Tinder for orang-utans: comparing sexually selective cognition among Bornean orang-utans (Pongo pygmaeus) and humans (Homo sapiens)

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Chapter 1

General introduction

Choosing a partner is one of the most critical decisions that humans make during their life. Even though it is important, the mechanisms underlying mate choice remain a mystery, because mate choice is such a complex and multifaceted phenomenon. Nevertheless, it has been established that cognition plays a pivotal role in finding a suitable mate. A broad definition of cognition encompasses perception, learning, memory, and decision making, and refers to all mechanisms that allow an individual to acquire, process, store, and act on external information (Shettleworth, 2010). This definition encompasses both fast, reflexive, subconscious processes, also referred to as implicit cognition, and slower, more versatile processes, also referred to as explicit cognition (Frith & Frith, 2008). In the case of mate choice, reflexive attention towards an attractive face could for instance be considered implicit cognition, while selecting the most attractive face out of a set would be considered explicit cognition.

The importance of cognitive processes in mate choice can clearly be observed in humans: when asking people to describe how they feel about their loved one or the first encounter with their loved one, they often refer to specific cognitive processes, such as attention, memory, and implicit associations. “I could not get my eyes off him”, “She immediately caught my attention”, or “I cannot get him out of my head”: almost everybody has used or heard such statements about a romantic partner. These cognitive processes in the context of mate choice have been termed *sexually selective cognition* (Maner & Ackerman, 2015; Box 1), which implies that exploring the cognitive mechanisms involved in mate choice and attractiveness can provide valuable insights into a complex phenomenon like mate choice.

Even though humans find it very easy to speak about mate choice in cognitive terms, we seem relatively reluctant to apply similar terminology to non-human mate choice. This is also reflected in research: while a plethora of studies has investigated the interplay between cognition and mate choice in humans, only few studies have started to explore this topic in our closest animal relatives. However, from an evolutionary perspective one would expect non-human animals to have analogous or homologous cognitive mechanisms that could help navigating the mate choice process (Bateson & Healy, 2005; Billington et al., 2020; Grammer et al., 2003). Interestingly, the impressive technological developments (e.g., touchscreens and eye-trackers) of the last two decades now allow us to study non-human cognition in more depth, and these developments have enabled researchers to investigate topics like emotion perception (e.g., Kret et al., 2016, 2018; Pritsch et al., 2017; van Berlo et al., 2023), theory of mind (e.g., Krupenye et al., 2016), and ingroup-outgroup bias (e.g., Kret et al., 2014; Lewis et al., 2021; van Berlo et al., 2023) in primates. Up until now, however, very few studies have applied these technologies to study cognition and mate choice in non-human animals, and especially great apes.

Box 1: sexually selective cognition
Sexually selective cognition (Maner & Ackerman, 2015) can be considered as an integration of evolutionary psychology, cognitive psychology, and motivation science. More specifically, the approach is concerned with how mating motivations influence cognitive processes in an evolutionarily adaptive manner. Sexually selective cognition aligns with evolutionary psychology because it assumes that the mind has been shaped by adaptive problems, which over time has resulted in mental adaptations to handle these problems (Tooby & Cosmides, 2015). It is a cognitive approach in the sense that it focuses on multiple aspects of how the brain processes information: perception, encoding, and decision-making. Furthermore, it encompasses both implicit, reflexive, cognitive processes and explicit, more flexible, cognitive processes (Maner et al., 2003). In addition, it takes a fundamental motives approach to cognition (Kenrick et al., 2010; Schaller et al., 2017) by investigating how a specific motivational state, in this case, related to mate choice, results in functional cognitive biases or attunements. From a Tinbergian perspective (Tinbergen, 1963), the approach is mainly concerned with identifying mechanistic explanations while assuming a functional basis. Maner & Ackerman (2015) discuss multiple examples related to different aspects of mate choice motivation and cognition. They discuss how people who look for a partner are more sensitive to cues of attractiveness (Maner et al., 2003), how differential reproductive costs for men and women result in sex differences in overestimating sexual interest (Haselton & Buss, 2000; Samara et al., 2021), and how being in a relationship results in lower sensitivity to attractive conspecifics (e.g., Karremans et al., 2011). In this dissertation, I will mainly focus on the first topic: how does mating motivation relate to cognitive attunement towards attractiveness or attractive traits?

This thesis addresses this research gap by investigating the interplay between cognition and mate choice in humans and Bornean orang-utans (*Pongo pygmaeus*). From a fundamental perspective, orang-utans are an interesting taxon to study this topic for two reasons. First, they are characterised by male bimaturism, meaning that adult males come in two distinct phenotypes (Utami et al., 2002). Second, orang-utan females seem to clearly prefer one type of male over the other when it comes to mating (Knott et al., 2009). From a practical perspective, the captive orang-utan population has relatively low breeding success (Kaumanns et al., 2004), and identifying cognitive tasks that can help to identify preferred mates could potentially help refining the orang-utan breeding programme.

To comparatively investigate the interplay between cognition and mate choice, both humans and Bornean orang-utans took part in various computerized tasks, eye-tracking studies and auditory playback setups. Additionally, humans were asked to provide attractiveness ratings of conspecifics, and went on speed-dates designed to resemble the natural mate choice context as much as possible (Finkel & Eastwick, 2008). Across different empirical studies, I investigated how immediate attention, voluntary attention and preferences were modulated by ratings of attractiveness (humans) or presence of secondary sexual characteristics (orang-utans).

Overall, the aim of this thesis is two-fold: to investigate to what extent attractiveness affects human cognition by employing different test paradigms, and to explore whether we can extend these paradigms to a closely-related great ape species. Such a comparison between related species will not only result in deeper understanding of the evolutionary emergence of cognitive phenomena (Panksepp et al., 2002; Smith et al., 2018), such as mate-related cognitive biases, and how they relate to socio-ecological differences between species, but the results of this thesis could also inspire practical applications, such as test paradigms that can identify individual mate preferences of zoo-housed animals. To start, I first provide an introduction to several concepts that are key to this thesis, after which I will provide an overview of the main themes discussed in this thesis.

Sexual selection and the evolution of attractiveness

From a biological perspective, evolved mate preferences are likely the result of sexual selection. In *The Descent of Man* (1871), Charles Darwin proposed his theory of sexual selection to explain the evolution of exaggerated secondary sexual characteristics, which are common in the animal kingdom. Darwin defined sexual selection as selection on “*the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction*” (Darwin, 1871, p. 256). Sexual selection can generally be divided into two types: intersexual selection, where traits make an individual more attractive to the opposite sex, and intrasexual selection, where traits are useful in competition between members of the same sex for access to mates. The sex that exerts these different types of sexual selection depends strongly on parental investment (Trivers, 1972), with females typically investing more energy in reproduction, leading to male-male competition and female choice. However, in species with biparental care, such as humans, mutual mate choice might be more common (Courtiol et al., 2016), because both sexes invest valuable energy in caring for their offspring.

Darwin’s ideas about sexual selection remain remarkably relevant to current research (Jones & Ratterman, 2009). More specifically, his work has inspired many to apply sexual selection theory to the topic of attractiveness (Grammar et al., 2003; Rhodes, 2006). Such evolutionary theories of attractiveness rely on two main assumptions. First, attractiveness, or attractive characteristics should reflect an individual's ability to provide benefits either directly or indirectly (Jones & Ratterman, 2009). For example, an attractive individual might offer *direct benefits* to a partner (e.g., a good territory or defense against intruders). Alternatively, attractiveness might reflect *indirect benefits*, meaning that high levels of attractiveness correspond to genetic quality. Second, evolutionary theories assume that selecting attractive individuals as a partner is adaptive, because it might affect the number, health, or attractiveness of offspring (Grammer et al., 2003; Little, Jones, et al., 2011). Thus, attractiveness should reflect the quality of the partner, which in turn might affect the quality and/or quantity of offspring.

Both of these assumptions can be relatively easily tested in non-human animal species. For instance, in non-human primates, several examples of potentially attractive traits can be found. First, symmetry of either the face or the whole body has been hypothesized to indicate stable development, thereby serving as an indicator of genetic quality (Gangestad et al., 1994; Little, Jones, et al., 2011). In line with this, facial symmetry positively correlated with health and body condition in chimpanzees (*Pan troglodytes*: Sefcek & King, 2007) and rhesus macaques (*Macaca mulatta*: Little et al., 2012). Second, many male primates are characterized by secondary sexual characteristics preferred by females or associated with more reproductive output. For example, male gorillas (*Gorilla gorilla gorilla*) with more prominent sagittal crests, larger bodies, and larger gluteal muscles tend to have more mates and more offspring, reflecting female preferences for extreme sexual dimorphism (Breuer et al., 2012). Third, in some species, males show dynamic changes in appearance. Such changes in appearance often covary with competitive ability or health (reviewed in Petersen & Higham, 2020), and can covary with female preferences (e.g., Setchell, 2005). Thus, in line with the first assumption of evolutionary theories of attractiveness, specific male characteristics can be predictive of male quality, and might be preferred by females.

An overwhelming amount of evidence supports the second assumption, that selecting attractive individuals should result in healthier and/or more offspring. Most studies investigating this topic used a mate preference test to identify preferred mates. In this test, individuals are placed in a mate preference arena (e.g., Anderson et al., 2007; Pogány et al., 2014). These arenas allow an individual to inspect multiple conspecifics of the opposite sex. Based on different criteria, such as proximity, affiliative behavior, courtship behavior, and agonistic behavior, the preference of the chooser can be assessed. In most studies, half of the choosers are then paired with their preferred mate, while the other half is paired with a non-preferred mate. A qualitative review across taxa that examined results from such setups showed that quantitative and qualitative measures of reproductive output were almost exclusively higher for animals that were allowed to choose their partner (Martin-Wintle et al., 2019). This suggests that selecting individuals based on attractive traits might indeed facilitate successful reproduction.

Concluding, studies on non-human animals provide evidence for the assumption that attractive traits might inform conspecifics about mate quality, and that selecting for attractive traits might increase reproductive success. This raises the question of whether these assumptions also hold for humans.

Human mate choice

When considering evidence for both assumptions in human populations, a more complex pattern emerges. With regard to the first assumption, a clear link between visual attractiveness and markers of health has not been established yet: while some studies claim a positive association (Hönekopp et al., 2004; Mengelkoch et al., 2022; Nedelec & Beaver, 2014), other studies found null results (Cai et al., 2019; Jones et al., 2021; Pátková et al., 2022). When looking at specific traits that are considered attractive, a similar pattern emerges. A clear example of this is facial symmetry: humans rate symmetrical faces as more attractive (Rhodes, 2006) and healthy looking (Rhodes et al., 2007). It has also been suggested that symmetry might be a reliable indicator of health (Valen, 1962). However, studies have mostly failed to identify such a relationship (Hönekopp et al., 2004; Pound et al., 2014; Rhodes et al., 2001). It is important to note that these null results only show that the association between health and attractiveness is unclear in our *current* environment. A potential explanation for these equivocal findings is that health and attractiveness were related in our evolutionary past, but that this association has been obfuscated by recent innovations, such as modern medicine and beauty products (Thornhill & Gangestad, 1999). Altogether, there is no unequivocal evidence for a link between attractiveness and health in current human populations.

With regard to the second assumption, attractive humans seem to have more reproductive success, although the results are somewhat equivocal and the underlying mechanisms remain poorly understood. Some studies report a positive association between attractiveness and proxies of reproductive success, such as number of sexual partners (Rhodes et al., 2005), sexual activity (Karraker et al., 2017), probability of marriage (Prokop & Fedor, 2011), and number of offspring (Jokela, 2009; Pflüger et al., 2012; Prokop & Fedor, 2011). However, other studies report no association. For example, Sorokowski et al. (2017) found no significant difference in reproductive success between arranged marriages and non-arranged marriages in three indigenous societies, and Silva et al. (2012) even found a negative association between attractiveness and reproductive success in one population. Altogether, these results suggest that attractiveness and reproductive success are linked in humans, but the results are somewhat inconsistent.

One potential reason for the inconsistent findings on the topic of attractiveness and reproductive success is that human mate choice is a multifaceted phenomenon. One can imagine human mate choice as an enormous jigsaw puzzle, with attractiveness being just one of the pieces. To better understand the role of attractiveness in human mate choice, I will consider human mate choice as a two-stage process (Dixson, 2012; Fisher, 1998; Figure 1). When two potential mates meet, they will first judge each other on easily observable cues. This first stage can be considered an initial filter, and is especially driven by fast perception and appraisal of attractiveness (Dixson, 2012). Passing this first filter is required for *attraction* (Fisher, 1998). Ample evidence indeed shows that humans employ such a first filter when choosing a partner (Asendorpf et al., 2011; Eastwick & Finkel, 2008; Luo & Zhang, 2009; Sidari et al., 2021). Consequently, this first filter is also where we expect *sexually selective cognition* (e.g., or attention, memory, and implicit associations) to play a large role.

The importance or threshold of the first filter may differ between individuals. For instance, previous research has suggested that men and women might differ in the strength of their initial attraction-filter. More specifically, differential evolutionary costs are at play for men and women, resulting in different priorities during mate choice (Buss & Schmitt, 1993). One common conclusion from cross-cultural studies is that men value attractiveness more than women, while women put a stronger emphasis on resources (Buss, 1989; Li & Meltzer, 2015). While some studies indeed find indications of sex differences in cognitive biases towards attractiveness (e.g., Maner et al., 2003; Mitrovic et al., 2018; Zhang et al., 2017), this effect does not always replicate in ecologically valid studies of human mate choice, such as speed-date paradigms, were attractiveness is a good predictor of mate choice for both men and women (Eastwick & Finkel, 2008; Luo & Zhang, 2009; Selterman et al., 2015). Thus, while the attraction-filter may somewhat differ between men and women, the results are far from conclusive.

Only when a potential mate "passes" the first filter, the second filter will be applied. This filter corresponds to *attachment* (Fisher, 1998), and focuses more on perception and appraisal of personality traits and behavioural compatibility, and explicit judgements about a potential partner (Dixson, 2012). Attachment filters might be especially common in pair-bonding species like humans, where compatibility and behavioural coordination are essential for successful reproduction (Eastwick et al., 2023; Roth, Samara, Tan, et al., 2021). Concluding, from a temporal perspective, humans first "filter" their potential partners based on attractiveness, only after which they consider other factors, such as personality and behavioural alignment.

Although the second filter might be especially relevant for pair-bonding species, a first filter based on perception of attractiveness and the associated cognitive biases should also be present in other species. Therefore, in addition to investigating the influence of attractiveness on cognitive mechanisms in humans, this thesis will also investigate whether this is the case for Bornean orang-utans.

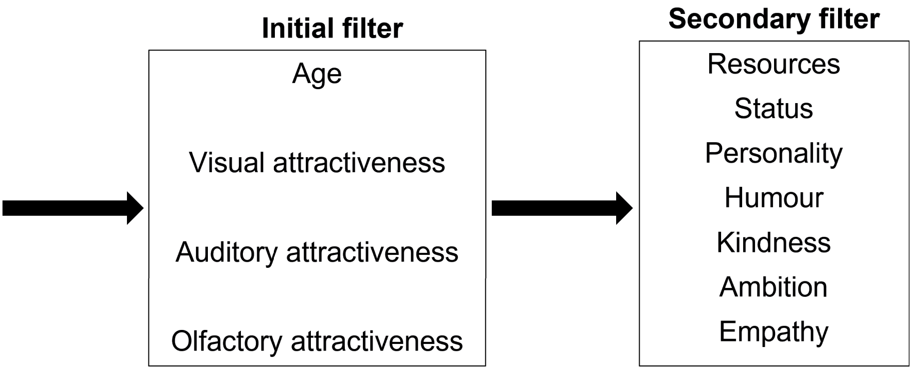

Figure 1. Schematic depiction of a two-stage model of human mate choice. Adapted from Dixson (2012).

Orang-utan socio-ecology

Orang-utans (*Pongo* spp.) are arboreal great apes that are native to Borneo and Sumatra. They share a last common ancestor with humans, that lived approximately 14 million years ago (Goodman et al., 1998). Currently, three species of orang-utans are distinguished (Figure 2): Bornean orang-utans (*P. pygmaeus*), Sumatran orang-utans (*P. abelii*) and Tapanuli orang-utans (*P. tapanuliensis*). Even though differences in behaviour can be found between different orang-utan species (Delgado & Schaik, 2000; van Schaik et al., 2008), recent work has emphasized their similarities (van Noordwijk et al., 2018) and suggests that some of the behavioural differences might result from plastic responses to local fruit availability (Roth et al., 2020). In general, orang-utans are characterized by a semi-solitary lifestyle, which is unique among the great apes (Mitra Setia et al., 2008; Roth et al., 2020; van Schaik, 1999). However, occasional social interactions do occur, and provide opportunities for socializing, playing, and mating (van Schaik, 1999). In some populations, the frequency of socialization seems linked to the availability of fruit, with more social interactions occurring during times of abundance (Roth et al., 2020).

Besides their peculiar social system, orang-utans are characterized by another uncommon trait, namely *male bimaturism*. This means that adult male orang-utans can be categorized in two distinct morphs: unflanged males and flanged males (Utami et al., 2002). Unflanged males experience a period of arrested development. They are sexually mature and can produce offspring, but are non-preferred mates for adult females (Knott et al., 2009; Kunz et al., 2022). In contrast, flanged males have fully developed secondary sexual characteristics, such as an extremely large body size, long hair, a large throat sac, and conspicuous flanges on the sides of their faces (Kunz et al., 2022). Furthermore, flanged males can produce long calls that seem to have a dual function: coordinating distance between males and attracting females (Mitra Setia & van Schaik, 2007). Importantly, orang-utan females seem to apply an *attraction filter* during mate choice: they prefer to mate with flanged males during their ovulation, potentially reflecting selection for good genes (Knott et al., 2009). Thus, the two male morphs are easily distinguishable based on visual and auditory cues, and females seem to discriminate between the morphs during their fertile phase.

Because orang-utans are characterized by two distinct male morphs, they provide an excellent species to study the interplay between secondary sexual traits and attention. While we know that secondary sexual characteristics affect cognitive processes such as attention in humans (Garza & Byrd-Craven, 2023; Yang et al., 2015), this topic has been virtually unexplored in great apes. However, to develop a full understanding of the evolutionary underpinnings of such attentional biases, it is important to test a wide range of species (Smith et al., 2018), ideally with different mating systems (Petersen & Higham, 2020). Because orang-utans are a suitable model organism for this topic, part of this thesis investigates whether Bornean orangutans show cognitive biases towards flanged males.

Figure 2. Pictures of flanged males of each orang-utan species. Left picture: courtesy of Ronald van der Beek. Middle picture: Tom Roth. Right picture: Tim Laman (redistributed under CC BY 4.0).

Dissertation outline

This dissertation consists of one review chapter and six empirical research chapters that investigate the influence of attractiveness or attractive traits on cognitive mechanisms that underly mate choice in either humans or orang-utans. The thesis is divided into three sections and a general discussion. Section 1 (Chapter 2) presents a literature review summarizing experimental paradigms that are relevant to the thesis. Section 2 (Chapters 3-5) provides evidence for biased visual attention towards attractive conspecifics in humans. Section 3 (Chapters 6-8) investigates visual attention and preference towards flanged males in Bornean orang-utans (*Pongo pygmaeus*). Chapter 9 concludes this thesis with a general discussion. I want to emphasize that, while the chapters are logically ordered in this thesis, most of them were performed in parallel. Based on the pattern that emerges from the chapters, I have placed them in a logical order. Furthermore, because the chapters were written as independent research articles, they contain some theoretical overlap.

Chapter 2 provides a theoretical basis for the empirical chapters, by reviewing previous research that investigated how attractiveness modulates cognition in humans and cognitive biases towards attractive characteristics in primates. Furthermore, I discuss test paradigms that can potentially be used to study mate preferences in primates, some of which will be used in the empirical chapters, and I discuss the practical relevance of applying such tasks to refine zoo breeding programmes.

Chapter 3 examines the role of visual, auditory and olfactory attractiveness in human mate choice, using a naturalistic speed-date paradigm and attractiveness rating tasks. The main aim of this chapter was to investigate the notion that human attraction is multimodal, by comparing the relative importance of visual, auditory and olfactory attractiveness on willingness to date again.

Taking into account the results of Chapter 3, **Chapter 4** specifically focuses on visual cognition by investigating how immediate attention and reflexive gaze cueing in humans are modulated by general ratings of facial attractiveness, and facial symmetry, a trait that is often associated with attractiveness. The goal of this chapter is to test whether attractiveness-driven implicit cognitive biases exist in a community sample, irrespective of idiosyncratic attractiveness preferences. Furthermore, we explored whether such biases were driven by sex and age.

Chapter 5 follows up on this work by not relying on pre-defined attractiveness categories, and taking idiosyncratic preferences into account instead. By combining cognitive tasks, attractiveness rating tasks, and speed-dating, I explore to what extent immediate and voluntary visual attention are driven by idiosyncratic attractiveness preferences, and how they relate to human mate choice in a speed-date context.

Chapter 6 is the first chapter that moves away from humans. Here, I apply cognitive tasks to measure immediate attention and preference to investigate whether zoo-housed Bornean orang-utans have an immediate attentional bias towards flanges and symmetrical faces, and a choice bias for pictures of flanged males. To study this, I used two well-established computerized task: the dot-probe task to study immediate attention, and a preference test to study choice bias.

Chapter 7 extends this work by testing Bornean orang-utans using a non-invasive eye-tracking setup, similar to the setup that was used to test humans (Chapter 5). Across two experiments, I explored whether orang-utans showed biased immediate and voluntary attention towards flanged males. Furthermore, the design of the second experiment allowed to explore whether the orang-utans showed a stronger attention bias towards certain conspecifics.

In **Chapter 8,** the thesis shifts its focus from visual to auditory information by investigating the effect of orang-utan long calls on female behaviour. More specifically, I describe two case reports of ovulation-induced vocalization and behavioural sensitivity towards male long calls in female Bornean orang-utans. These two cases suggest a potential role for male long calls in orang-utan female mate choice. Furthermore, these cases are the first to indicate that female orang-utans might produce ovulation vocalizations that communicate their proceptivity.

Finally, **Chapter 9** closes the thesis with a general discussion and conclusion, where I emphasize and integrate the main findings from this thesis, and compare my findings in humans and Bornean orang-utans. I also propose relevant directions for future research and discuss practical applications.