applied zoo animal welfare science. *Journal of Applied Animal Welfare Science*, *21*(sup1), 23–33. https://doi.org/10.1080/10888705.2018.1513842

Wark, J., Cronin, K., Niemann, T., Shender, M., Horrigan, A., Kao, A., & Ross, M. (2019). Monitoring the behavior and habitat use of animals to enhance welfare using the

ZooMonitor app. *Animal Behavior and Cognition*, *6*(3), 158–163. https://doi.org/10.26451/abc.06.03.01.2019

Warneken, F., Hare, B., Melis, A. P., Hanus, D., & Tomasello, M. (2007). Spontaneous altruism by chimpanzees and young children. *PLOS Biology*, *5*(7), Article e184. https://doi.org/10.1371/journal.pbio.0050184

Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science*, *311*(5765), 1301–1303. https://doi.org/10.1126/science.1121448

Warren, M. A. (1997). *Moral status: Obligations to persons and other living things*. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198250401.001.0001

Waters, R. M., Bowers, B. B., & Burghardt, G. M. (2017). Personality and individuality in reptile behavior. In J. Vonk, A. Weiss, & S. A. Kuczaj (Eds.), *Personality in nonhuman animals* (pp. 153–184). Springer International Publishing. https://doi.org/10.1007/978-3-319-59300-5_8

Webb, C. E., Romero, T., Franks, B., & de Waal, F. B. M. (2017). Long-term consistency in chimpanzee consolation behaviour reflects empathetic personalities. *Nature Communications*, *8*(1), Article 292. https://doi.org/10.1038/s41467-017-00360-7

Weinstein, T. A., & Capitanio, J. P. (2012). Longitudinal stability of friendships in rhesus monkeys (*Macaca mulatta*): individual- and relationship-level effects. *Journal of Comparative Psychology*, *126*(1), 97–108. https://doi.org/10.1037/a0025607

Weinstein, T. A. R., Capitanio, J. P., & Gosling, S. D. (2008). Personality in animals. In O. P. John, R. W. Robins, & L. A. Pervin (Eds.), *Handbook of personality: Theory and research* (3rd ed., pp. 328–348). The Guilford Press.

Weiss, A. (2017a). Exploring factor space (and other adventures) with the Hominoid Personality Questionnaire. In J. Vonk, A. Weiss, & S. A. Kuczaj (Eds.), *Personality in* *nonhuman animals* (pp. 19–38). Springer. https://doi.org/10.1007/978-3-319-59300-5_2

Weiss, A. (2017b). A human model for primate personality. *Proceedings of the Royal Society B*, *284*(1864), Article 20171129. https://doi.org/10.1098/rspb.2017.1129

Weiss, A. (2018). Personality traits: A view from the animal kingdom. *Journal of Personality*, *86*(1), 12–22. https://doi.org/10.1111/jopy.12310

Weiss, A. (2022). Dominance in human (*Homo sapiens*) personality space and in hominoid phylogeny. *Journal of Comparative Psychology*, *136*(4), 236–254. https://doi.org/10.1037/com0000322

Weiss, A., & Adams, M. J. (2013). Differential behavioral ecology. The structure, life history and evolution of primate personality. In C. M. Carere, Dario (Ed.), *Animal personalities: behavior, physiology and evolution* (pp. 96–123). The University of Chicago Press. https://doi.org/10.7208/chicago/9780226922065.003.0005

Weiss, A., & Costa, P. T., Jr. (2014). Re: "Personality and all-cause mortality: Individual-participant meta-analysis of 3,947 deaths in 76,150 adults". *American Journal of Epidemiology*, *179*(6), 791–792. https://doi.org/10.1093/aje/kwt300

Weiss, A., Feldblum, J. T., Altschul, D. M., Collins, D. A., Kamenya, S., Mjungu, D., Foerster, S., Gilby, I. C., Wilson, M. L., & Pusey, A. E. (2023). Personality traits, rank attainment, and siring success throughout the lives of male chimpanzees of Gombe National Park. *PeerJ*, *11*, Article e15083. https://doi.org/10.7717/peerj.15083

Weiss, A., Gartner, M. C., Gold, K. C., & Stoinski, T. S. (2013). Extraversion predicts longer survival in gorillas: an 18-year longitudinal study. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1752), Article 20122231. https://doi.org/10.1098/rspb.2012.2231

Weiss, A., Inoue-Murayama, M., King, J. E., Adams, M., & Matsuzawa, T. (2012). All too human? Chimpanzee and orang-utan personalities are not anthropomorphic projections. *Animal Behaviour*, *83*(6), 1355–1365. https://doi.org/10.1016/j.anbehav.2012.02.024

Weiss, A., Inoue-Murayama, M., Hong, K. W., Inoue, E., Udono, T., Ochiai, T., Matsuzawa, T., Hirata, S., & King, J. E. (2009). Assessing chimpanzee personality and subjective well-being in Japan. *American Journal of Primatology*, *71*(4), 283–292. https://doi.org/10.1002/ajp.20649

Weiss, A., & King, J. E. (2015). Great ape origins of personality maturation and sex differences: a study of orangutans and chimpanzees. *Journal of Personality and Social Psychology*, *108*(4), 648–664. https://doi.org/10.1037/pspp0000022

Weiss, A., King, J. E., & Hopkins, W. D. (2007). A cross-setting study of chimpanzee (*Pan troglodytes*) personality structure and development: zoological parks and Yerkes National Primate Research Center. *American Journal of Primatology*, *69*(11), 1264–1277. https://doi.org/10.1002/ajp.20428

Weiss, A., King, J. E., & Murray, L. (2011). *Personality and temperament in nonhuman primates*. Springer. https://doi.org/10.1007/978-1-4614-0176-6

Weiss, A., Wilson, M. L., Collins, A. D., Mjungu, D., Kamenya, S., Foerster, S., & Pusey, A. E. (2017). Personality in the chimpanzees of Gombe National Park. *Scientific Data*, *4*, Article 170146. https://doi.org/10.1038/sdata.2017.146

Whitehouse, J., Micheletta, J., Powell, L. E., Bordier, C., & Waller, B. M. (2013). The impact of cognitive testing on the welfare of group housed primates. *PLOS ONE*, *8*(11), Article e78308. https://doi.org/10.1371/journal.pone.0078308

Whiten, A., Harrison, R. A., McGuigan, N., Vale, G. L., & Watson, S. K. (2022). Collective knowledge and the dynamics of culture in chimpanzees. *Philosophical Transactions of* *the Royal Society B: Biological Sciences*, *377*(1843), Article 20200321. https://doi.org/10.1098/rstb.2020.0321

Whitham, J. C., Hall, K., Lauderdale, L. K., Bryant, J. L., & Miller, L. J. (2023). Integrating reference intervals into chimpanzee welfare research. *Animals*, *13*(4), Article 639. https://doi.org/10.3390/ani13040639

Whitham, J. C., & Wielebnowski, N. (2013). New directions for zoo animal welfare science. *Applied Animal Behaviour Science*, *147*(3), 247–260. https://doi.org/10.1016/j.applanim.2013.02.004

Wilke, C., Lahiff, N. J., & Sabbi, K. H. (2022). Declarative referential gesturing in a wild chimpanzee (*Pan troglodytes*). *Proceedings of the National Academy of Sciences of the United States of America*, *119*(47), Article e2206486119. https://doi.org/10.1073/pnas.2206486119

Wilson, D. (1998). Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *353*(1366), 199–205. https://doi.org/10.1098/rstb.1998.0202

Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, *9*(11), 442–446. https://doi.org/10.1016/0169-5347(94)90134-1

Wilson, M. L., Hauser, M. D., & Wrangham, R. W. (2001). Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Animal Behaviour*, *61*(6), 1203–1216. https://doi.org/10.1006/anbe.2000.1706

Wilson, V. A. D., Inoue-Murayama, M., & Weiss, A. (2018). A comparison of personality in the common and Bolivian squirrel monkey (*Saimiri sciureus* and *Saimiri boliviensis*). *Journal of Comparative Psychology*, *132*, 24–39. https://doi.org/10.1037/com0000093

Witt, L. A., Burke, L. A., Barrick, M. A., & Mount, M. K. (2002). The interactive effects of conscientiousness and agreeableness on job performance. *Journal of Applied Psychology*, *87*(1), 164–169. https://doi.org/10.1037/0021-9010.87.1.164

Woerle, S. (2020). *Effects of olfactory enrichment on the stereotypic behaviors of owl monkeys* (*Aotus nancymaae*) [Doctoral dissertation, Florida Southern College]. Florida Southern College Repository. http://hdl.handle.net/11416/522

Wolfensohn, S., Shotton, J., Bowley, H., Davies, S., Thompson, S., & Justice, W. S. (2018). Assessment of welfare in zoo animals: Towards optimum quality of life. *Animals*, *8*(7), Article 110. https://doi.org/10.3390/ani8070110

World Association of Zoos and Aquariums. (2023). *WAZA Code of ethics*. https://www.waza.org/wp-content/uploads/2023/10/FINAL_WAZA-Code-of-Ethics.pdf

Wowk, Z. M., & Behie, A. M. (2023). The influence of olfactory enrichment on the behavior of two captive New World primates: Black-capped capuchin (*Sapajus apella*) and common marmoset (*Callithrix jacchus*). *Zoo Biology*, *42*(2), 231–242. https://doi.org/10.1002/zoo.21731

Yamamoto, S., Humle, T., & Tanaka, M. (2013). Basis for cumulative cultural evolution in chimpanzees: Social learning of a more efficient tool-use technique. *PLOS ONE*, *8*(1), Article e55768. https://doi.org/10.1371/journal.pone.0055768

Yamanashi, Y., & Hayashi, M. (2011). Assessing the effects of cognitive experiments on the welfare of captive chimpanzees (*Pan troglodytes*) by direct comparison of activity budget between wild and captive chimpanzees. *American Journal of Primatology*, *73*(12), 1231–1238. https://doi.org/10.1002/ajp.20995

Yamanashi, Y., Matsunaga, M., Shimada, K., Kado, R., & Tanaka, M. (2016). Introducing tool-based feeders to zoo-housed chimpanzees as a cognitive challenge: Spontaneous acquisition of new types of tool use and effects on behaviours and use of space. *Journal of Zoo and Aquarium Research*, *4*(3), 147–155. https://doi.org/10.19227/jzar.v4i3.235

Yamanashi, Y., & Matsuzawa, T. (2010). Emotional consequences when chimpanzees (*Pan troglodytes*) face challenges: individual differences in self-directed behaviours during cognitive tasks. *Animal Welfare*, *19*(1), 25–30. https://doi.org/10.1017/S0962728600001123

Yerkes, R. M., & Yerkes, A. W. (1936). Nature and conditions of avoidance (fear) response in chimpanzee. *Journal of Comparative Psychology*, *21*(1), 53–66. https://doi.org/10.1037/h0058825

Young, R. (2003). *Environmental enrichment for captive animals*. Blackwell Science. https://doi.org/10.1002/9780470751046

Young, R. J., de Azevedo, C. S., & Cipreste, C. F. (2020). Environmental enrichment. In V. A. Melfi, N. R. Dorey, & S. J. Ward (Eds.), *Zoo animal learning and training* (pp. 101–118). Wiley-Blackwell. https://doi.org/10.1002/9781118968543.ch6

Zaragoza, F., Ibañez, M., Mas, B., De Laiglesia Gil, S., & Anzola Delgado, B. (2011). Influence of environmental enrichment in captive chimpanzees (*Pan troglodytes spp.*) and gorillas (*Gorilla gorilla gorilla*): Behavior and faecal cortisol levels. *Revista Cientifica de la Facultad de Ciencias Veterinarias de la Universidad del Zulia*, *21*(5), 447–456. https://www.redalyc.org/articulo.oa?id=95919362011

Zhang, B., Li, Y. M., Li, J., Luo, J., Ye, Y., Yin, L., Chen, Z., Soto, C. J., & John, O. P. (2022). The Big Five Inventory–2 in China: A comprehensive psychometric evaluation in four diverse samples. *Assessment*, *29*(6), 1262–1284. https://doi.org/10.1177/10731911211008245

Zuckerman, M. (1993). Personality from top (traits) to bottom (genetics) with stops at each level between. In J. Hettema & I.J. Deary (Eds.), *Foundations of Personality* (Vol. 72, pp. 73–100). Springer. https://doi.org/10.1007/978-94-011-1660-2_7