

CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Tropical AgriSciences



**Analysis of the Cognitive Abilities of Captive Sumatran orangutans
(*Pongo abelii*) Regarding the Use of Puzzle Feeders**

MASTER'S THESIS

Prague 2023

Author: Adulusi Adesewa

Supervisor: doc. Francisco Ceacero, PhD

Consultant: Mgr. Markéta Lavická

Declaration

I hereby declare that I have done this thesis entitled “Analysis of the Cognitive Abilities of Captive Sumatran orangutans (*Pongo abelii*) Regarding the Use of Puzzle Feeders” independently, all texts in this thesis are original, and all the sources have been quoted and acknowledged by means of complete references and according to Citation rules of the FTA.

In Prague date

17.04.2023

Adesewa Adelusi

Acknowledgements

My profound gratitude goes to my supervisor, doc. Francisco Ceacero (Paco as everyone fondly calls him) for his immense help and guidance during the period of this study. Not forgetting the staffs at the Prague Zoo, Mgr. Markéta Lavická and Ing. Michal Papež for being so patient, welcoming and not hesitating to render their kind assistance.

I would also like to acknowledge my colleagues, Divyadharshini Shanthakrishnan and Joshi Kundankumar for their moral support in our quest to complete this phase.

Saving the best for the last, I would not have had this privilege without God, my amazing parents (Prince Alade Adelusi and Mrs. Bolanle Adelusi), my Uncle Abbeykoko and his beautiful family and my annoying brother (Segun Adelusi). Finally, I am forever grateful in a million ways to Noheem Tijani (a.k.a. My Meme) for being indescribable and extremely supportive and to me of course, for not giving up.

Abstract

This research examined the captive Sumatran orangutans' cognitive ability. The study was conducted at the Indonesian Jungle – Orangutans' Enclosure at Prague Zoo. The study included three Sumatran orangutans, two females (older and younger) and one male, aged 9-33 years. The purpose of the puzzle feeder was to provide enrichment and measure the orangutans' puzzle-solving abilities. Two cameras were used to observe the orangutans during the trial, which lasted six months. The length of behaviours, preferred handling method, and frequency of success were all recorded. Kolmogorov-Smirnov, Shapiro-Wilk, Mann-Whitney U, and Kruskal-Wallis tests were the statistical procedures employed to analyse the data. According to the study's findings, each animal tested exhibited a unique style of exploratory behaviour. Diru was consistently the first animal to explore and manipulate the puzzle feeder, while Mawar was always the last. The animals also displayed differences in latency time to explore the fourth pattern of the puzzle feeder compared to the first pattern, with Diru taking longer to explore the fourth pattern, indicating a sign of diminished interest. The study also found that there may be individual differences in how animals respond to changes in their environment, with Diru and Pagi displaying less explorative behaviour during the fourth pattern than the first one. According to the study, social learning behaviour may not be influenced by the type of puzzle feeder design, and social cues did not impact the animals' performance on the task. The fact that Diru, the most successful animal at extracting rewards, exhibited the highest level of social learning behaviour, however, shows that social learning may have been a key factor in developing new skills.

Keywords: Cognitive abilities, Sumatran orangutans, Puzzle-feeder, Enrichment, Puzzle-solving abilities, Social learning behaviour, Rewards, Tools.

Table of Contents

1. Introduction	1
1.1. Background to the study.....	1
1.2. Aims and objectives	3
2. Literature Review	4
2.1. Evolution of Intelligence	4
2.2. Development of Intelligence	5
2.3. The role of experience.....	7
2.4. Primate Cognition	10
2.4.1. Social cognition and apes.....	11
2.4.2. Physical cognition of apes.....	12
2.5. Orangutans as a model species for intelligence testing.....	14
2.6. The study species: Sumatran Orangutan (<i>Pongo abelii</i>).....	15
2.6.1. Phylogeny.....	15
2.6.2. Ecology, characteristic features, and social structure	16
2.6.3. Orangutans in captivity	19
2.7. Environmental enrichment	19
3. Methodology.....	21
3.1. Study facilities	21
3.2. The Indonesian Jungle – Orangutans’ Enclosure	22
3.3. Subjects	23
3.4. Enrichment procedure	27
3.5. Collection of data.....	32
3.6. Data Extraction	34
3.7. Statistical analyses	35
4. Results	38
4.1. Behaviour and puzzle-solving	38
4.2. Temporal changes in techniques used.....	39
5. Discussion.....	41
5.1. Behaviour and puzzle-solving	41

5.2.	Temporal changes in techniques used.....	43
6.	Conclusions	45
6.1.	Recommendations.....	46
7.	References	47
8.	Appendix	66
8.1.	Appendix I – Images of test subjects and test tool	66

List of tables

Table 1: Behavioural Ethogram	32
Table 2: Different handling techniques used during manipulation.....	34
Table 3: Normality tests for the studied variables	36

List of figures

Figure 1: Map of Prague Zoo.....	21
Figure 2: Puzzle design and time taken to solve per day.....	39
Figure 3: Techniques used to extract rewards.....	40

List of Plates

Plate 1: Puzzle feeder in the enclosure with demarcated panelled glass window for public viewing	22
Plate 2: Outer view of the Orangutans' enclosure.	23
Plate 3: Mawar (the oldest female in the group), date of birth - 16.3.1989 and Kawi (infant male), date of birth -17.11.2020. Mother: Mawar, father: Pagy.....	24
Plate 4: Diri (the youngest female in the group), date of birth - 3.2.2013. Mother: Mawar, father: Padang, Padang is absent at the facility.	25
Plate 5: Pagy (only adult male in the group), date of birth - 23.7.2001. Parents are not known.	26
Plate 6: First puzzle setting. An easy setting with small rewards to motivate the orangutans.	28
Plate 7: Second Puzzle setting, arrows are indicating movable elements while other elements are fixed and immovable.....	29
Plate 8: Third Puzzle setting, arrows are indicating movable elements while other elements are fixed and immovable.....	30
Plate 9: Fourth Puzzle setting, arrows are indicating movable elements while other elements are fixed and immovable.....	31

1. Introduction

1.1. Background to the study

Cognition encompasses all mental processes that involve the brain and are responsible for acquiring, processing, and storing information, ultimately leading to behavioral actions. A more specific definition of cognition is limited to mental processes that involve some type of mental representation (van Schaik et al., 2016). These cognitive processes are particularly critical when dealing with new ecological and social situations, also known as novel problems (Mayer & Wittrock, 2006), where an individual must discover new solutions to overcome these challenges. Therefore, cognitive abilities are strongly linked to problem-solving abilities. Although it is challenging to directly measure cognitive abilities in any species, it is possible to infer an animal's inherent cognitive potential by evaluating its problem-solving skills (Burkart et al., 2017).

It is commonly believed that animals with higher cognitive abilities have minds that are adapted to their specific environments through domain-specific abilities or modules (Duchaine et al., 2001). Similarly, human cognition also consists of domain-specific components (Cosmides & Tooby, 2013). These specialized cognitive mechanisms or adaptive specializations are genetically based and developmentally canalized solutions that have evolved to address particular adaptive problems (Burkart et al., 2017). They cannot be applied across different domains, and thus the solutions to specific problems are fixed, lacking flexibility and exhibiting no effects of learning through experience on performance.

In ethology, domain-general ability refers to a cognitive capacity, such as general intelligence or speed of information processing, that affects performance across a broad range of tasks and situations (Lambert et al., 2022). Unlike domain-specific abilities, which operate within specific contexts, domain-general abilities, such as learning or behavioral flexibility, function across multiple domains and contexts and form the foundation of intelligence. For humans, intelligence encompasses reasoning, problem-solving, abstract thinking, planning, comprehension, and the ability to learn from

experience (Gottfredson, 1997). Psychometric and factor-analytical methods are commonly used to measure intelligence, yielding a primary factor, independent of content, that spans different tasks and domains, known as the general factor or "g" (Hunt, 2011; Johnson et al., 2004). According to McCloskey et al. (2012), the "g" factor (also called general intelligence, general mental ability, or general intelligence factor) is a construct derived from psychometric investigations of cognitive abilities and human intelligence.

The general ability of intelligence, originally proposed by Spearman (1904), was later subdivided by Cattell into two distinct sub-abilities: crystallized intelligence and fluid intelligence (Geary, 2005; Blair, 2006; Horn & McArdle, 2007). Crystallized intelligence refers to the knowledge and skills that have been acquired through learning and experience over an individual's lifetime. In contrast, fluid intelligence describes the underlying abilities that enable individuals to acquire new knowledge and skills, such as the ability to solve novel problems and reason inductively (Jensen, 2002). The ability to learn new information flexibly throughout life is particularly associated with fluid intelligence (Cattell, 1971; Ackerman, 1986, 1988).

While intelligence in animals may not be as broadly defined as in humans, it is still evident that intelligence is not limited to biologically constrained learning of specific solutions. Instead, animal intelligence encompasses the acquisition of knowledge, behavioural flexibility, and problem-solving in both familiar and novel environments (Yoerg, 2002; Rumbaugh et al., 2008). For example, many animal species exhibit flexible feeding behaviour, adjusting their diet or foraging strategies in response to changes in food availability. Social animals, such as primates, modify their social behaviour in response to changes in group dynamics or the social environment. Some animals also demonstrate problem-solving abilities, using trial-and-error learning to overcome new challenges. These examples show that animals are capable of learning, adapting, and evolving their behaviour, underscoring the importance of considering behavioural plasticity in animal research and conservation efforts (Reader et al., 2011). Thus, as in humans, the core features of animal intelligence include learning ability and problem-solving in novel contexts (Yoerg, 2002; Rumbaugh et al., 2008).

1.2. Aims and objectives

The aim of this thesis is to analyse the cognitive abilities of captive Sumatran orangutans. The specific objectives are to:

1. Determine the capability of orangutans for solving puzzle feeders, and the transmission of information through social learning.
2. Explore the adaptation of orangutans to different levels of difficulty in the puzzles, and the influence of motivation due to the feed reward.
3. Evaluate the tool (puzzle feeder) as a valuable cognitive enrichment for the species.

2. Literature Review

2.1. Evolution of Intelligence

The relationship between brain size and cognitive ability has been the subject of extensive research, and it is widely accepted that the evolution of intelligence is directly linked to an evolutionary increase in relative brain size, or encephalization. In fact, studies have shown that species with larger brains generally exhibit greater cognitive abilities, such as flexible learning and problem-solving (Lefebvre et al. 2004; Deaner et al. 2007; Burkart et al. 2017). While brain size alone does not necessarily determine cognitive ability, it has been suggested that the additional brain tissue required for domain-general cognitive abilities, such as learning and behavioral flexibility, may be a driving force behind the evolution of larger brains (Deaner et al. 2007; Reader et al. 2011). However, maintaining a larger brain is energetically costly (Bauernfeind & Babbitt, 2014; Kuzawa et al. 2014), and therefore requires a stable energy supply to be maintained (Navarrete et al. 2011).

Despite the metabolic and developmental costs associated with larger brains, some species, including primates, have evolved relatively large brains, likely due to the adaptive benefits conferred by increased cognitive abilities (Isler & Van Schaik, 2014). This suggests that ecological and social pressures have played a significant role in driving the evolution of encephalization (Reader et al., 2011). Understanding the factors that contribute to the evolution of large brains and advanced cognition is an important area of research, as it can shed light on the mechanisms that underlie the development of intelligence in both humans and non-human animals.

The Social Brain Hypothesis proposes that group living, with its social constraints and challenges, played a crucial role in driving the evolution of enhanced cognitive abilities (Dunbar, 1998). The dynamics of social bonding and coalition formation are especially cognitively demanding (Dunbar & Shultz, 2007), and the ability to effectively transmit social information is also important (Whiten & van Schaik, 2007; Pradhan et al., 2012). These factors are thought to have been instrumental in driving the evolution of intelligence.

In addition, ecological factors were also suggested to have acted as selective pressures for the evolution of larger brains. Maximizing a stable energy income through the fluctuating seasons required individuals to be behaviourally flexible to prevent food scarcity (the Cognitive Buffer Hypothesis: Allman et al., 1993, Deaner et al. 2007; Sol, 2009), and also required special techniques and higher levels of cognition for the extraction and processing of difficult-to-acquire food (the Technical Intelligence Hypothesis, Byrne, 1997). Thus, both ecological and social factors were likely important drivers in the evolution of enhanced cognitive abilities and larger brains in some species, particularly primates.

Recent research on brain size evolution in primates suggests that ecological preconditions were the main driver for the evolution of large brains, rather than social ones (Heldstab et al., 2022). However, lineages that had favourable ecological conditions that drove encephalization could also develop enhanced cognitive abilities in the social domain. The evidence of correlated evolution of socio-cognitive and eco-cognitive abilities found by Heldstab et al. (2022) strongly suggests the presence of domain-general cognitive abilities, which can be applied to both ecological and social domains.

It is worth noting that there is overlap between the ecological and social domains, such as in the case of social learning. Once a particular set of social skills has evolved, it might indirectly favour the evolution of enlarged brains by improving the access and energy intake of important food resources. This hypothesis can also be applied to the development of cognitive abilities. Conditions that favour learning and experiences during an individual's development are likely to shape their cognitive abilities. Therefore, the interplay between ecological and social factors, along with individual experiences, play a crucial role in the evolution and development of cognitive abilities.

2.2. Development of Intelligence

The development of proficient problem-solving abilities and cognitive understanding of ecological challenges is considered beneficial for individuals, leading to fitness benefits in challenging environments. However, species with higher cognitive capacities do not inherently possess intelligence, but rather acquire cognitive abilities through learning experiences during ontogeny (Wilson, 1991, Reader & Laland, 2002;

Whiten & van Schaik, 2007; van Schaik & Burkart, 2011; Galef, 2015). Intelligence has a genetic foundation (e.g., Neisser et al., 1996; Bouchard, 2004; Deary et al., 2009; Davies et al., 2011; Nisbett et al., 2012; Bates et al., 2013; Joshi et al., 2015 for humans; Hopkins et al., 2014 for apes; Galsworthy et al., 2005 for mice), particularly in terms of the ability to learn (Rumbaugh et al., 2008). However, social and environmental inputs during development are critical for the construction of intelligence (Nisbett et al., 2012).

The importance of learning becomes more apparent when considering the benefits of enhanced learning abilities. Through learning, individuals can acquire knowledge and develop learned skills that are essential for survival. Natural selection acts on an individual's skill set relevant for survival, i.e., the products of learning, rather than on learning ability per se. social learning, in particular, is a crucial tool that enables individuals to learn from others more efficiently and with fewer risks than individual learning (van Schaik & Burkart, 2011).

Furthermore, social learning enables the transmission of skill knowledge not only horizontally, but also vertically between generations. Depending on the environment and the skill pool size of the population, social learning opportunities can play a significant role in determining an individual's skill set. In demanding environments with varying conditions, socially acquired knowledge of hidden food resources and foraging techniques can be a major advantage. Social environment influences during ontogeny are critical for the development of cognitive abilities, defining the learning conditions, determining the scope of an individual's actions and responses, and shaping the skills to be learned. The Cultural Intelligence Hypothesis suggests that social-cultural environmental influences during development shape an individual's cognitive abilities and learned skills (Tomasello, 1999; Herrmann et al. 2007; Whiten & van Schaik, 2007; van Schaik & Burkart, 2011). Initially proposed to explain the development of uniquely human cognitive abilities (Tomasello, 1999; Herrmann et al., 2007), this hypothesis was later applied to non-human animals (Whiten & van Schaik, 2007; van Schaik & Burkart, 2011).

The Cultural Intelligence Hypothesis predicts that in a stimulating social-cultural environment with increased social learning opportunities, individuals will develop larger skill repertoires and minds capable of better cognitive performance, both on a

developmental and an evolutionary level (van Schaik & Burkart, 2011; van Schaik, 2016). This idea was recently confirmed in orangutans (Forss et al., 2016). Knowledge and learned skills are referred to as crystallized intelligence, while the underlying current learning ability is comparable to fluid intelligence. Under stimulating external conditions, these two forms of intelligence show a strong positive correlation when compared to Cattell's model of intelligence.

2.3. The role of experience

The process of learning is fundamental to acquiring knowledge and experience, both of which are strongly influenced by the surrounding environment. It follows that the greater the opportunities provided by the learning environment, the larger the pool of learned skills that an individual can acquire, either through social learning from others or through asocial learning via personal experience. These learned skills and knowledge of affordances gained through experience can significantly impact an individual's current learning ability, irrespective of whether the knowledge was acquired through social or asocial learning. Interestingly, it has been shown that the cognitive mechanisms underlying social and asocial learning are quite similar, which suggests that the beneficial effects of experience on learning may apply to both forms of learning (Heyes, 2012).

The acquisition of knowledge and experience is a cumulative process that strongly influences an individual's approach, exploration, and understanding of the world. This feedback loop also impacts the quality and quantity of learning opportunities available to the individual. The way in which an individual approaches its environment, interacts with novel situations, and engages with social and asocial opportunities for learning are all essential factors in this process. In the absence of a social learning partner, an individual's approach to a stimulus can significantly affect the learning experience. To effectively explore, the individual must first approach the resource, making the approach and response style a crucial factor in learning, exploration, and the development of cognitive abilities. Thus, the individual's learning experience is shaped by a complex interplay of factors, including the learning environment, cognitive mechanisms, and approach style (Greenberg & Mettke-Hofmann, 2001; Reader & Laland, 2003).

Research has shown that a lower degree of neophobia, or fear of novelty, is positively associated with better problem-solving skills in nonhuman animals (Auersperg et al., 2011; Benson-Amram & Holekamp, 2012; Sol et al., 2012; Cauchard et al., 2013). Individuals with a greater tendency for novelty-seeking exhibit different attentional patterns towards their surroundings, enabling them to recognize learning opportunities more easily and explore their environment more effectively. For instance, in chimpanzees, higher levels of temperamental openness, or willingness to experience new things, have been linked to successful problem-solving (Hopper et al., 2014), as well as in capuchin monkeys (Morton et al., 2013). It is plausible that motivational factors and curiosity play a role in learning and innovation processes (Reader & Laland, 2003). Therefore, individual differences in neophobia and temperament may influence learning, problem-solving, and cognitive abilities in nonhuman animals.

Exploration and curiosity play an essential role in the development of cognitive abilities. Intrinsic exploration, which refers to exploration for its own sake, has been observed in various species, including humans (Reader & Laland, 2003). This tendency for exploration can be self-rewarding, as individuals may enjoy the process of discovering and learning new things. Additionally, the presence of novel stimuli can elicit a curious response in humans, indicating the motivational aspects underlying exploration (Berlyne, 1950). To better understand the factors that influence cognition and problem-solving skills, it is important to investigate the interplay between intrinsic motivation and external conditions. However, the relationship between these factors remains poorly understood. It is therefore necessary to further explore the internal motivational factors that influence cognition, how they interact with external conditions, and how they impact an individual's behaviour and problem-solving abilities. Such research may provide insights into the mechanisms that underlie the development of cognitive abilities and the emergence of innovation.

The importance of socio-cultural and environmental factors in shaping an individual's behaviour and cognitive abilities cannot be overstated. Research has shown that both deprivation and enculturation can have long-lasting effects on primates, with captive individuals raised in a more stimulating sociocultural environment exhibiting more advanced developmental outcomes. Studies have indicated that primates raised in enriched environments demonstrate increased cognitive abilities, such as enhanced

problem-solving skills, tool use, and social learning (Call & Tomasello, 1996; Tomasello & Call, 2004; Björklund, 2006; Fredman & Whiten, 2008; Furlong et al., 2008; van Schaik & Burkart, 2011). Additionally, these individuals exhibit more complex social behaviour and have more extensive social networks than those raised in less stimulating environments (Fragaszy et al., 1998; Whiten et al., 1999; Mancini et al., 2011). These findings suggest that social and environmental factors play a crucial role in shaping the cognitive development of primates. Therefore, it is important to consider the effects of these factors when studying learning and cognition in primates and other animals. Further research into the underlying mechanisms of these effects may provide valuable insights into the development of cognitive abilities and enhance our understanding of the factors that influence learning and cognition.

In addition to the extreme cases of deprivation and enculturation, within-species variation in cognitive performance has been documented in primates. This variation can be attributed to differences in environmental conditions and social experiences during development. For example, in chimpanzees, the quality of the mother-infant relationship during early development has been shown to have a significant impact on the development of socio-cognitive abilities (Lonsdorf & Hopkins, 2005; Lonsdorf et al., 2014). Similarly, social rank and access to resources can influence cognitive performance in primates (Reader & Laland, 2002; MacLean et al., 2012). Moreover, research has shown that exposure to different types of environmental stimuli can have a significant impact on cognitive abilities. For example, exposure to music has been linked to improvements in spatial reasoning and attention (Hetland, 2000; Schellenberg, 2004). In addition, exposure to visual art has been associated with improvements in visual-spatial processing and creative thinking (Winner et al., 1987; Gombrich, 2002). Moreover, these studies do not reveal the processes involved in producing these outcomes. Even subtle variation in opportunities for learning and variation in experiences during development beyond the species-typical repertoire might lead to changes in behaviour and learning. This is most evident when comparing captive versus wild individuals of the same species. In captivity, the reduced overall risk, increased free time and increased social interaction, including contact with humans, were suggested to underlie the increase in exploration and cognitive abilities, a phenomenon commonly known as the captivity effect (Laidre, 2008; Benson-Amram et al., 2013; Forss et al., 2015).

The exposure to humans and their artifacts offers broader exploration opportunities (Shumaker et al., 2011). According to the Cultural Intelligence Hypothesis, these opportunities for learning can change the knowledge and skill repertoire of an individual, explaining variation in problem-solving performance. Increased contact with humans can additionally change the social understanding of individuals: usually primates perform very poorly at locating hidden food using social cues and social communication from humans. However, individuals that grew up with humans perform far better (Anderson et al., 1995; Call et al., 2000; Lyn, 2010).

The developmental construction of intelligence has consequences for how we think about its evolution. Little is still known about the interaction between factors influencing the individual's style of approach, response and exploration of previously unexplored features of the environment, leading to differences in opportunities for learning, which in turn shape the knowledge and skill repertoire of an individual. This provides selection with a great number of variables to act upon. Especially because we not only find between-, but also within-species variation in cognitive performance, the study of developmental influences might lead to insight in the selective pressures driving the evolution of cognition. It is therefore very important to investigate the developmental conditions that favour learning abilities, behavioural flexibility, and cognition during development. This is most promising in nonhuman primates, our closest relatives.

2.4. Primate Cognition

Much primate cognition research is focused on understanding the highest achievements of apes and monkeys and involve studying only a few subjects. Researchers train their subjects rigorously and extensively, driving them to learn and display abilities, which are impressive, and occasionally unmatched. For example, Ayumu and other members of Project Ai (research targeted at comprehending chimpanzees' cognition) display numeral chaining abilities that no human could perform (Inoue & Matsuzawa, 2007). If the goal is to show that a species can master a particular task, then studying the extreme aptitudes of selected individuals can be informative. However, the conclusions of these studies rely on the assumption that the task is a valid indicator of an underlying cognitive ability, and that the ability exists in the species in the first place. What we have

established from test theory is that a single test is not likely to be reliable, hence the use of batteries in human intelligence testing. If the goal is to understand the average or range of capacities in a species, then the issues inherent to studies of small samples are compounded.

To study the variation of cognitive ability in animals, we need to determine how to operationalize this ability. Can cognitive ability be captured with one central domain, or many? Do many domains tap into a common, shared aptitude? As mentioned, research in humans (Carroll, 1993) supports this model with multiple correlated domains. However, evidence from other species is mixed, and even within chimpanzees, the structure of intelligence is not yet clear (Herrmann et al., 2010; Hopkins et al., 2014).

Researchers and theorists have often posited that two domains of intelligence exist in apes: social and physical (Bluff et al., 2007; Cheney et al., 1995; Penn et al., 2008; Penn & Povinelli, 2007; Povinelli & Vonk, 2004; Tomasello & Call, 1997). Some investigations of the social domain involve observing and interpreting another's behaviour, such as one's ability to follow another's gaze, and understand cues communicated by another to indicate the location of a reward (Tomasello et al., 1998). With the physical domain, researchers have questioned subjects' understanding of causality, quantity, and space. Relevant studies have required that subjects implement a variety of problem-solving tasks, e.g., tasks which necessitate tool use to retrieve an out of reach object or keep track of a reward after the location has been changed (Albiach-Serrano et al., 2010; Povinelli, 2000).

Chimpanzee social cognitive abilities and tool-use abilities were the focus of a particular study, and compared directly with the performance of bonobos, orangutans, and young children (Herrmann et al., 2007; Herrmann et al., 2010). Chimpanzees are particularly an important candidate for these investigations, for they are one of humanity's closest living relatives, and display impressive comprehension of physical and social relations.

2.4.1. Social cognition and apes

In the wild, apes must be able to recognize group members after being apart for long periods; this is because of the high rate of fission-fusion within groups. When groups

reunite, it is crucial for individuals to be able to recognize and remember other group members, as opposed to non-group members. It is also essential for individuals to be able to recognize fluctuations in dominance rank among group members, which may have occurred during a period of separation. Inaccurate inference of group membership or asymmetrically hierarchical relationships could result in stressful conflict. When individuals of different groups do come into contact, violent acts of aggression often occur (Wilson et al., 2014) wherein group members gang up on non-members, and attack and sometimes kill the non-member (Goodall, 1986).

Social awareness and recognition are crucial for chimpanzees, so they do not needlessly kill known, or even related individuals. Tracking and monitoring conspecifics' interactions is also useful for primate survival (Jolly, 1966). As suggested above, chimpanzees are adept at inferring rank and relationship fluctuations from observing conspecifics' behaviour (Kendal et al., 2015; Pika & Mitani, 2006; Subiaul et al., 2008). Chimpanzees also appear to be skilled in deception: subordinate males will mate with fertile females when the alpha or other dominant males are absent (Mitani et al., 2002). This behaviour suggests that the chimpanzees understand the risks of their actions and know when to take advantage of the absence of dominant individuals. In captivity, researchers have found that chimpanzees can predict the actions of individuals based on physical signals (i.e., hair standing up, swaying, body orientation), follow the gaze of humans and conspecifics, and they can assist a human to achieve a clear goal such as obtaining an out of reach object (Barth et al., 2005; Hare et al., 2001; Warneken & Tomasello, 2006). Gaze following is of particular note, as it allows individuals to extract information from one another. This information may concern social relations within the group, or activity of outsiders, including conspecifics and predators. And yet, not all chimpanzees are proficient at following gaze or gestures, so in other words, individual differences are present.

2.4.2. Physical cognition of apes

Problem solving, especially concerning tool-use, is of primary interest for investigators of apes' physical cognition. Moreover, researchers have argued that tool-use reflects causal understanding of the relationship between the tool, the target, and the actions required to put the tool into use to obtain the target reward (Deaner et al., 2006).

Tool-use, such as using a twig to extract termites from a colony mound, has been studied in the wild (Boesch & Boesch, 1990) and in captivity (Celli et al., 2003). Goodall (1964) first observed chimpanzees using tools to feed on insects in this way, and since then, observations of this behaviour have been frequent and widespread in wild populations (Boesch & Boesch, 1990; McGrew, 1974; Nishida, 1973).

The materials and methods of tool-use had been found to vary among wild chimpanzee populations (McGrew, 1992). Wild chimpanzees modify sticks for use as tools, but the modification depends on the purpose of the tool. For instance, chimpanzees fashion tools from sticks of two different sizes: longer, thicker sticks used to probe for ants and honey, and smaller sticks for picking out and eating bone marrow. In almost all instances, the chimpanzees modified the sticks for the task before making any attempts to use the stick, which suggests that chimpanzees understood the relationship between these tools and the task (Boesch & Boesch, 1990).

In captivity, the strengths and limitations of chimpanzee tool-use has been the subject of much research (Mulcahy & Call, 2006; Murray et al., 2009). To enhance understanding of the limitations governing chimpanzees' reasoning skills regarding tool use, many researchers have used tasks wherein subjects must select the correct tool from a set of tools, some of which are functional for solving the task, and some of which are not (Povinelli et al. 2000; Yocom & Boysen, 2011).

Other researchers have employed tasks which require that their subjects modify the tool to solve the task (Visalberghi et al. 1995). In the early study by Visalberghi et al. (1995), chimpanzees (and other apes, and capuchins) were tested with a perspex tube containing a food reward in the centre. The researchers provided the chimpanzees with a varying selection of tools, some of which could be easily used to solve the problem, and others which required modification. The chimpanzees were able to solve both types of problems, but small individual differences in performance were present, which the researchers did not interpret. In a later variant of the test, even stronger differences in performance were apparent, but the researchers chose to focus on the number of errors that each subject made, rather than examining overall performance, which varied considerably.

2.5. Orangutans as a model species for intelligence testing

Orangutans in the wild and captivity show great cognitive plasticity and are known to be very good problem solvers (Lehner et al., 2011). A systematic investigation of individual variation in orangutans' cognitive performance will thus most likely significantly increase the understanding of the evolution of primate intelligence. *Pongo tapanuliensis*, is the smallest population number of orangutan species (Kuswanda, 2014; Wich et al., 2016) and considered to be evolutionarily distinct from its closest relatives in the Borneo lowlands (Nater et al., 2017). *Pongo pygmaeus* and *Pongo abelii* are the two well-known pongo species. The two species shared a common ancestor approximately 0.9–1.1 Ma (Greminger, 2015). The evolutionary divergence between orangutans and humans is estimated to have taken place 9-13 million years ago (Hobolth et al., 2011; Prado-Martinez et al., 2013). Although this divergence took place much earlier than that between hominids and the chimpanzee-bonobo ancestor, orangutans and humans share a variety of traits, such as a long-life history, omnivorous ecology with a strong extractive element, and similar basic cognitive abilities (Herrmann et al., 2008).

Furthermore, both orangutan species evolved large brains, with Sumatran orangutans' relative brain size being slightly larger than that of Borneans' (Taylor & van Schaik, 2007; van Schaik et al., 2009). This difference is also reflected in their innate problem-solving ability (Forss et al. 2016). In general, their large brains are good preconditions for having general cognitive abilities (Burkart et al., 2017). If we assume evolutionary continuity of general intelligence, orangutans might also possess some level of domain-general abilities (measured in humans through factor g). In fact, orangutans seem to have all the requirements for having factor g - as suggested for other primate species (Banerjee et al., 2009; Hopkins et al., 2014; Woodley of Menie et al., 2015). However, given uncertainties in interpretation and a clear risk that some results represent false positives (Burkart et al., 2017), there is a need for research that assesses the extent of evolutionary continuity of general intelligence, and orangutans are an excellent species for this.

Also, orangutans live in an environment with fluctuating food availability (Marshall et al. 2009). They are specialized in complex food processing techniques that reflect their complex foraging niche (Jaeggi et al., 2010; Schuppli et al., 2012; Schuppli

et al., 2016). However, this knowledge has to be acquired via learning. The mother is an especially important role model (van Noordwijk et al., 2009; Schuppli et al., 2016). Therefore, like us humans, orangutans are characterized by sophisticated social learning skills (Stoinski and Whiten, 2003; Dindo et al., 2010) and the presence of role models during ontogeny for knowledge transfer (Jaeggi et al., 2010; Schuppli et al., 2016). As a result, behavioural variation between populations qualifies as cultural variation (van Schaik et al., 2003; van Schaik et al., 2009; Krützen et al., 2011).

In addition, intraspecific variation in behaviour, novelty response and cognitive abilities were found between wild and captive orangutans (Forss et al., 2015). Still, little is known about the influences of socio-cultural and housing conditions on the cognitive abilities and problem-solving mechanisms under non-extreme conditions. Orangutans with their slow development (Wich et al., 2004; Wich et al., 2009), socially learned skill repertoires and innate learning competence are ideal to investigate the internal and external influences on cognitive performance.

Furthermore, wild orangutans are highly neophobic (Forss et al., 2015). It is very hard to conduct experimental studies in the wild, and almost impossible to conduct cognition-studies under controlled, comparable settings in nature. Consequently, almost all studies investigating orangutans' cognitive abilities and behavioural flexibility were conducted under captive settings, e.g., zoological gardens. However, being born and raised in captivity, these individuals might consequently not show the same abilities as their wild conspecifics. In order to investigate the full range of influences on cognitive performance on a developmental level, individuals with various backgrounds are needed. Therefore, studies that determine different social-cultural influence during ontogeny due to e.g., subtle background differences are needed to investigate what influences during development shape cognition.

2.6. The study species: Sumatran Orangutan (*Pongo abelii*)

2.6.1. Phylogeny

Orangutans belong to the hominid genus *Pongo* that is most distantly related to humans. Their phylogenetic lineage diverged from the common lineage of all other

modern great apes about 12- 16 million years ago (Locke et al., 2011). The recently completed sequencing of the orangutan genome shed new light onto the phylogeny of orangutans and the genetic proximity of modern great apes (Locke et al., 2011). Based on sequence identity, the divergence of the two extant orangutan species, Bornean and Sumatran orangutan (*Pongo pygmaeus* and *Pongo abelii*, respectively; Brandon-Jones et al., 2004), has been estimated as having taken place between 0.6 and 6.4 million years ago, depending on the particular approach and used molecular markers (Goossens et al., 2009).

A more recent study estimates that the split up of these lineages has taken place less than 1 million years ago, comparable to the divergence of chimpanzees and bonobos (*Pan troglodytes* and *Pan paniscus*, respectively) (Prüfer et al., 2012). Findings from a genetic comparison indicate that the evolution of the genetic structure proceeded much faster in *Pan* and *Homo* after the *Pongo* lineage split apart. This strongly supports the view that the modern orangutan genome resembles the genome of the common hominid ancestor more than any other extant great ape species' genome does (Locke et al., 2011), which alone means that orangutans should be of special interest for a comparative perspective on prosociality.

2.6.2. Ecology, characteristic features, and social structure

Orangutans are the only non-human great apes that naturally occur outside of Africa. During the Pleistocene, orangutan populations spread across a range throughout southern Asia including the mainland (Delgado & van Schaik, 2000). Today, there are only fragmented populations left in the rain forests of the northern part of Sumatra and across Borneo (Husson et al., 2009; Marshall et al., 2009), forming the three species of Sumatran and Bornean orangutans (Groves, 2001; Brandon-Jones et al., 2004). Estimating orangutan densities is methodologically highly demanding (Spehar et al., 2010). The most recent estimation of Sumatran orangutans took place in 2015 (Wich et al., 2016) and of Bornean orangutans in 2003 (Ancrenaz et al., 2008). According to these estimations, the total number of Sumatran orangutans is about 14.600 individuals (conservation status: critically endangered; IUCN Red List of Threatened Species. Version 2016-2) and of Bornean orangutans between 45.000 and 69.000 individuals (conservation status recently re-assessed as: critically endangered; IUCN Red List.

Version 2016-2). The population trend is still decreasing due to the rapidly ongoing deforestation and fragmentation of their habitat, mainly for the sake of oil palm plantations as well as for the claims of the timber and paper industry, but also due to poaching and the illegal trade of orangutan infants as pets after killing their mothers (Marshall et al., 2009; Wich et al., 2016). Therefore, there are probably even fewer orangutans left today.

Compared to the African great apes, both orangutan species reveal several unique physical and behavioural characteristics. Despite their heavy body mass and size (adult males can reach a body weight of 80 kg), they are truly arboreal and show several anatomical and behavioural adaptations to the life in the canopy of the tropical rainforests (Thorpe & Crompton, 2006). Especially in Sumatra where large terrestrial predators like the Sumatran tiger (*Panthera tigris*) are present, orangutans barely leave the canopy. In Borneo, where tigers are absent, particularly male orangutans come down from the trees more often to travel terrestrially (Ancrenaz et al., 2014).

Orangutans show a strong sexual dimorphism, with adult males being twice the size of females. They also show a male bimaturism. Only fully developed (or flanged) males display specific secondary sexual characteristics, such as cheek pads (so called flanges), a large throat sac or a long coat of hair, and they are able to produce the characteristic long calls. Unflanged males on the other hand, though being fertile and sexually active, stay in an “arrested” condition which may last up to 20 years after reaching sexual maturity (Fox, 2002; Utami et al., 2002). These two male morphs follow different, but successful mating strategies (Utami et al., 2009). While dominant flanged males usually prefer the “sitting, calling, waiting” strategy, which includes reproductive consortships and cooperative mating, the main strategy of unflanged males can be described as “going, searching, finding” often including coerced mating (Utami et al., 2002).

Females often resist copulations with particular individuals, often unflanged males, while cooperatively associating and mating with others, suggesting there is a form of female partner choice (Utami et al., 2009). Orangutans have a slower life history than African great apes. At about eight years of age, orangutans of both species have the largest interbirth interval of all modern non-human primates and weaning takes place around the

seventh year of age, about two years later than in chimpanzees (Wich et al., 2009). Immature orangutans crucially depend on their mothers regarding feeding and protection, and to acquire dietary, foraging and other essential survival skills via social learning (van Noordwijk & van Schaik, 2005; van Noordwijk et al., 2009; Jaeggi et al., 2010).

The dependence of orangutan infants and juveniles on their mothers is especially strong due to the social organization of orangutans, which is unique among diurnal primates and can be described as an individual-based fission fusion society (van Schaik, 1999) with a mean party size of less than two individuals. This semi-solitary lifestyle of orangutans is probably an adaptive strategy to cope with feeding competition. Being large, primarily frugivorous animals (Rijksen, 1978), orangutans need sizable amounts of fruits, which the South-Asian rainforests cannot provide continuously in such quantities that would allow orangutans to live in permanent groups (Delgado & van Schaik, 2000). However, orangutans are not as solitarily or even “anti-social” (Sugardjito & Nurhuda, 1981) as assumed earlier; in periods of high fruit abundance, they aggregate in large fruit trees and occasionally form travel bands. Furthermore, recent findings revealed that, in orangutans in contrast to other great apes, females are the philopatric sex (Arora et al., 2012; van Noordwijk et al., 2012), which means that mature males disperse, orangutan females tend to stay in their natal area (Mitra, 2009).

Adult females and their dependent offspring live in large, overlapping home ranges which overlap with the larger home range of a resident flanged male (Singleton, 2009). Females and males temporarily engage in consortships which are characterised by coordinated traveling, cooperative mating, and other social interactions. Comparative studies on Sumatran and Bornean study populations revealed considerable variations in the degree of social tolerance and party size between the two orangutan species and even between different populations of one species (Delgado & van Schaik, 2000; van Schaik et al., 2009).

Sumatran orangutans are generally more sociable than Bornean orangutans; especially in Suaq Balimbing where reproductive synchrony results in large parties during the pre-birth period, featuring an almost stable composition for more than two weeks (van Schaik, 1999). After giving birth, females – joined by their infant and their older offspring – associate among each other and are unusually tolerant, exhibiting behaviours including

feeding in close proximity and occasional food sharing among adult females (Singleton & van Schaik, 2002). In Bornean orangutans, maternally related females with dependent offspring also associate with each other. Though the females themselves usually do not engage in affiliative interactions, they tolerate and sometimes even enable social play among their offspring (van Noordwijk et al., 2012).

2.6.3. Orangutans in captivity

The circumstances for orangutans in captivity differ dramatically from natural conditions. In modern zoos, orangutans are usually kept in permanent groups, mostly comprising an adult male, several adult females, and their offspring. Since the relationship between flanged males is always hostile (Utami et al., 2009), adult males cannot be kept together in a single group. The usual group structure in zoos account for the natural dispersal strategy of male orangutans (Knott, 2009), and simultaneously precludes the occurrence of any interactions among adult males as well as any female partner choice.

Furthermore, in contrast to female clusters in the wild, which are formed by related individuals (Singleton et al., 2009), zoo-groups comprise also unrelated females. In their natural habitat, associated unrelated females show more aggressions among each other. These aggressions usually result in breaking up the association. In contrast, related females in the wild show more social tolerance, enable social play of their infants and sometimes even share food, (van Noordwijk et al., 2012). Notwithstanding their social behaviour in the wild, captive orangutans generally seem to cope surprisingly well with group life. In zoos, they engage in affiliative interactions, such as social play, contact sitting, sometimes also grooming and even third-party interventions to prevent or cease conflicts (Tajima & Kurotori, 2010).

2.7. Environmental enrichment

Environmental enrichment is a tool used by animal care staff to improve the welfare of cetaceans under professional care. Environmental enrichment is designed to provide opportunities for mental and physical stimulation and to encourage species-appropriate behaviour through the addition of stimuli (White et al., 2003). The goals of

enrichment are to promote engagement, increase behavioural diversity, provide opportunities for behavioural choice, and give the animals control over their environment (Miller et al., 2016). To achieve these objectives, environmental enrichment programs can incorporate enrichment types that function to stimulate cognitive, visual, auditory, feeding, and social systems (Hoy et al., 2010).

Enrichment is one tool that has been used to increase active behaviours and locomotion in several species in zoo environments. For example, food enrichment increased activity by 30% on days when it was provided to Asian elephants (Soulsby, 2013). Hiding food inside objects and throughout the enclosure of harbour seals (*Phoca vitulina*) increased the rate of species-appropriate foraging behaviours (Grindrod & Cleaver, 2001). Food enrichment also increased the active behaviours of six species of felids (Skibieli et al., 2007). Enrichment objects and problem-solving tasks are effective tools for increasing positive social play for chimpanzees (Clark & Smith, 2013).

Environmental enrichment can include introducing new objects into an enclosure, altering the enclosure, which may mean a major renovation, or moving the animal to a new enclosure (Shepherdson & Swaisgood, 2005). Positive reinforcement training is also a form of enrichment in captive animals as it stimulates cognition and creates an opportunity for the animal to make choices (Shepherdson & Swaisgood, 2005). There are multiple categories of enrichment objects, including food puzzles, toys, and novel objects. Gronqvist et al. (2013) found that toys and food enrichment may decrease aggressive behaviours and increase affiliative behaviours in captive animals. Food enrichment is one of the most feasible options of enrichment for gibbons, considering they are primarily arboreal, and toys are not as easy to manipulate if swinging from rope to tree (Irwin & Wells, 2008).

Sensory enrichment can be auditory, visual, or tactile, such as use of scents, oils, and spices (Gronqvist et al., 2013). These can be mats that are dipped in different scents, such as lavender and peppermint, and hung for the animals inside the enclosure. Olfactory enrichment has been shown to increase species-typical behaviours and reduce levels of inactivity (Gronqvist et al., 2013). Additionally, manipulation, puzzle, sensory and other forms of enrichment can be paired with food (Young, 2003).

3.2. The Indonesian Jungle – Orangutans' Enclosure

The pavilion is large, transparent (acrylic), and dome-shaped with a surface area of 1900m² covering a volume of 14700m³ with a warm and humid jungle-like indoor environment. The indoor enclosure was modelled to represent a considerable section of flora and fauna typical for the tropical Indonesian jungle. The daytime indoor temperature is maintained between 22 and 25 °C all year round. The relative humidity should be over 70% (Bartak, *et al.* 2000).

The exhibit area where observations were done had public viewing demarcated via panelled glass windows on the front walls, as shown in Plate 1. The exhibit consists of multiple vertical levels with permanent climbing structures. The side walls are concrete, and the entire front area has wooden crafted patterns, (Plate 2). Clear panels above the flexible mesh allow sunlight into the enclosure.



Plate 1: Puzzle feeder in the enclosure with demarcated panelled glass window for public viewing. (Credit: Adesewa Adelusi)



Plate 2: Outer view of the Orangutans' enclosure. (Credit: Adesewa Adelus)

3.3. Subjects

The study included three Sumatran orangutans (*Pongo abelii*) housed at Prague Zoo, including two females (older and younger) and one male, as presented in plates 3-5. The subjects' ages at testing ranged from 9 – 33 years.



Plate 3: Mawar (the oldest female in the group), date of birth - 16.3.1989 and Kawi (infant male), date of birth -17.11.2020. Mother: Mawar, father: Pagy. (Credit: Prague Zoo)



Plate 4: Diri (the youngest female in the group), date of birth - 3.2.2013. Mother: Mawar, father: Padang, Padang is absent at the facility. (Credit: Prague Zoo)



Plate 5: Pagy (only adult male in the group), date of birth - 23.7.2001. Parents are not known. (Credit: Prague Zoo)

3.4. Enrichment procedure

A puzzle-feeder was newly installed and offered to the animals. It consisted of a board measuring 27×25×6 cm, hung on one side of the enclosure (about mid-height). The puzzle-feeder is covered by plexiglass with several holes, through which the orangutans could insert their slender fingers or tools (sticks or tiny branches) to retrieve pieces of rewards (feed rewards like nuts), or to manipulate the pieces so that they would fall, via a series of horizontal shelves, finally landing at the bottom of the feeder with a larger outlet which allows easier retrieval. The puzzle was prepared with different degrees of difficulty (four in total), including traps or dead ends. There are two constantly running cameras to keep track of the activities of the orangutans once the puzzle with rewards is set by the keepers, one focusing on the activities of the orangutans and the other focusing on the puzzle feeder.

The zookeepers and the animal welfare and enrichment specialist set the type and number of rewards placed in the puzzle feeder and the puzzle patterns. It started with the easiest setting and smaller rewards, keeping the same design of the puzzle and the same kind and amount of feed rewards for a period no shorter than 20 days (exceptions were included based on the number of days the orangutans were released from the inner enclosure either due to weather conditions, reconstruction, or inability to refill the puzzle feeder). This was necessary to initially evaluate the puzzle-solving abilities of the three adults in the group, quantify the learning process (decrease of the time needed to solve the puzzle) and potential transmission of information between individuals (like teaching each other the use of tools or specific techniques). Along this initial period, the latency time (time between setting the puzzle and interaction) would allow quantifying the loss of motivation due to habituation to the enrichment tool. The patterns were mostly set early morning (7 am – 8 am) before releasing the orangutans to the outdoor enclosure. Later, two variations were introduced to the original setting. Firstly, based on increasing the difficulty of the puzzle by including more complex elements and dead ends. Secondly, based on changes in the feed reward (bigger rewards with an increase in difficulty), the feed preferences already well-known by the keepers, which may lead to increased/decreased motivation. The following (Plates 6-9) describes different puzzle settings used in this study with increase in level of difficulty.



Plate 6: First puzzle setting. An easy setting with small rewards to motivate the orangutans.



Plate 7: Second Puzzle setting, arrows are indicating movable elements while other elements are fixed and immovable.



Plate 8: Third Puzzle setting, arrows are indicating movable elements while other elements are fixed and immovable.



Plate 9: Fourth Puzzle setting, arrows are indicating movable elements while other elements are fixed and immovable.

3.5. Collection of data

This experiment lasted six months (May 2021 to October 2021) with four different puzzle patterns. The cameras present were connected to Aviligon Control Centre, which serves as remote storage access used at the zoo. The video recordings of the activities of the Orangutans were downloaded and stored at the Head of Operations department, Prague Zoo.

Upon collection of the recorded data, the behavioural ethogram was extracted by watching the videos. The behaviour types were further grouped into four basic categories, Exploring, Interacting, Extracting and Not interacting. Whereby, exploring, interacting, and extracting relate to the direct use of the puzzle feeder. The behaviours included in each category are described in Table 1. In addition, during manipulation, the information on the various techniques used was recorded, indicated in Table 2.

Table 1: Behavioural Ethogram

Categories	Behaviour Types	Description
Exploring	Playing	Licking the installed camera
Exploring	Climbing	Movement along the puzzle feeder
Exploring	Investigation	Licking/sniffing around the puzzle feeder, trying to figure out the manipulation technique to be used
Interacting	Manipulation	Use of tools, picking, poking, or handling with the fingers, tongue, toes and/or mouth
Interacting	Connection	Activity involving interaction with another member(s); embracing, patting, extending the hand or touching with hand or foot
Interacting	Observation	Searching for food, monitoring the surroundings and another member(s) in the group
Extracting	Feeding	Achieving success by removing rewards from the feeder, making chewing movements

Not Interacting	Walking	Locomotion on the ground
Not Interacting	Swinging	Dangling down a rope, moving back and forth or from side to side
Not Interacting	Grooming Others	Removing particles from fur, combing through the fur with fingers of another member(s) in the group
Not Interacting	Out of sight	Away from site
Not Interacting	Hanging	Suspending below an item using hands or legs or both
Not Interacting	Standing	Remaining relatively motionless in bipedal or quadrupedal stance
Not Interacting	Attack/Display/Threat	Biting or striking, slapping, stamping the outer glass reacting to a stimulus or putting up a quick show for the public
Not Interacting	Avoidance	Rapid flight, bending away, bowing and/or crouching
Not Interacting	Self-Groom	Picking through the hair with fingers or mouth, or carefully picking off the teeth, eyes, ears, or nose
Not Interacting	Scratching	Any rapid, casual drawing of the fingernails over the body
Not Interacting	Parenting	Infant being secured by an adult by being carried, including clinging to the chest of the adult
Not Interacting	Relaxation	The state of being at rest, not exploring, interacting, or extracting

The behavioural categories were grouped based on the most interactive behaviours relating to the use of the puzzle feeder.

Table 2: Different handling techniques used during manipulation.

Handling Techniques
Mouth only
One finger
Finger + Tool
Tool only
Two fingers
Mouth + Tool
Finger(s) + toe
Mouth + Finger

3.6. Data Extraction

The recorded data was extracted using BORIS software by logging in the necessary information related to the day of interest, such as observation ID, observation date, description of observation, weather conditions, number of individuals in the group and behavioural ethogram.

The duration of each video ranges from 30 minutes at the least to 6 hours at most. Each video was uploaded on the software and events were coded by selecting the related behaviours on the table. On BORIS software, an event is either a “State event” when the behaviour has a duration (start and stop time) or a “Point event” when the behaviour has

no duration. The coded events from BORIS were exported in an excel format for statistical analyses.

The data extracted included latency time, time spent interacting or not interacting with the puzzle feeder, preferred handling technique used, and the frequency of achieving success (*Category – Extracting*).

3.7. Statistical analyses

Two datasets were prepared with the data extracted from BORIS software. The first dataset summarized the latency time until a given behaviour starts, the total time dedicated to each behaviour, the number of events for each behaviour (occurrence), and the order among the three studied animals (who was the first, second or third animal performing each behaviour) for the studied behavioural categories: Exploration, Manipulation and Extraction. For activities connected to social learning, just the total time and occurrence were recorded. Since the duration of the enrichment was different every experimental day, these two variables (total time and occurrence) were standardized per hour.

The second dataset summarized the techniques used for each successful extraction throughout the whole experiment, n=109, together with the time that Diri needed to solve the puzzle and extract each reward (the other two adults were never observed to extract any reward).

Kolmogorov-Smirnov (for variables over 50 observations) and Shapiro-Wilk tests (for variables under 50 observations) were used to test the normality of the studied variables (Table 3). According to these results, nonparametric statistic was used for the following analyses.

Table 3: Normality tests for the studied variables

		df	Sig.
Exploration Latency (sec)	W=0.704	27	<0.001
Exploration Order	W=0.741	27	<0.001
Exploration Time (sec/h)	W=0.595	45	<0.001
Exploration Occurrence (n/h)	W=0.658	45	<0.001
Manipulation Latency (sec)	W=0.678	27	<0.001
Manipulation Order	W=0.753	27	<0.001
Manipulation Time (sec/h)	W=0.727	45	<0.001
Manipulation Occurrence (n/h)	W=0.725	45	<0.001
Extraction Latency (sec)	W=0.869	13	0.051
Extraction Time (sec/h)	W=0.474	45	<0.001
Extraction Occurrence (n/h)	W=0.580	45	<0.001
Time to solve (sec)	D=0.395	109	<0.001
Social Learning Time (sec/h)	W=0.833	45	<0.001
Social Learning Occurrence (n/h)	W=0.878	45	<0.001

Kolmogorov-Smirnov (D) was used for those variables over 50 observations, while Shapiro-Wilk (W) was used for variables under 50 observations.

Mann-Whitney U test was used for detecting differences in the distribution of the data for latency time, and time and occurrence per hour for each studied behaviour between the first and fourth puzzle feeding patterns. It was similarly used for detecting differences in social learning activities.

Kruskal-Wallis test was used to test differences in the distribution of the display of different behaviours among the three studied individuals, as well as for the order of displaying each studied behaviour and the time needed to extract each reward along the study and between the different techniques used: one finger, two fingers, one finger +

mouth, and only mouth. Only mouth was observed just once and thus was not used for further analyses. Seven outliers were excluded from the analyses as well since the extraction took much longer time than usual since Dirí was more interested in playing with the reward than in extracting it. Mood's Median test was also used for the data about reward extraction in order to have more robust results.

4. Results

4.1. Behaviour and puzzle-solving

Kruskal-Wallis test showed that Diri was systematically and significantly being the first animal exploring (KW=9.117, $p=0.010$) and manipulating (KW=9.099, $p<0.001$) the puzzle feeder, followed by Pagy. Mawar was always the last animal displaying these behaviours. These two last animals never succeeded in extracting a reward, and thus no analysis was conducted about this behaviour.

Mann-Whitney tests show that the latency time that took the animals to start exploring the puzzle feeder was different for the first and the fourth patterns ($U=135$, $p<0.001$), being this time higher for the fourth pattern. On the contrary, the latency times to start manipulating and successfully extracting the rewards was not different between these two patterns ($U=100$, $p=0.0217$ for manipulation; $U=18$, $p=1.000$ for extraction). Very similar pattern was observed for Diri ($p=0.007$, $p=0.240$, $p=1.000$ respectively for exploration, manipulation, and extraction), the animal more interested in the puzzle feeders; but these differences were not found for Mawar ($p=1.000$, $p=0.133$) and Pagy ($p=0.073$ and $p=1.000$ for exploration and manipulation respectively). The longer latency time to start exploring the fourth pattern of the puzzle feeder suggest a reduced interest for the tool by that period. However, Spearman's ranked correlations do not show a similar tendency during the display of the first pattern ($\rho=-0.024$, $p=0.923$ for exploration; $\rho=-0.131$, $p=0.594$ for manipulation; $\rho=-0.067$, $p=0.865$ for extraction).

Similar analyses showed that the number of times that the animals displayed explorative ($U=155$, $p=0.084$), manipulative ($U=191$, $p=0.404$), or extractive behaviours ($U=214$, $p=0.752$) were not different between the first and fourth pattern. Furthermore, the total time (per hour) dedicated to these three behaviours were neither significantly different ($U=164$, $p=0.132$; $U=186$, $p=0.326$; $U=206$, $p=0.578$). However, different patterns arise when the three animals were analysed individually. Diri performed less explorative behaviours ($U=7$, $p=0.028$) and for shorter time ($U=5$, $p=0.013$) during the display of the fourth pattern compared to the first one. Pagy also performed less explorative behaviour to explore ($U=4$, $p=0.005$) and dedicated less time to it for the

fourth pattern of the puzzle feeder ($U=5$, $p=0.008$) compared to the first one. No differences were found for Mawar, and neither for the rest of variables.

The occurrence of social learning behaviour and the time dedicated to them were not different between the two puzzle feeder patterns ($U=202$, $p=0.595$ and $U=182$, $p=299$, respectively). Just Pagy dedicated less time to social learning while pattern four was displayed ($U=6$, $p=0.019$). Similarly, no differences were found on the time dedicated to social learning among the three individuals ($KW=1.707$, $p=0.426$). However, surprisingly, the occurrence of this behaviour was higher in Dir, followed by Pagy and then Mawar ($KW=7.686$, $p=0.021$); that is, the most successful animal extracting rewards was the one paying more attention to the attempts of her groupmates.

4.2. Temporal changes in techniques used.

The time to extract the reward (time to solve) that Dir needed along the study showed a tendency to decrease as the study advanced, both for the distribution of the data ($KW=35.859$, $p<0.001$) and the medians ($\chi^2=23.189$, $p=0.026$) (Figure 2).

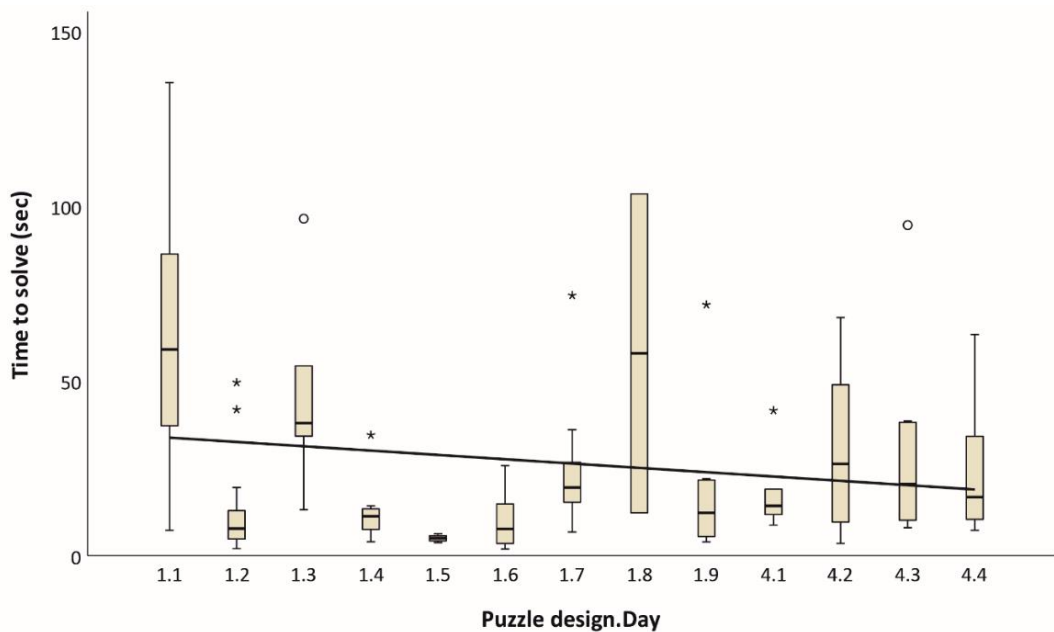


Figure 2: Puzzle design and time taken to solve per day.

Differences in the time to extract a reward were also observed, both for the distribution of the data (KW=37.965, $p < 0.001$) and the medians ($\chi^2=30.269$, $p < 0.001$). It was longer when Diri used just one finger to extract the reward (39.6 ± 5.0 sec), shorter when using two fingers (25.5 ± 5.4) and shortest when using finger and mouth (10.9 ± 1.7). The development of the time to solve may be connected to the changes along the study in the techniques used by Diri. During the first part of the study (first puzzle pattern), there was a tendency to change from one finger to finger + mouth. Similarly, in the second part of the study (fourth puzzle pattern), there was a tendency to change from one finger to two fingers (Figure 3). In both cases, that means transitioning from the less effective to a more effective technique.

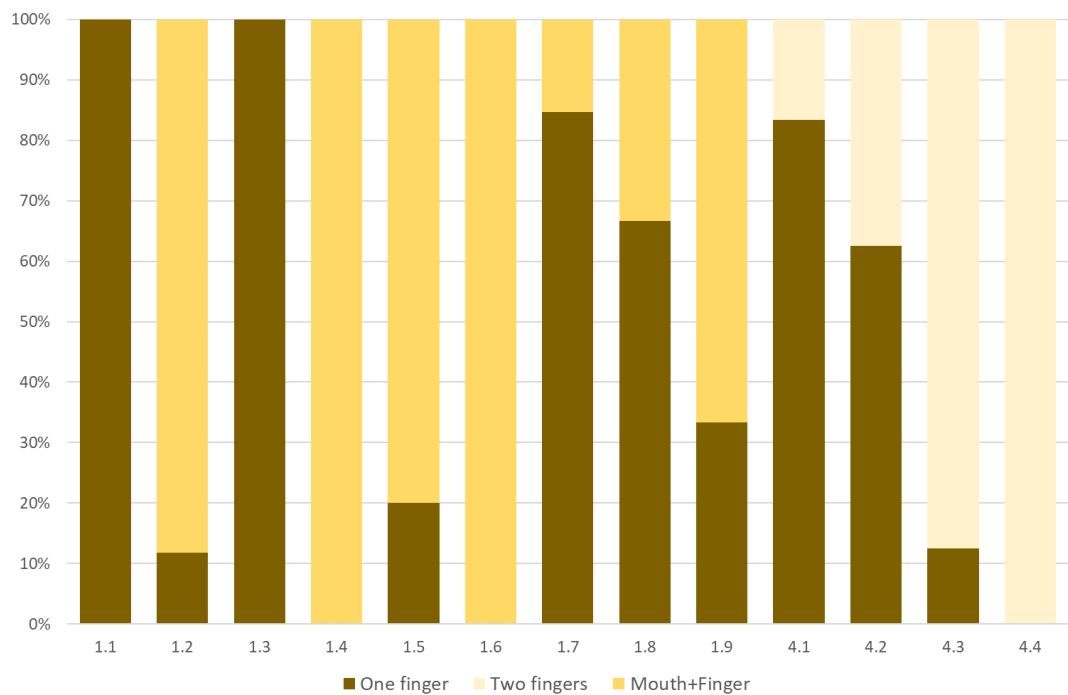


Figure 3: Techniques used to extract rewards.

5. Discussion

5.1. Behaviour and puzzle-solving

The result of this study suggests that there are individual differences in exploration behaviour among the animals. Specifically, the Kruskal-Wallis test showed that Dirí was consistently the first animal to explore and manipulate the puzzle feeder, while Mawar was always the last. This suggests that Dirí may be more exploratory and motivated to engage with the task than Mawar. Similar findings have been reported in previous studies. For example, a study on rats found that some were more willing to explore a novel environment than others (Einion et al., 1978). These studies suggest that individual differences in exploration behaviours are not unique to the animals tested in this study but rather a common phenomenon across species.

The fact that Dirí was the first animal to extract a reward from the puzzle feeder successfully is also consistent with previous research. A study on chimpanzees found that some animals were better at using tools to obtain rewards than others (Hopper et al., 2016). This suggests that individual differences in cognitive abilities may underlie individual differences in exploration and problem-solving behaviour. The finding that Mawar and Pagy never succeeded in extracting a reward from the puzzle feeder is also consistent with previous research. For example, a study on monkeys found that some individuals were better at learning a novel task than others (Cole et al., 2013). This suggests that individual differences in learning and memory may underlie individual differences in exploration and problem-solving behaviour.

This study's findings imply differences in animals' latency time to explore a novel task. Specifically, the Mann-Whitney test showed that animals took longer to explore the puzzle feeder's fourth pattern than the first pattern. However, there were no differences in the latency times to start manipulating and successfully extracting the rewards between these two patterns. Additionally, these differences were only observed for Dirí, the animal that showed the most interest in the puzzle feeders, while no significant differences were found for Mawar and Pagy.

These results are consistent with previous studies that found individual differences in exploration behaviour. For example, a study conducted on rats found that some individuals are more exploratory than others, and these individual differences in behaviour are consistent across different testing environments (Einon et al., 1978). Similarly, a study on monkeys found that some individuals are more willing to explore a novel object than others and that this behaviour is associated with differences in brain activity (Bellgowan et al., 2009).

The finding that animals took longer to explore the fourth pattern of the puzzle feeder suggests a reduced interest in the enrichment tool by that period. This is consistent with the concept of habituation, which refers to a decrease in responsiveness to a stimulus as a result of repeated exposure (Thompson & Spencer, 1966). However, it is important to note that Spearman's ranked correlations did not show a similar tendency during the display of the first pattern. This suggests that the reduced interest observed in the fourth pattern may not be a general phenomenon but specific to the particular task or stimulus used in this study.

Furthermore, the results of this study suggest that there may be individual differences in how animals respond to changes in their environment. Specifically, while the analysis did not find any significant differences in the number of explorative, manipulative, or extractive behaviours displayed by the animals between the first and fourth patterns of the puzzle feeder, further analysis of the individual animals revealed that Diri and Pagy showed less explorative behaviour during the fourth pattern compared to the first one. This finding is consistent with previous research on animal behaviour. For example, a study on dogs found that some individuals were more sensitive to environmental changes than others (Marshall-Pescini et al., 2017). Another study found that some rats were more flexible in their behaviour and better able to adapt to environmental changes than others (Birrell et al., 2018). These studies suggest that individual differences in how animals respond to environmental changes are not unique to the animals tested in this study but rather a common phenomenon across species. The fact that Diri and Pagy displayed less explorative behaviour during the fourth pattern of the puzzle feeder may indicate a reduced interest or motivation to engage with the task. This could be due to factors such as fatigue or decreased novelty value. Alternatively, it could reflect a difference in the animals' cognitive abilities or problem-solving strategies.

The results further suggest that social learning behaviour may not be affected by the type of puzzle feeder pattern, as there were no significant differences in occurrence and time dedicated to social learning behaviour between the two patterns. These findings are consistent with previous studies that have found similar results. For example, a study by Hopper et al. (2013) showed that the presence of social cues did not affect the performance of captive chimpanzees in a tool-use task. Similarly, a study by Whiten et al. (2005) found that the presence of a model chimpanzee did not affect the performance of young chimpanzees in a foraging task. However, the finding that Diri, the most successful animal at extracting rewards, also showed the highest occurrence of social learning behaviour is noteworthy. This suggests that Diri may have learned from her group mates' attempts and adjusted her behaviour accordingly, leading to her higher success rate. This finding is consistent with previous studies that have found that social learning can play a critical role in acquiring new skills in non-human primates, including chimpanzees (Hopper et al., 2013; Whiten et al., 2005). Furthermore, it highlights the importance of considering individual differences in learning and problem-solving abilities when studying animal behaviour.

5.2. Temporal changes in techniques used

The observed trend in this study is consistent with findings from other studies that suggest animals can improve their problem-solving abilities with repeated exposure to similar tasks. For instance, a study conducted by Joly et al. (2012) on capuchin monkeys showed that with repeated exposure to a particular task, the monkeys demonstrated an improved ability to solve the task more quickly and efficiently. Another study by Lonsdorf et al. (2014) on chimpanzees also found that they were able to solve complex tasks faster with repeated exposure. However, it is important to note that the observed trend in this study could also be influenced by other factors such as increased motivation, improved familiarity with the testing environment, or even fatigue. These factors could potentially affect the animal's problem-solving ability and the time taken to extract the reward. Further studies could investigate these factors to better understand the observed trend.

This result suggests that the technique used to extract the reward significantly affected the time taken to solve the puzzle feeder. This finding is consistent with previous studies showing that using different techniques can affect the success rate of solving puzzles by animals. For example, a study on orangutans showed that they use various techniques to extract food rewards and that the success rate was highest when using more effective techniques such as tools (Fox et al., 2013). Another study on chimpanzees showed that they use a range of techniques to extract food rewards and that the success rate was higher when using more efficient techniques, such as using a stick (Mulcahy and Call, 2006). The observed tendency to change techniques throughout the study suggests that Diri was learning from experience and adapting her strategies to become more efficient in solving the puzzle feeder. This finding is consistent with other studies showing that animals can improve their problem-solving abilities through learning and experience (e.g., Lonsdorf et al., 2009; Seed et al., 2012).

6. Conclusions

The cognitive abilities of non-human animals have long been a subject of scientific investigation, and the study presented here adds to the growing body of research in this field. Over the course of six months, we were able to test the captive Sumatran orangutans' puzzle-solving abilities and study their behaviour by employing a puzzle feeder as an enrichment item. The results of the study shed light on individual differences in exploration behaviour, response to changes in the environment, and social learning behaviour among the animals.

The study results indicate individual differences in exploration behaviour among the animals tested. Diru was consistently the first animal to explore and manipulate the puzzle feeder, while Mawar was always the last, suggesting that Diru may be more exploratory and motivated than Mawar. The animals also displayed differences in latency time to explore the fourth pattern of the puzzle feeder compared to the first pattern, with Diru taking longer to explore the fourth pattern, indicating reduced interest in the tool.

Furthermore, the study found that there may be individual differences in how animals respond to changes in their environment, with Diru and Pagy displaying less explorative behaviour during the fourth pattern than the first one. The study also suggested that social learning behaviour may not be affected by the type of puzzle-feeder pattern, and the presence of social cues did not affect the performance of the animals in the task. However, the finding that Diru, the most successful animal at extracting rewards, showed the highest occurrence of social learning behaviour suggests that social learning may have played a critical role in acquiring new skills.

In conclusion, this study provides valuable insights into the cognitive abilities of Sumatran orangutans in captivity and highlights the importance of enrichment activities to enhance their problem-solving skills. The findings of this study also suggest that individual differences in exploration behaviour and social learning behaviour may play a significant role in the acquisition of new skills. Further research in this area may help improve captive orangutans' welfare and inform conservation efforts for this endangered species. The study also underscores the need for continued research in this field, as our

understanding of the cognitive abilities and behaviours of non-human animals continues to evolve.

6.1. Recommendations

The following recommendations were made based on the findings of this study:

- 1 Enrichment activities, such as puzzle-feeders, should be provided regularly to captive Sumatran orangutans in order to promote their cognitive abilities and encourage exploration behaviour.
- 2 Caretakers and researchers should pay attention to individual differences among the animals, as they may have varying levels of motivation and interest in enrichment activities. This knowledge could help tailor enrichment activities to better suit individual animals' needs and preferences.
- 3 The findings suggest that social learning behavior may play a critical role in the acquisition of new skills, therefore social interactions should be encouraged among captive orangutans.
- 4 Researchers should continue to investigate individual differences in exploration and manipulation behavior, as well as how animals respond to changes in their environment, in order to gain a better understanding of cognitive abilities and motivations in captive Sumatran orangutans.
- 5 Further studies could investigate the potential benefits of using different types of puzzle-feeders and other forms of enrichment activities to promote cognitive development and prevent boredom and stress in captive orangutans.

7. References

- Ackerman, P. L. (1986). Individual differences in information processing: An investigation of intellectual abilities and task performance during practice. *Intelligence*, **10**(2), 101-139.
- Ackerman, P. L. (1988). Determinants of individual differences during skill acquisition: Cognitive abilities and information processing. *Journal of experimental psychology: General*, **117**(3), 288.
- Albiach-Serrano, A., Call, J., & Tomasello, M. (2010). Chimpanzees (*Pan troglodytes*) flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities. *PLoS One*, **5**(5), e10573.
- Allman, J., McLaughlin, T., & Hakeem, A. (1993). Brain weight and life-span in primate species. *Proceedings of the National Academy of Sciences*, **90**(1), 118-122.
- Ancrenaz, M., Dabek, L., Brewer, S., Kler, H., Leighton, M., & O'Neil, S. (2008). Orangutan population and habitat viability assessment: final report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.
- Anderson, J. R., Awazu, S., & Fujita, K. (1995). Can squirrel monkeys (*Saimiri sciureus*) learn self-control?. *Journal of Comparative Psychology*, **109**(2), 133.
- Arora, N., van Noordwijk, M. A., Ackermann, C., Willems, E. P., & van Schaik, C. P. (2012). The effects of sex, rank and group size on food competition in Bornean orang-utans. *Behavioral Ecology and Sociobiology*, **66**(2), 261-272.
- Auersperg AMI, von Bayern AMP, Gajdon GK, Huber L, Kacelnik A. 2011. Flexibility in problem solving and tool use of kea and new caledonian crows in a multi access box paradigm. *PLoS ONE* **6**(6): e20231.
- Banerjee, S., Chabris, C. F., Johnson, V. E., Lee, J. J., & Hauser, M. D. (2009). General intelligence in another primate: Individual differences across cognitive task performance in a new world monkey (*Saguinus oedipus*). *PloS one*, **4**(8), e5883.

- Barth, J., Reaux, J. E., & Povinelli, D. J. (2005). Chimpanzees' (Pan troglodytes) use of gaze cues in object-choice tasks: different methods yield different results. *Animal cognition*, 8(2), 84-92.
- Bates, T. C., Lewis, G. J., & Weiss, A. (2013). Childhood socioeconomic status amplifies genetic effects on adult intelligence. *Psychological Science*, 24(10), 2111-2116.
- Bauernfeind, A. L., & Babbitt, C. C. (2014). The appropriation of glucose through primate neurodevelopment. *Journal of human evolution*, 77, 132-140.
- Bellgowan, P. S., Buffalo, E. A., Bodurka, J., & Martin, A. (2009). Lateralized spatial and object memory encoding in entorhinal and perirhinal cortices. *Learning & memory*, 16(7), 433-438.
- Benson-Amram S, Holekamp KE. 2012. Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences* 279(1739): 4087-4095.
- Benson-Amram, S., Dantzer, B., Stricker, G., Swanson, E. M., & Holekamp, K. E. (2013). Brain size predicts problem-solving ability in mammalian carnivores. *Proceedings of the National Academy of Sciences*, 110(9), 3519-3523.
- Birrell J., M., & Brown V., J. (2018). Medial frontal cortex mediates perceptual attentional set shifting in the rat. *Journal of Neuroscience*, 38(11):2699-2710.
- Björklund, A. (2006). The role of experience in the development of cognitive systems and its relevance to social learning in primates. In S. Suomi, C. Harlow & H. Van Tilburg (Eds.), *Primate Origins of Human Cognition and Behavior* (pp. 123-146). Springer.
- Blair, C. (2006). How similar are fluid cognition and general intelligence? A developmental neuroscience perspective on fluid cognition as an aspect of human cognitive ability. *Behavioral and Brain Sciences*, 29(2), 109-125.
- Bluff, L. A., Weir, A. A., Rutz, C., & Kacelnik, A. (2007). Tool-related cognition in New Caledonian crows. *Comparative Cognition & Behavior Reviews*, 2, 1–25.

- Boesch, C., & Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia primatologica*, 54(1-2), 86-99.
- Bouchard Jr, T. J. (2004). Genetic influence on human psychological traits: A survey. *Current directions in psychological science*, 13(4), 148-151.
- Brandon-Jones, D., Eudey, A. A., Geissmann, T., Groves, C. P., Melnick, D. J., Morales, J. C., ... & Zhang, Y. (2004). Asian primate classification. *International Journal of Primatology*, 25(1), 97-164.
- Burkart, J. M., Schubiger, M. N., & van Schaik, C. P. (2017). The evolution of general intelligence. *Behavioral and Brain Sciences*, **40**, e195.
- Byrne, R. W. (1997). The technical intelligence hypothesis: an additional evolutionary stimulus to intelligence?.
- Call, J. & Tomasello, M. (1996). The effect of humans on the cognitive development of apes. In W.C. McGrew, L.F. Marchant & T. Nishida (Eds.), *Great Ape Societies* (pp. 355-367). Cambridge University Press.
- Call, J., Brauer, J., Kaminski, J., & Tomasello, M. (2000). Domestic dogs (*Canis familiaris*) are sensitive to the attentional state of humans. *Journal of comparative psychology*, 114(3), 337.
- Carroll, J. B. (1993). *Human cognitive abilities: A survey of factor-analytic studies*. Cambridge University Press.
- Cattell, R. B. (1971). *Abilities: Their structure, growth, and action*.
- Cauchard L, Boogert NJ, Lefebvre L, Dubois F, Doligez B. 2013. Problem-solving performance is correlated with reproductive success in a wild bird population. *Animal Behaviour* 85(1): 19-26.
- Celli, M. L., Tomonaga, M., Udono, T., & Teramoto, M. (2003). Tool use by captive chimpanzees (*Pan troglodytes*): do they use us as tools?. *Primates*, 44(2), 115-118.
- Cheney, D. L., & Seyfarth, R. M. (1995). Constraints and preadaptations in the earliest stages of language evolution. *Linguistics*, 33(1), 1-14.

- Clark, F.E. & Smith, J.A. (2013). Play and problem-solving using enrichment in captive chimpanzees (*Pan troglodytes*). *Journal of Applied Animal Welfare Science*, 16(4), 378-393.
- Cole, M. W., Laurent, P., & Stocco, A. (2013). Rapid instructed task learning: A new window into the human brain's unique capacity for flexible cognitive control. *Cognitive, Affective, & Behavioral Neuroscience*, 13, 1-22.
- Cosmides, L., & Tooby, J. (2013). Evolutionary psychology: New perspectives on cognition and motivation. *Annual review of psychology*, 64, 201-229.
- Davies, G., Tenesa, A., Payton, A., Yang, J., Harris, S. E., Liewald, D., ... & Visscher, P. M. (2011). Genome-wide association studies establish that human intelligence is highly heritable and polygenic. *Molecular psychiatry*, 16(10), 996-1005.
- Deaner, R. O., Isler, K., Burkart, J., & Van Schaik, C. (2007). Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain, behaviour and evolution*, 70(2), 115-124.
- Deaner, R. O., van Schaik, C. P., & Johnson, V. E. (2006). Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. *Evolutionary psychology*, 4(3), 149-196.
- Deary, I. J., Penke, L., & Johnson, W. (2010). The neuroscience of human intelligence differences. *Nature Reviews Neuroscience*, 11(3), 201-211.
- Delgado, R. A., & van Schaik, C. P. (2000). The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): a tale of two islands. *Evolutionary Anthropology*, 9(5), 201-218.
- Dindo, M., Whiten, A., & De Waal, F.B.M. (2010). In-group conformity sustains different foraging traditions in capuchin monkeys (*Cebus apella*). *PLOS One*, 5(4), e10368.
- Duchaine, B., Cosmides, L., & Tooby, J. (2001). Evolutionary psychology and the brain. *Current opinion in neurobiology*, 11(2), 225-230.

- Dunbar, R. I. M. (1989). Machiavellian intelligence. Social expertise and the evolution of intellect in monkeys, apes, and humans: Edited by Richard Byrne & Andrew Whiten. Oxford: Clarendon Press (1988). Pp. xiv+ 413.
- Dunbar, R. I., & Shultz, S. (2007). Evolution in the social brain. *science*, **317(5843)**, 1344-1347.
- Einon, D. F., Morgan, M. J., & Kibbler, C. C. (1978). Brief periods of socialization and later behaviour in the rat. *Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology*, **11(3)**, 213-225.
- Forss, S. I. F., Willems, E. P., Call, J., & van Schaik, C. P. (2016). Cognitive differences between orangutan species: a test of the cultural intelligence hypothesis. *Scientific Reports*, 6(1), 30516.
- Forss, S. I., Schuppli, C., Haid, N., Zweifel, N., Schnell, A., Bugnyar, T., & Kotrschal, K. (2015). Cognitive differences between wild and captive individuals of a same species: insights into the effects of captivity on cognition. *Animal Behaviour*, 102, 75-87.
- Fox, E. A. (2002). Female tactics to reduce sexual harassment in the Sumatran orangutan (*Pongo pygmaeus abelii*). *Behavioral Ecology and Sociobiology*, 52(2), 93-101.
- Fox, E. A., Sitompul, A. F., & van Schaik, C. P. (2013). Intelligent tool use in wild Sumatran orangutans. *Nature*, **479(7372)**, 497-499.
- Fragaszy, D.M., Visalberghi, E., Fedigan, L.M. & Mackintosh, N.J. (1998). The complete capuchin: The biology of the genus *Cebus*. Cambridge University Press.
- Fredman, T. & Whiten, A. (2008). What can we learn from the study of wild chimpanzee tool-use relevant to the evolution of cognition in early hominids? *International Journal of Primatology*, 29(3), 715-741.
- Furlong, E.E., Boose, K.J., Boysen, S.T. & Schapiro, S.J. (2008). Effects of cognitive testing on welfare measures in captive chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, 70(9), 871-883.
- Galef Jr, B. G. (2015). Whither tradition?. *Animal Behaviour*, 110, e1-e7.

- Galsworthy, M. J., Paya-Cano, J. L., Monleon, S., Plomin, R., & Fenton, A. A. (2005). Evidence for general cognitive ability (g) in heterogeneous stock mice and an analysis of potential confounds. *Genes, Brain and Behavior*, 4(5), 364-375.
- Geary, D. C. (2005). *The origin of mind: Evolution of brain, cognition, and general intelligence*. American Psychological Association.
- Gombrich, E. H. (2002). The visual image: Its place in communication. *Journal of Aesthetics and Art Criticism*, 60(1), 17-25.
- Goodall, J. (1964). Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature*, 201(4923), 1264-1266.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behaviour*. Belknap Press.
- Goossens, B., Chikhi, L., Ancrenaz, M., et al. (2009). Genetic signature of anthropogenic population collapse in orang-utans. *PLoS Biology*, 7(5), e1000055. doi: 10.1371/journal.pbio.1000055
- Gottfredson, L. S. (1997). Mainstream science on intelligence: An editorial with 52 signatories, history, and bibliography. *Intelligence*, 24(1), 13-23.
- Greenberg, R., & Mettke-Hofmann, C. (2001). Ecological aspects of neophobia and neophilia in birds. *Current ornithology*, 119-178.
- Greminger, M. P. (2015). Evolutionary history of orang-utans and humans. *Nature*, 525(7569), 399-400.
- Grindrod, J. & Cleaver, M. (2001). The effect of hiding food on the behaviour of captive harbour seals (*Phoca vitulina*). *Applied Animal Behaviour Science*, 71(3), 321-330.
- Gronqvist, G., Wikman, I., & Strandberg, E. (2013). Effects of enrichment on activity and social behaviour in a group of captive gibbons. *Folia Primatologica*, 84(2), 73-85.
- Groves, C. P. (2001). *Primate taxonomy*. Smithsonian Institution Press, Washington DC.

- Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know?. *Animal Behaviour*, 61(1), 139-151.
- Heldstab, S. A., Isler, K., Graber, S. M., Schuppli, C., & van Schaik, C. P. (2022). The economics of brain size evolution in vertebrates. *Current Biology*, 32(12), R697-R708.
- Herrmann, E., Call, J., Hernandez-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.
- Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B., & Tomasello, M. (2008). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science*, 317(5843), 1360-1366.
- Herrmann, E., Hare, B., Call, J., & Tomasello, M. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PLoS One*, 5(8), e12438.
- Hetland, L. (2000). Listening to music enhances spatial-temporal reasoning: Evidence for the “Mozart Effect”. *Journal of Aesthetic Education*, 34(3/4), 105-148.
- Heyes, C. (2012). What's social about social learning?. *Journal of comparative psychology*, 126(2), 193.
- Hobolth, A., Christensen, O. F., Mailund, T., Schierup, M. H., & Jensen, J. D. (2011). Genomic relationships and speciation times of human, chimpanzee, and gorilla inferred from a coalescent hidden Markov model. *PLoS genetics*, 7(2), e1002137.
- Hopkins, W. D., Russell, J. L., & Cantalupo, C. (2007). Neuroanatomical correlates of handedness for tool use in chimpanzees (*Pan troglodytes*). *Behavioural Brain Research*, 183(2), 315-320.
- Hopper LM, Schapiro SJ, Lambeth SP, Brosnan SF. 2014. Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Animal Behaviour* 95: 85-93.

- Hopper, L. M., Lambeth, S. P., Bernacky, B. J., & Brosnan, S. F. (2013). The ontogeny of social comparisons by rhesus macaques (*Macaca mulatta*).
- Hopper, L. M., Shender, M. A., & Ross, S. R. (2016). Behavioral research as physical enrichment for captive chimpanzees. *Zoo Biology*, **35**(4), 293-297.
- Horn, J. L., & McArdle, J. J. (2007). Understanding human intelligence since Spearman. In *Factor analysis at 100* (pp. 219-262). Routledge.
- Hoy, J.M., Jenkins, S.R. & Tidwell, L.A. (2010). Enrichment and training techniques that enhance animal welfare. *International Journal of Comparative Psychology*, **23**(2), 111-127.
- Hunt, E. (2011). *Human intelligence*. Cambridge University Press.
- Husson, S. J., Wich, S. A., Marshall, A. J., Dennis, R. D., Ancrenaz, M., Brassey, R., ... & van Schaik, C. P. (2009). Orangutan distribution, density, abundance and impacts of disturbance. In *Orangutans* (pp. 77-96). Springer, Boston, MA.
- Inoue, S., & Matsuzawa, T. (2007). Working memory of numerals in chimpanzees. *Current Biology*, **17**(23), R1004-R1005.
- Irwin, M.T. & Wells, J.P. (2008). The effects of food distribution on foraging and activity in a group of captive gibbons (Hylobatidae). *Journal of Applied Animal Welfare Science*, **11**(2), 134-149.
- Isler, K., & Van Schaik, C. P. (2014). How humans evolved large brains: comparative evidence. *Evolutionary Anthropology: Issues, News, and Reviews*, **23**(2), 65-75.
- Jaeggi, A.V., Dunkel, L.P., Van Noordwijk, M.A., Wich, S.A., Sura, A.A.L., & Van Schaik, C.P. (2010). Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. *American Journal of Primatology*, **72**(1), 62-71.
- Jensen, A. R. (2002). Psychometric g: Definition and substantiation. In *The general factor of intelligence* (pp. 51-66). Psychology Press.
- Jolly, A. (1966). Lemur social behaviour and primate intelligence. *Science*, **153**(3735), 501-506.

- Joly, M., Schell, A. M., & Wimmer, M. C. (2012). Problem solving and learning in capuchin monkeys. *Animal Cognition*, **15**(6), 923-930.
- Joshi, P. K., Esko, T., Mattsson, H., Eklund, N., Gandin, I., Nutile, T., ... & Wilson, J. F. (2015). Directional dominance on stature and cognition in diverse human populations. *Nature*, *523*(7561), 459-462.
- Kendal, R., Custance, D., Kendal, J., Vale, G., & Stoinski, T. (2015). Orangutans modify their gestural signaling according to their audience's comprehension. *Current Biology*, *25*(10), 1342-1346.
- Krützen, M., Willems, E.P., van Schaik, C.P., & Van Noordwijk, M.A. (2011). Culture and geographic variation in orangutan behaviour. *Current Biology*, *21*(21), 1808-1812.
- Kuswanda, B. (2014). Preliminary study of population of Tapanuli Orangutan (*Pongo tapanuliensis*). Orangutan Republik Foundation.
- Kuzawa, C. W., Chugani, H. T., Grossman, L. I., Lipovich, L., Muzik, O., Hof, P. R., ... & Lange, N. (2014). Metabolic costs and evolutionary implications of human brain development. *Proceedings of the National Academy of Sciences*, **111**(36), 13010-13015.
- Laidre, M. E. (2008). The captive environment and its relationship to the wild: implications for the welfare of captive cetaceans. *Journal of Applied Animal Welfare Science*, *11*(3), 169-183.
- Lambert, M., Farrar, B., Garcia-Pelegrin, E., Reber, S., & Miller, R. (2022). ManyBirds: A multi-site collaborative Open Science approach to avian cognition and behaviour research. *Animal Behavior and Cognition*, **9**(1), 133-152.
- Lefebvre, L., Reader, S. M., & Sol, D. (2004). Brains, innovations and evolution in birds and primates. *Brain, behaviour and evolution*, **63**(4), 233-246.
- Lehner, S. R., Burkart, J. M., van Schaik, C. P., & Haun, D. B. M. (2011). The cognitive skills of early orangutans (*Pongo pygmaeus*). *Animal cognition*, *14*(4), 549-560.

- Locke, D. P., Hillier, L. W., Warren, W. C., et al. (2011). Comparative and demographic analysis of orangutan genomes. *Nature*, 469(7331), 529-533. doi: 10.1038/nature09687
- Lonsdorf, E. V., & Hopkins, W. D. (2005). Wild chimpanzees show population-level handedness for tool use. *Proceedings of the National Academy of Sciences*, 102(35), 12634-12638.
- Lonsdorf, E. V., Anderson, K. E., Stanton, M. A., Shender, M. A., Heintz, M. R., Goodall, J., & Murray, C. M. (2014). Boys will be boys: sex differences in wild infant chimpanzee social interactions. *Animal Behaviour*, **88**, 79-83.
- Lonsdorf, E. V., Eberly, L. E., Pusey, A. E., & Vigilant, L. (2009). Spatial complexity, patch departure rules, and group size in the chimpanzees of Gombe National Park. *American Journal of Physical Anthropology*, **140(2)**, 373-384.
- Lyn, H. (2010). *How monkeys find their way: leadership, coordination, and cognitive maps of African baboons*. University of Chicago Press.
- MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., ... & Visalberghi, E. (2012). The evolution of self-control. *Proceedings of the National Academy of Sciences*, 109(36), 21316-21323.
- Mancini, G., Saporiti, M. & Palagi, E. (2011). Social relevance affects prosociality in capuchin monkeys. *Scientific Reports*, 1, 183.
- Marshall, A.J., Leighton, M., Mengersen, K., & Ancrenaz, M. (2009). Orangutan population biology, life history, and conservation. In S. Wich, S.S. Utami Atmoko, T. Mitra Setia, and C.P. van Schaik (Eds.), *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 47-66). Oxford: Oxford University Press.
- Marshall-Pescini, S., Schwarz, J. F., Kostelnik, I., Virányi, Z., & Range, F. (2017). Importance of a species' socioecology: Wolves outperform dogs in a conspecific cooperation task. *Proceedings of the National Academy of Sciences*, **114(44)**, 11793-11798.

- Mayer, R. C., & Wittrock, R. (2006). Problem Solving in PA Alexandria and PH Winn eds Handbook of Educational Psychology.
- McCloskey, G., Whitaker, J., Murphy, R., & Rogers, J. (2012). Intellectual, cognitive, and neuropsychological assessment in three-tier service delivery systems in schools.
- McGrew, W. C. (1974). Tool use by wild chimpanzees in feeding upon driver ants. *Journal of human evolution*, 3(6), 501-508.
- McGrew, W. C. (1992). Chimpanzee material culture: implications for human evolution. Cambridge University Press.
- Miller, L.J., Bettinger, T.L. & Bexell, S.M. (2016). Environmental enrichment for captive aquatic animals: Recent advances and future directions. *Aquatic Mammals*, 42(3), 253-266.
- Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., Silk, J. B., & Snyder-Mackler, N. (2010). The evolution of nonhuman primate societies: past, present, and future. *Evolutionary Anthropology: Issues, News, and Reviews*, 19(4), 136-149.
- Morton FB, 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): 282-298.
- Mulcahy, N. J., & Call, J. (2006). Apes save tools for future use. *Science*, **312(5776)**, 1038-1040.
- Murray, E. D., Machado, C. J., & Knight, R. T. (2009). Orbitofrontal cortex, cognitive bias, and social decision-making in nonhuman primates. In *The Cognitive Neuroscience of Social Behaviour* (pp. 209-232). Psychology Press.
- Nater, A., Mattle-Greminger, M. P., Nurcahyo, A., Nowak, M. G., de Manuel, M., Desai, T., ... & Krützen, M. (2017). Morphometric, behavioral, and genomic evidence for a new orangutan species. *Current Biology*, 27(22), 3487-3498.

- Navarrete, A., Van Schaik, C. P., & Isler, K. (2011). Energetics and the evolution of human brain size. *Nature*, **480(7375)**, 91-93.
- Neisser, U., Boodoo, G., Bouchard Jr, T. J., Boykin, A. W., Brody, N., Ceci, S. J., ... & Urbina, S. (1996). Intelligence: Knowns and unknowns. *American psychologist*, *51(2)*, 77-101.
- Nisbett, R. E., Aronson, J., Blair, C., Dickens, W., Flynn, J., Halpern, D. F., ... & Turkheimer, E. (2012). Intelligence: new findings and theoretical developments. *American Psychologist*, *67(2)*, 130-159.
- Nishida, T. (1973). The ant-gathering behaviour by the use of tools among wild chimpanzees of the Mahali Mountains. *Journal of Human Evolution*, *2(5)*, 357-370.
- Penn, D. C., & Povinelli, D. J. (2007). On the lack of evidence that non-human animals possess anything remotely resembling a 'theory of mind.' *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362(1480)*, 731-744.
- Penn, D. C., Holyoak, K. J., & Povinelli, D. J. (2008). Darwin's mistake: Explaining the discontinuity between human and nonhuman minds. *Behavioral and Brain Sciences*, *31(2)*, 109–130.
- Pika, S., & Mitani, J. C. (2006). Referential gestural communication in wild chimpanzees (*Pan troglodytes*). *Current Biology*, *16(6)*, R191-R192.
- Povinelli, D. J. (2000). *Folk physics for apes: The chimpanzee's theory of how the world works*. Oxford University Press.
- Povinelli, D. J., & Vonk, J. (2004). We don't need a microscope to explore the chimpanzee's mind. *Mind & Language*, *19(1)*, 1–28.
- Povinelli, D. J., Reaux, J. E., Theall, L. A., & Giambrone, S. (2000). Exploring chimps' cognitive abilities with the rope-cleaning task. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *51(1)*, 1-11.

- Pradhan, G. R., Tennie, C., & van Schaik, C. P. (2012). Social organization and the evolution of cumulative technology in apes and hominins. *Journal of human evolution*, **63**(1), 180-190.
- Prado-Martinez, J., Sudmant, P. H., Kidd, J. M., Li, H., Kelley, J. L., Lorente-Galdos, B., ... & Wall, J. D. (2013). Great ape genetic diversity and population history. *Nature*, 499(7459), 471-475.
- Prüfer, K., Munch, K., Hellmann, I., et al. (2012). The bonobo genome compared with the chimpanzee and human genomes. *Nature*, 486(7404), 527-531. doi: 10.1038/nature11128
- Reader SM, Laland KN. 2003. Animal innovation: An introduction. In: *Animal innovation*. Oxford University Press. Pp. 3-35.
- Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences*, **99**(7), 4436-4441.
- Reader, S. M., Hager, Y., & Laland, K. N. (2011). The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**(1567), 1017-1027.
- Rijksen, H. D. (1978). A field study on Sumatran orang utans (*Pongo pygmaeus abelii*, Lesson 1827): ecology, behaviour and conservation. Wageningen: H. Veenman and Zonen.
- Rumbaugh, D. M., & Washburn, D. A. (2008). *Intelligence of apes and other rational beings*. Yale University Press.
- Schellenberg, E. G. (2004). Music lessons enhance IQ. *Psychological Science*, 15(8), 511-514.
- Schuppli, C., Burkart, J.M., & van Schaik, C.P. (2016). Co-occurrence of orangutan tool-use and social learning is rare. *American Journal of Primatology*, 78(3), 309-318.

- Schuppli, C., van Schaik, C.P., & Burkart, J.M. (2012). Effect of travel costs and age on natural food choice in wild immature orangutans. *Behavioral Ecology*, 23(1), 67-73.
- Seed, A. M., Clayton, N. S., & Emery, N. J. (2012). Cooperative problem solving in rooks (*Corvus frugilegus*). *Proceedings of the Royal Society B: Biological Sciences*, 279(1739), 4940-4945.
- Shepherdson, D.J. & Swaisgood, R.R. (2005). Environmental enrichment as a strategy for mitigating welfare problems in zoos: a review and prospectus. In G. Mason & J. Rushen (Eds.), *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare* (pp. 212-233). Wallingford, UK: CABI Publishing.
- Shumaker, R. W., Walkup, K. R., & Beck, B. B. (2011). *Animal tool behavior: the use and manufacture of tools by animals*. JHU Press.
- Singleton, I. & van Schaik, C.P. (2002). Orangutan home range size and its determinants in a Sumatran swamp forest. *International Journal of Primatology*, 23(3), 487-513.
- Singleton, I. (2009). Orangutan population biology: food, parasites, and pregnancies. In S. Wich, S. Utami Atmoko, T. Mitra Setia, & C.P. van Schaik (Eds.), *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 161-171). Oxford University Press.
- Skibieli, A.L., Trevino, H.S. & Naugher, K. (2007). Evaluation of three forms of enrichment for captive felids. *Zoo Biology*, 26(5), 371-381.
- Sol D, Griffin AS, Bartomeus I, Boyce H. 2012. Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PLoS ONE* 7(2): e31735.
- Sol, D. (2009). The cognitive-buffer hypothesis for the evolution of large brains'. *Cognitive ecology II*, 111-136.
- Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences*, 102(15), 5460-5465.

- Soulsby, A. (2013). The effectiveness of food enrichment in elephants. Unpublished dissertation, Duke University, Durham, NC.
- Spearman, C. (1961). " General Intelligence" Objectively Determined and Measured.
- Spehar, S. N., Campbell-Smith, G., & Nardiyono, N. (2010). Estimating orangutan densities using the standing crop and marked nest count methods: lessons learned for conservation. *Endangered Species Research*, 12(3), 249-256.
- Stoinski, T.S., & Whiten, A. (2003). Social learning by great apes. In F.B.M. de Waal, & P.L. Tyack (Eds.), *Animal social complexity: Intelligence, culture, and individualized societies* (pp. 333-352). Harvard University Press.
- Subiaul, F., Vonk, J., & Okamoto-Barth, S. (2008). Testing the social intelligence hypothesis: A comparative study on visual cooperative problem solving in 12-month-old humans (*Homo sapiens*) and orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, 122(1), 45-54.
- Sugardjito, J., & Nurhuda, T. (1981). Orangutan sociality, with special reference to the Tanjung Puting population. *Animal Behaviour*, 29(3), 974-978.
- Taylor, A. B., & van Schaik, C. P. (2007). Variation in brain size and ecology in *Pongo*. *Journal of human evolution*, 52(1), 59-71.
- Thompson, R. F., & Spencer, W. A. (1966). Habituation: a model phenomenon for the study of neuronal substrates of behaviour. *Psychological review*, 73(1), 16.
- Tomasello, M. & Call, J. (2004). The study of primate cognition: Lessons from Capuchin monkeys for understanding the evolution of human cognition. In M.J. de Waal & P.L. Tyack (Eds.), *Animal Social Complexity: Intelligence, Culture, and Individualized Societies* (pp. 183-202). Harvard University Press.
- Tomasello, M. (1999). The human adaptation for culture. *Annual review of anthropology*, 28(1), 509-529.
- Tomasello, M., & Call, J. (1997). *Primate cognition*. Oxford University Press.
- Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, 55(4), 1063–1069.

- Utami, S. S., Goossens, B., Bruford, M. W., de Ruiter, J. R., & van Hooff, J. A. R. A. M. (2009). Male bimaturism and reproductive success in Sumatran orangutans. *Behavioral Ecology*, 20(1), 54-63.
- Utami, S. S., Goossens, B., Bruford, M. W., de Ruiter, J. R., van Hooff, J. A., & van Schaik, C. P. (2002). Male bimaturism and reproductive success in Sumatran orangutans. *Behavioral Ecology*, 13(5), 643-652.
- van Noordwijk, M. A., Arora, N., Willems, E. P., Dunkel, L. P., & Utami Atmoko, S. S. (2009). Female philopatry and its social benefits among Bornean orangutans. *Behavioral Ecology and Sociobiology*, 63(6), 827-839.
- van Noordwijk, M. A., Willems, E. P., Utami Atmoko, S. S., Kuzawa, C. W., & van Schaik, C. P. (2012). Multi-year lactation and its consequences in Bornean orangutans (*Pongo pygmaeus wurmbii*). *Behavioral Ecology and Sociobiology*, 66(4), 565-578.
- van Noordwijk, M.A. & van Schaik, C.P. (2005). Development of ecological competence in Sumatran orangutans. *American Journal of Physical Anthropology*, 127(1), 79-94.
- van Noordwijk, M.A., van Schaik, C.P., Suci Utami, S.S., & Rijksen, H.D. (2009). Feeding competition in female orangutans: Why are females more likely to join a new group after a male take-over? In S. Wich, S. Utami Atmoko, T. Mitra Setia, & C.P. van Schaik (Eds.), *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 187-200). Oxford University Press.
- van Schaik, C. P. (1999). The socioecology of fission-fusion sociality in orangutans. *Primates*, 40(1), 69-86.
- van Schaik, C. P. (2016). *The primate origins of human nature*. John Wiley & Sons.
- van Schaik, C. P., & Burkart, J. M. (2011). Social learning and evolution: the cultural intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 1008-1016.

van Schaik, C. P., Burkart, J., Damerius, L., Forss, S. I., Koops, K., van Noordwijk, M. A., & Schuppli, C. (2016). The reluctant innovator: orangutans and the phylogeny of creativity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **371**(1690), 20150183.

van Schaik, C. P., Fox, E. A., & Sitompul, A. F. (1996). Manufacture and use of tools in wild Sumatran orangutans. *International Journal of Primatology*, *17*(3), 309-325.

van Schaik, C.P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C.D., Singleton, I., ... & Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science*, *299*(5603), 102-105.

van Schaik, C.P., Djojosedharmo, S., & Willems, E.P. (2009). Long-term orangutan—habitat relationships. In S. Wich, S. Utami Atmoko, T. Mitra Setia, & C.P. van Schaik (Eds.), *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 111-120). Oxford University Press.

Visalberghi, E., Fragaszy, D. M., & Savage-Rumbaugh, E. S. (1995). Performance in a tool-using task by common chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), an orangutan (*Pongo pygmaeus*), and capuchin monkeys (*Cebus apella*). *Journal of comparative psychology*, *109*(1), 52-60.

Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science*, *311*(5765), 1301-1303.

White, M.L., Porter, L.J. & Duffield, D. (2003). Environmental enrichment for marine mammals in captivity. *Journal of Applied Animal Welfare Science*, *6*(1), 27-47.

Whiten, A., & Van Schaik, C. P. (2007). The evolution of animal ‘cultures’ and social intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362**(1480), 603-620.

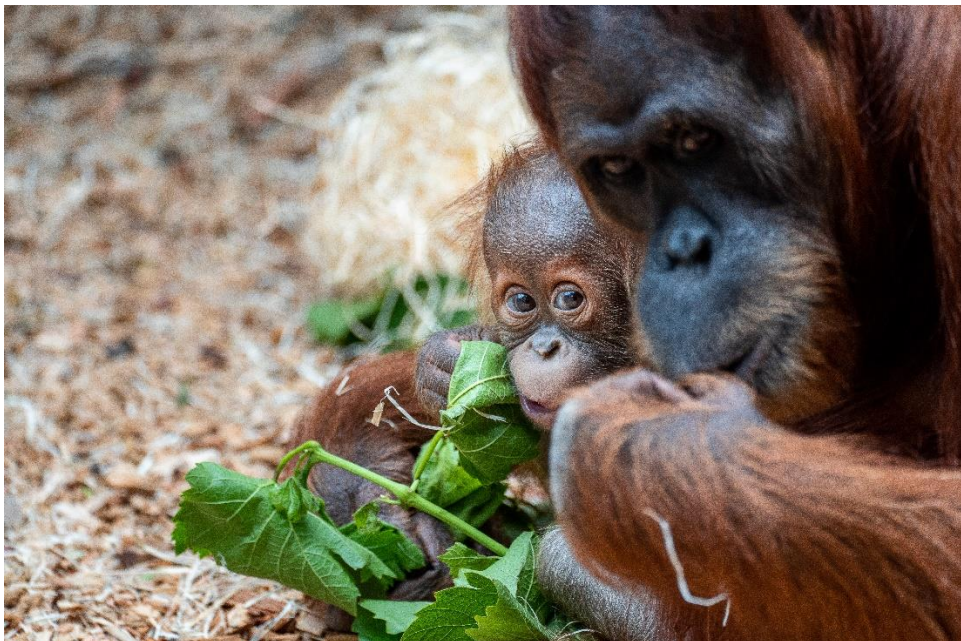
Whiten, A., Byrne, R.W., Henzi, S.P. & Johnstone, R.A. (1999). Teaching strategies in wild baboons. *International Journal of Primatology*, *20*(6), 853-871.

- Whiten, A., Horner, V., & De Waal, F. B. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, **437(7059)**, 737-740.
- Wich, S. A., Meijaard, E., Marshall, A. J., Husson, S., Ancrenaz, M., Lacy, R., ... & Nardiyono, N. (2016). Distribution and conservation status of the orangutan (*Pongo* spp.) on Borneo and Sumatra: how many remain?. *Oryx*, **50(2)**, 1-14.
- Wich, S. A., Utami, S. S., Setia, T. M., Rijksen, H. D., Schürmann, C., van Hooff, J. A. R. A. M., & van Schaik, C. P. (2009). Life history of wild Sumatran orangutans (*Pongo abelii*). *Journal of Human Evolution*, **56(5)**, 471-485.
- Wich, S. A., Utami-Atmoko, S. S., Setia, T. M., Rijksen, H. D., Schürmann, C., Van Hooff, J. A. R. A. M., & van Schaik, C. P. (2004). Life history of wild Sumatran orangutans (*Pongo abelii*). *Journal of human evolution*, **47(6)**, 385-398.
- Wilson, E. O. (1991). *The diversity of life*. Harvard University Press.
- Wilson, M. L., Hauser, M. D., & Wrangham, R. W. (2014). Chimpanzees and the limits of animal rights. In *The Ethics of Animal Research* (pp. 77-97). Springer, Cham.
- Winner, E., Cooper, M. M., & Gardner, H. (1987). Perception of art by chimpanzees (*Pan troglodytes*). *Journal of Aesthetics and Art Criticism*, **46(4)**, 369-375.
- Woodley of Menie, M. A., Fernandes, H. B. F., & Madison, G. (2015). The eminence of g in the 21st century: Reaffirming the dominance of general intelligence in predicting important life outcomes. *Personality and Individual Differences*, **86**, 139-144.
- Yocom, A. M., & Boysen, S. T. (2011). The influence of perceptual similarity and category membership on proactive interference in a cross-modal tool use task in chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Journal of Comparative Psychology*, **125(4)**, 445-454.
- Yoerg, S. I. (2002). *Clever as a fox: animal intelligence and what it can teach us about ourselves*. Harvard University Press.

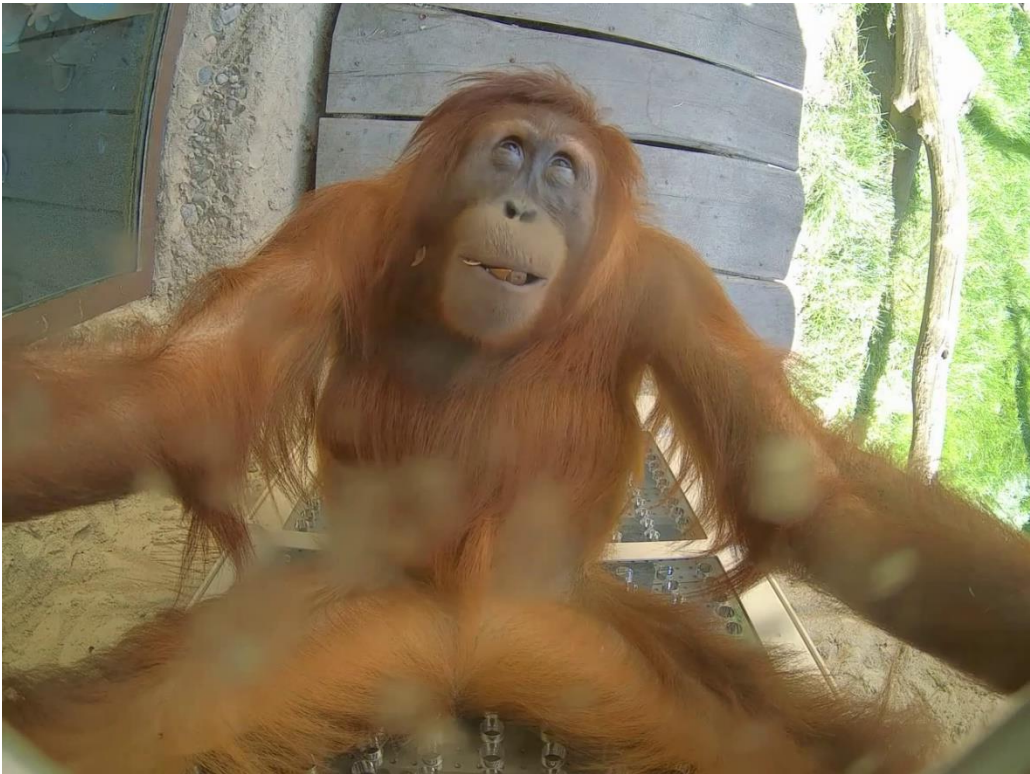
Young, R.J. (2003). Environmental enrichment for captive animals. Oxford, UK:
Blackwell Science.

8. Appendix

8.1. Appendix I – Images of test subjects and test tool









sf

