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

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Chapter 9

General discussion

Primates, including humans, often rely on visually conspicuous traits to judge the quality of a potential mate (Petersen & Higham, 2020; Rhodes, 2006). Because choosing a good-quality mate has a significant bearing on an individual's biological fitness, it has been suggested that such traits have a strong influence on the cognitive processes of humans (Maner & Ackerman, 2015) and other animals (Bateson & Healy, 2005). Consequently, Maner & Ackerman (2015) proposed the term *sexually selective cognition* for cognitive attunements and biases related to mate choice. However, to date, sexually selective cognition has almost exclusively been studied in humans, whereas systematic studies in non-human primates are rare. This is unfortunate because a more comparative approach would allow for a better understanding of the phylogenetic history of sexually selective cognition. Moreover, this understanding can have practical implications for the management of primate populations in zoos.

This thesis addresses this fundamental research gap by investigating the interplay between cognition and mate choice in humans and Bornean orang-utans (*Pongo pygmaeus*) while simultaneously considering practical implementations within zoo breeding programmes. More specifically, I investigated whether humans and Bornean orang-utans show similar cognitive biases for mate-relevant information when presented with similar tasks, with an emphasis on attentional biases. I begin by summarizing the main findings of each chapter. The primary objective of the chapter summary is to offer a succinct overview of the main discoveries in each chapter, without integrating the results across chapters or with the existing body of literature. Following this, the subsequent sections will integrate the findings from various chapters and compare them to the existing literature, encompassing theoretical implications, methodological considerations, and practical implications. Finally, the chapter will conclude with a comprehensive summary.

Summary of main findings

In **Chapter 2**, I reviewed the literature on sexually selective cognition in humans and non-human primates. While a plethora of methods have been employed to investigate the interplay between attractiveness and cognition in humans, encompassing attentional processes, memory, and motivational processing, relatively few studies have investigated this phenomenon in non-human

primates. Moreover, the few studies that have investigated the link between attractiveness and cognition have mainly focused on visual attention, employing a preferential looking paradigm, even though a wide range of test paradigms has been developed to study primate cognition in recent decades. To close this gap, I suggested test paradigms that can be used across species to study sexually selective cognition from a comparative perspective. Furthermore, I discussed how these paradigms can be applied to investigate partner preferences in conservation breeding programmes, which may benefit well-being of captive animals and increase their reproductive success.

Primates are characterised by visual specialisation (Barton, 1998; DeCasien & Higham, 2019), and thus studies investigating sexually selected traits tend to focus on conspicuous visual traits (e.g., Petersen & Higham, 2020; Rhodes, 2006). Nevertheless, it has been suggested that research on human attractiveness should also embrace olfactory and auditory attractiveness, as voices and smells can convey a large amount of information about a person (Groyecka et al., 2017). In **Chapter 3**, I therefore investigated the unique role of visual, auditory, and olfactory attractiveness in human mate choice by combining multimodal attractiveness rating tasks with speed-dating, an ecologically valid paradigm to study human mate choice (Finkel & Eastwick, 2008). Sixty-seven heterosexual adolescents participated in the experiment, resulting in a total of 277 speed dates. The results indicate a strong positive link between idiosyncratic ratings of visual attractiveness before the date and the willingness to date again after the date. However, I found only equivocal effects for the idiosyncratic auditory and olfactory ratings. These findings provide strong evidence for the notion that attractiveness is especially in the eye of the beholder. That is, mainly visual information influences whether we perceive conspecifics as attractive or not. This is in line with a plethora of previous studies.

In **Chapter 4**, I investigated how general ratings of facial attractiveness or variation in attractive traits modulate implicit cognition in humans. Zoo visitors ($N = 450$ across the three experiments) participated in a dot-probe task (MacLeod et al., 1986) with stimuli varying in attractiveness category, a dot-probe task with stimuli varying in facial symmetry, or a gaze cueing task (Deaner et al., 2007) with stimuli varying in attractiveness category. The stimuli were obtained from a large standardized dataset (Ma, Correll, et al., 2015). In Experiment 1, I presented participants with attractive or unattractive faces paired with intermediately attractive faces. In line with our expectations, the implicit attention of participants

was drawn to attractive but away from unattractive faces. In Experiment 2, I presented participants with faces that varied in symmetry, a trait often considered to be correlated with facial attractiveness. Contrary to our expectations, I found no robust effect of facial symmetry on implicit attention. In Experiment 3, I employed a gaze-cueing paradigm (Deaner et al., 2007) to investigate whether participants would more readily follow the gaze of attractive faces. While I found a strong gaze cueing effect, this effect did not vary according to attractiveness category. Furthermore, I found no evidence of age or sex effects in either of the experiments. The findings presented in this chapter suggest that implicit attention but not gaze cueing is modulated by attractiveness. In addition, this attentional bias was present across age groups, and in both male and female participants. Previous studies on implicit attention have incorporated only attractive and intermediately attractive stimuli, and could not therefore investigate the differential effects of attractive and unattractive stimuli on implicit attention. Our findings showed that attention was specifically drawn to attractive faces but not to unattractive faces. This suggests that the attentional bias is not solely driven by the deviation of attractive faces from the average face, as unattractive faces also deviate from the average face but do not receive preferential attention.

In Chapter 4, I defined attractiveness categories based on previous ratings by an independent group of raters. Although humans strongly agree on attractiveness ratings (Langlois et al., 2000), 50% of the variation can be explained by individual preferences (e.g., Hönekopp, 2006). Therefore, **Chapter 5** examined the relationship between idiosyncratic attractiveness preferences and visual attention in a realistic mate choice context. I combined visual attractiveness rating tasks with two well-established attentional paradigms: a dot-probe paradigm to investigate immediate attention, and a preferential looking paradigm to investigate voluntary attention. Furthermore, all participants went on speed dates after completing the tasks. In line with previous studies, I found considerable inter-rater variability in the attractiveness ratings. With regard to immediate attention, idiosyncratic ratings of visual attractiveness were a good predictor of immediate attention in males, but not in females ($N = 57$ participants), although I found no robust sex effect. However, both male and female participants ($N = 35$ participants) showed a strong bias towards attractive faces in the preferential looking paradigm. Moreover, I found no consistent relationship between speed date outcome and immediate attention ($N = 56$ participants), whereas I found a robust association between speed-date outcome and voluntary attention for

both male and female participants ($N = 35$ participants). Our results complement previous studies that have found an association between general attractiveness ratings on attention (Ma, Zhao, et al., 2015; Roth et al., 2022) by showing that the same applies for idiosyncratic attractiveness ratings. Furthermore, our findings suggest that biases in voluntary attention concord with mate choice.

In **Chapter 6**, I moved away from humans and focused on Bornean orang-utans (*Pongo pygmaeus*). Across three touchscreen experiments, I investigated whether Bornean orang-utans showed an implicit attentional bias towards males with larger flanges or more symmetrical faces using the dot-probe paradigm. Furthermore, I presented orang-utans with a choice task that allowed them to view a picture of either a flanged or unflanged male. Previous studies have suggested that orang-utan females prefer to mate with flanged males (Knott et al., 2009). Furthermore, facial symmetry has been linked to health in multiple primate species (Little et al., 2012; Sefcek & King, 2007). Therefore, I expected individuals to immediately attend to males with larger flanges and symmetrical faces and to choose to look at flanged males. However, none of our expectations were confirmed: individuals had no clear attentional biases in the dot-probe paradigm and chose to look at flanged and unflanged males equally often in the choice task. Furthermore, the pattern in which they selected flanged and unflanged stimuli seemed random, as I did not find evidence for temporal clustering. However, I did find evidence for energy efficiency trade-offs and a colour bias in the preference task. The findings of this chapter cast doubt on the suitability of extrinsically rewarded touchscreen experiments to test partner preferences of zoo-housed orang-utans.

In **Chapter 7**, I employed non-invasive eye-tracking to investigate immediate and voluntary attention in Bornean orang-utans across two experiments. To this effect, I presented individuals ($N = 4$) with two stimuli that were presented simultaneously for four seconds. In Experiment 1, these presentations always consisted of one flanged and one unflanged male. In Experiment 2, I also presented pairs consisting of two flanged or two unflanged stimuli. Across the two experiments, I found that orang-utans (1) were more likely to fixate first on stimuli of flanged males, and (2) spent a larger proportion of time looking at flanged males. Furthermore, I found some indications of individual preferences in Experiment 2. Taken together, our results suggest that orang-utan attention is attuned toward flanged males, which suggests that sexual selection shaped attentional processes in orang-utans. However, our results should mainly be considered at the proximate level, as I cannot explain *why* orang-utans

specifically attended to flanged males. Their attentional bias might be driven by positive-valenced interest, but could also be the result of vigilance. This is also reflected in the fact that the participating male also had a bias towards flanged male stimuli. Therefore, future studies should further investigate the motivational drives behind this attentional bias.

While Chapters 6 and 7 focused on visual processing, **Chapter 8** reports the link between auditory signals and sociosexual behaviour of Bornean orang-utans. Because orang-utans are characterised by a dispersed social system, vocalisations might be crucial for social organisation and reproductive strategies (Delgado, 2006). I report anecdotal evidence of two zoo-housed Bornean orang-utan females which supports this idea. First, I described the behavioural response of Temmy to male long-call playbacks while she was ovulating. She showed a strong tendency to approach the origin of the sound, whereas she did not do so when I played control sounds. Furthermore, she responded by producing vocalisations. Second, I described the case of Eloise, who consistently showed an increase in proceptive behaviour during ovulation for at least over a decade. Similar to Temmy, she produced vocalisations during her ovulation. However, in contrast to Temmy, she proactively produced them. Both the vocalisations produced by Temmy and Eloise seem distinct from previously described orang-utan vocalisations. Thus, these observations suggest that the female vocal repertoire may be more extensive than previously thought. While conclusions about the function of these calls remain tentative, they may facilitate coordination between ovulating females and flanged males.

Overall, this thesis has shown that (1) sexually selective cognition has rarely been studied in non-human primates, even though suitable test paradigms are available, (2) human initial mate choice is strongly determined by visual attractiveness, and not auditory or olfactory attractiveness, (3) human attentional processes are attuned to visual attractiveness, both when using general ratings and idiosyncratic ratings of attractiveness, (4) Bornean orang-utans have an attentional bias in immediate and voluntary attention towards flanged males in an eye-tracking task, but no attentional biases or choice biases towards male flanges and/or facial symmetry in touchscreen tasks, and (5) Bornean orang-utan females can show both a behavioural and vocal response to visual or vocal indicators of flanged male presence during ovulation. Although these results have relevant theoretical and practical implications, methodological considerations and important knowledge gaps remain. This is discussed in the following section.

Theoretical implications

The multimodality of attraction

Human mate choice can be considered a two-stage process, consisting of two main filters (Dixson, 2012). While the first filter is thought to mainly focus on physical traits and attractiveness (attraction: Fisher, 1998), the second filter is more closely associated with personality traits and behavioural coordination (attachment: Fisher, 1998). In this thesis, I have specifically focused on the first filter, because *sexually selective cognition* is especially relevant at this point in time. Dixson (2012) postulates that the first filter consists of multimodal perception of attractiveness, encompassing olfactory, auditory and visual information. This is also in line with a recent paper that argued for a stronger integration of olfactory and auditory attractiveness in the study of human mate choice (Groyecka et al., 2017). However, the results of Chapter 3 strongly suggest that such a shift of focus is premature, at least in the context of initial mate choice. In contrast with the notion that multimodal attractiveness is important in human mate choice, I found strong evidence only for the role of visual attractiveness in initial mate choice, whereas attractiveness of smell and voice seemed to have little to no bearing on speed-date outcome.

This is not to say that olfactory and auditory information do not play a role in human mate choice at all. More specifically, these modalities could be especially relevant in early stages of inter-personal contact where auditory and olfactory information can be reliably perceived and evaluated, such as contexts in which no other people are present. However, during initial interactions this will often not be the case, and visual information may be the most reliable source of information in such a context. Therefore, I suggest splitting Dixson's (2012) attraction filter into two parts (Figure 1): potential mates are first discriminated based on visual attractiveness, because this is often the most conspicuous and reliable source of information. In the second attraction filter, auditory and olfactory information would play a larger role. Importantly, this filter could be applied simultaneously with the attachment filter. Furthermore, there might be trade-offs between the different filters, to the extent that 'scoring high' on one filter may to some extent compensate for 'lower scores' on another filter (Figure 1). However, these trade-offs require further investigation. A further point that requires attention is the link between culture and mate choice for odour. The effect of olfaction on mate choice could very well vary between cultures due to cultural variation in

the use of hygienic products and fragrances and attitudes towards natural body odour (Ferdenzi et al., 2020). However, recent work shows that variation in odour awareness is not well-explained by cultural differences, which suggests that there might be large individual differences in the importance of body odour for mate choice irrespective of culture (Sorokowska et al., 2018). In short, while multimodal perception of attraction might be at work during the early stages of inter-personal contact, my work suggests that existing models are not specific enough and require more finetuning.

In addition, Chapter 4 and 5 provide evidence for the notion that biases in attention are associated with this first attraction filter. This is in line with the idea that evolutionary relevant stimuli should receive preferential attention (Cosmides & Tooby, 2013). In Chapter 4 I have shown that an immediate bias towards generally attractive faces is present in a wide community sample, irrespective of sex and age of the perceiver. The results of Chapter 5 are somewhat in contrast with this result. More specifically, when testing adolescents that were motivated to find a partner, only men showed a robust immediate attentional bias towards more attractive opposite-sex stimuli. When considering voluntary attention, however, I identified a strong attentional bias towards attractive opposite-sex stimuli in both men and women. The results with regard to immediate attention are somewhat unexpected, because the attentional biases reported in Chapter 4 and 5 are very similar in effect size despite the fact that participants in Chapter 4 cover a wide age range and might have been in a relationship already, whereas the participants in Chapter 5 were all single and motivated to find a partner. This is in contrast with motivational approaches to cognition (Kenrick et al., 2010; Schaller et al., 2017), that suggest that motivational states bias cognitive processes in a functional way towards motivationally salient information. If that would be the case, one would have expected participants in the speed-date study to show a stronger attentional bias towards opposite-sex stimuli than participants from the community sample, because participants in the speed-date study were motivated to look for a partner. Thus, the findings of this thesis seem to point more towards a domain-general mechanism underlying bias towards attractive faces than a domain-specific mechanism that becomes only apparent in the context of mate choice (Principe & Langlois, 2012; Trujillo et al., 2014).

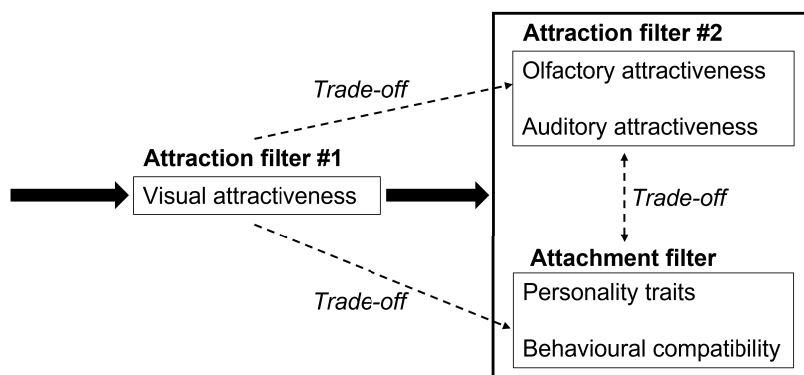


Figure 1. Schematic depiction of the updated two-stage model of human mate choice. The model still consists of two stages. However, stage two now consists of two separate filters. Furthermore, the model explicitly mentions trade-offs between different filters, allowing for a high 'score' on one filter to compensate for a lower 'score' on another.

The link between cognitive bias and behaviour

In addition, the results from Chapter 4 cast doubt on the link between attractive *traits* and immediate attentional biases. Whereas people did immediately attend to attractive faces, they did not show evidence of differential attention as a function of facial symmetry. This could be interpreted in two main ways. First, it could be argued that sexually selective cognition concerns attunement towards holistically attractive faces, and not specifically to slight variations in features that contribute to attractiveness. Second, it can be argued that facial symmetry is not as important for mate choice as has been argued in the past (e.g., Thornhill & Gangestad, 1999), and therefore does not receive preferential attention. The first interpretation cannot be rejected at the time of writing, because no cueing studies have been performed that use faces that vary in attractive traits other than symmetry, such as facial averageness or sexual dimorphism. The second interpretation, however, seems to concord with recent literature in multiple aspects. First, data-driven approaches to facial attractiveness have recently shown that facial symmetry does not contribute to attractiveness ratings (Holzleitner et al., 2019; Jones & Jaeger, 2019). Second, the link between mate quality and facial symmetry is heavily debated, given the lack of correlation between measures of health and facial symmetry (e.g., Foo et al., 2017; Pound et al., 2014). The results of Chapter 4 corroborate this interpretation, although it is not yet clear whether people show biases in immediate attention towards other traits that are linked to attractiveness, such as facial averageness.

One important assumption that underlies evolutionary approaches to cognition, is that cognitive adaptations or biases also translate into behavioural differentiation (Cosmides & Tooby, 1992). For example, attentional sensitivity to threats in the environment can guide avoidance behaviour, and thereby increase an individual's fitness. Such a link has not been established yet in the context of sexually selective cognition. However, Chapter 5 suggests that a link between attentional biases may exist. While many studies have investigated the interplay between cognition and attractiveness, very few studies have linked cognition to real-world mate choice. Admittedly, many studies have established a link between attentional processes and sexual behaviour, to the extent that heterosexual and homosexual participants show differential attention towards same- and opposite-sex stimuli (Dawson & Chivers, 2016, 2018). In addition, with regard to other topics, evidence suggests a strong link between substance abuse and attentional biases towards these substances (Field & Cox, 2008; Sharbanee et al., 2013; Weafer & Fillmore, 2013), suggesting a direct link between attentional biases and behaviours. However, these attentional biases all relate to general perceiver behaviour, and not specifically to an interactive effect of perceiver and stimulus on behaviour. Nevertheless, if sexually selective cognition would indeed aid people to identify suitable mates, a link between cognitive measures and valid measures of mate choice need to be firmly established. Recently, it has been established that initial impressions have a lasting effect on long-term mate choice in humans (Baxter et al., 2022), and functional cognitive biases potentially play a role in this. Accordingly, the results of Chapter 5 of this thesis are a first attempt to establish a link between attentional biases to preferred mates and mate choice based on speed-dates. Future work could try to further explore this line of research by combining cognitive tasks and speed-dating in order to get a better insight into the link between cognitive biases and mate choice. Such knowledge is essential to understand the role of cognitive processes in the first attraction filter.

The attraction filter in regard to orang-utan mate choice

With regard to this filter, it still has to be established whether such a multi-stage model applies to non-human primates as well, and whether they possess sexually selective cognition. In Chapter 1, I suggested that orang-utans very likely only possess an attraction-filter, because they do not form long-term pair bonds. If they indeed possess such a filter, the most likely visual traits that would be “filtered”, would be traits of fully developed flanged males, such as large cheek

pads on the side of the face. Therefore, I investigated whether Bornean orang-utan cognition would be biased towards stimuli depicting males bearing this trait. However, the results are mixed, with no evidence of cognitive attunement towards flanged males in Chapter 6, but evidence of immediate and voluntary attentional bias towards flanged males in Chapter 7. The eye-tracking results from Chapter 7 do indeed suggest that orang-utan cognition is attuned towards flanged males. This corroborates previous work in rhesus macaques, where systematic studies have established links between visual attention and visually conspicuous traits, such as facial masculinity (Rosenfield et al., 2019), facial coloration (Dubuc et al., 2016; Waitt et al., 2003), and facial symmetry (Waitt & Little, 2006). Thus, attentional biases towards conspicuous facial traits that are thought to play a role in mate choice seem not to be restricted to rhesus macaques, but might be more widespread across primate species, including great apes. It is important to note, though, that the results of Chapter 6 do not provide evidence for the notion that orang-utan cognition is biased towards flanged males. However, I will further elaborate on this in the section “Methodological considerations”.

Furthermore, Chapter 8 suggests that the first filter of orang-utans might also be sensitive to auditory information. From a functional cognition perspective, this would make sense, as orang-utans are considered semi-solitary (Roth et al., 2020; van Schaik, 1999). Because of their dispersed social system, auditory communication has a pivotal role in inter-individual coordination (Delgado, 2006). Consequently, orang-utan females will often have access to auditory information from males, but not visual information. Therefore, auditory information may have an important role in female orang-utan mate choice. While some evidence for this has been found in Sumatran orang-utans (Mitra Setia & van Schaik, 2007), results for Bornean orang-utans do not support this notion (Mitani, 1985; Spillmann et al., 2010). Nevertheless, this point underlines the need for a biocentric approach to animal cognition (Bräuer et al., 2020). While presenting identical tasks to different species may seem an objective approach to comparative cognition, this approach ignores the fact that each species has its uniquely adapted sensory systems. Therefore, it is crucial to consider the specific sensory modalities and environmental contexts of each species when studying animal cognition.

Caveats in interpreting the results of cognitive bias tasks

Thus, it is possible that orang-utans indeed possess an attraction-filter, and that sexually selective cognition is one of the mechanisms through which this filter

functions. However, I want to mention three caveats. First, the eye-tracking results cannot be considered evidence for an attentional bias that is driven by *positive evaluation*. It could also be the result of *vigilance* towards flanged males, because they can be a threat to both males, with whom they may compete, and females and their offspring. Therefore, future studies should further investigate this, for example by using physiological measures in combination with experiments (see “Future directions”). Second, it is possible that orang-utan females will especially employ an attraction-filter during ovulation. In Chapter 8, I have described two cases that suggest increased sensitivity for flanged male signals, visual or auditory, during ovulation. This idea is also in line with behavioural evidence from wild Bornean orang-utan females, who selectively mate with flanged males only during their ovulation (Knott et al., 2009). Third, the idea of an attraction-filter does not take into account potential socio-ecological constraints, even though such constraints are essential in shaping female sexual behaviour.

In the case of Bornean orang-utans, populations consist of a relatively large proportion of flanged males, many of which are semi-nomadic (Kunz et al., 2022). Furthermore, the dominance hierarchy between flanged males is often rather unstable (Spillmann et al., 2017). This results in a situation where females can be confronted with a large number of different males, none of which achieves absolute local dominance, and some of which may be infanticidal. Consequently, it may not be adaptive for female Bornean orang-utans to rely purely on an attraction-filter mechanism for mate selection. Instead, females need to strategically spread the probability of paternity across multiple flanged males, to decrease risk of infanticide (Kunz et al., 2022; Palombit, 2015). Still, employing such a sexual counterstrategy against infanticide does not fully rule out an attraction-filter. Because orang-utan females are characterised by concealed ovulation, they might still exert female preference by mating with their most preferred flanged male around ovulation. This would imply that their attraction-filter is activated specifically during their peri-ovulatory period, while outside of this period, females do not discriminate based on attractive traits as much. Importantly, this would allow females to ensure a mate with good genetic quality during their most fertile period, while at the same time reducing infanticide risk by spreading the probability of paternity.

The above-mentioned points are summarised in Figure 2. First, the attraction-filter of Bornean orang-utans encompasses both visual and auditory attractiveness. Second, the sensitivity of this filter is strongly modulated by the

ovulatory status of the female (dotted arrow). Third, exertion of female preference can be restricted by socio-ecological factors, such as the need to strategically mate with multiple males to reduce infanticide risk. Altogether, this model suggests that there is still a role for female mate choice despite the need to spread paternity probability, and thus the possibility that sexually selective cognition to some extent guides mate choice by Bornean orang-utan females.

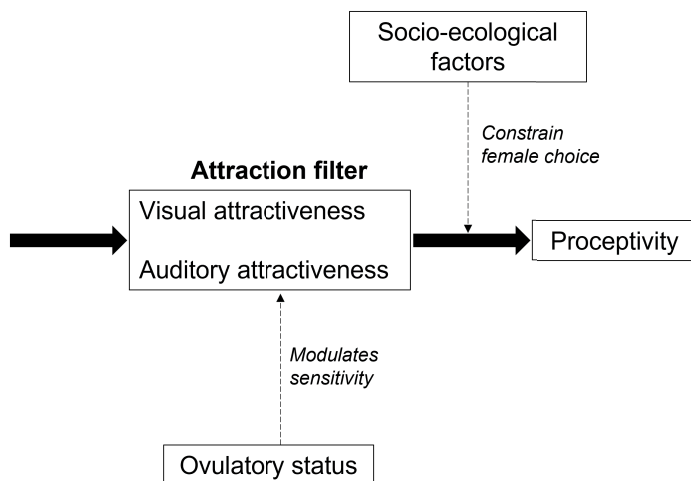


Figure 2. Schematic depiction of the attractiveness filter of female orang-utans, and the two important factors influencing it. First, ovulatory status influences the sensitivity of the filter, so that females are more biased towards specific males during ovulation. However, social-ecological factors, such as the need to reduce infanticide risk, may constrain the link between female preference and actual proceptive behaviour.

Methodological considerations

This thesis encompasses a range of paradigms employed in humans and Bornean orang-utans, each with their own methodological considerations. Since the literature on primates is scarce and new methods are continuously being developed, I therefore focus on the methodological considerations for testing primates, and specifically orang-utans.

Studies of sexually selective cognition in non-human primates remain rare, even though a more systematic approach could help reveal intriguing commonalities and differences between species. In this thesis, I have tried to

explore sexually selective cognition in Bornean orang-utans by employing similar test paradigms that have been used to study this topic in humans. However, I was able to employ these paradigms only with mixed success. Based on my experiences, future studies could consider improving their approach in several ways. In the section above, I already argued for a more biocentric approach to animal cognition (Bräuer et al., 2020). Taking such a perspective is essential to ensure that tasks are valid measures of the hypothesized cognitive processes involved in performing the task (Schubiger et al., 2020). I want to elaborate on this in the context of Chapter 6, where I tested Bornean orang-utans in two touchscreen tasks, that both yielded null results.

First, Bornean orang-utans have historically been exposed to extremely long periods of food scarcity (Vogel et al., 2017). As a consequence, orang-utans are extremely well-equipped to saving energy. For example, orang-utans have very low levels of daily energy expenditure compared to other mammals (Pontzer et al., 2010) and will minimise travel costs by adapting their locomotion style (Roth et al., 2017; Thorpe et al., 2007). Whereas sensitivity to food rewards has not been systematically studied yet, it is to be expected that Bornean orang-utans are extremely sensitive to and focused on food rewards. This is also what I noticed in the touchscreen task. At the end of each trial, individuals would receive a reward, in order to keep them motivated. However, it sometimes seemed that the anticipation of a reward distracted them from the task. More specifically, although they performed the task correctly, they showed little involvement in it, and seemed more focused on the reward. Such a finding is not unique to orang-utans, however. In quantity judgment tasks, primates are well-known to show improved performance when they need to discriminate between abstract tokens instead of actual food items (e.g., Boysen & Berntson, 1995). This suggests that primates are naturally inclined to respond to rewarding stimuli, which might disrupt their ability to focus on and complete tasks effectively. Interestingly, I did not encounter the same problem during the eye-tracking experiment (Chapter 7), where individuals received a reward continuously throughout the trial. This design might have avoided continuous anticipation of reward, thereby increasing involvement in the task. Therefore, I consider studies that can provide a reward to orang-utans while they are performing a test trial more likely to be successful.

Second, the touchscreen setup employed in Chapter 6 allowed orang-utans to only use their hands during the tasks. However, manual tasks may not be the most suitable tasks for orang-utans, as they often seem to employ their mouth

for manipulating objects or using tools (Bardo et al., 2017). Due to their almost exclusively arboreal life style, orang-utans often need most of their hands and feet to navigate the canopy. Their mouth functions as a ‘fifth’ hand for precise, motoric tasks (Lameira, 2023). Thus, when designing touchscreen tasks for orang-utans, it would be ideal to provide them with the opportunity to use their lips to control the screen. Luckily, systems that allow for this are already available (e.g., Schmitt, 2019), and could be applied more widely in future studies to better accommodate the preferences of participating orang-utans.

Another consideration for future studies refers to the cognitive processes that I have focused on. Whereas Chapter 2 outlines multiple promising methods to study sexually cognition, focusing on attention, memory, and motivational processing, I have mostly focused on attentional processes in this thesis. This is for a large part the result of the COVID-19 pandemic, which has considerably reduced opportunities for research with the orang-utans. While the initial idea was to also study memory for and motivational processing of flanged male stimuli, this became untenable due to the pandemic. However, future projects should ideally employ tasks that measure multiple aspects of sexually selective cognition, so that results can be compared for different aspects of sexually selective cognition. This will also help to elucidate the underlying motives for existing cognitive biases. For example, while an attentional bias can be reflective of both positive or negative interest in a stimulus, this is less likely to be the case in a motivational processing task, where an individual chooses to be exposed to a stimulus. Thus, employing multiple paradigms potentially allows for clearer understanding of the motives that guide cognitive biases.

I find it important to note that one of the methods employed in this thesis, namely the dot-probe paradigm, has come under scrutiny in the psychopathology literature in the last decade. The main issues with the paradigm are its relatively poor reliability (e.g., Kappenman et al., 2014; Rodebaugh et al., 2016), lack of ability to discriminate between different attentional processes (e.g., Belopolsky et al., 2011; Koster et al., 2004), and, consequently, discrepancies in findings. With regard to reliability, previous work has identified low internal (Chapman et al., 2019) and external consistency (Jones et al., 2018), while the discussion about attentional processes mainly revolves around the question whether the dot-probe paradigm measures engagement or disengagement of attention (Belopolsky et al., 2011; Fox et al., 2002; Koster et al., 2004). Interestingly, inconsistent results have also been found in primates with the dot-probe paradigm. While the paradigm

has been successful in elucidating the effect of emotion information on cognition in multiple primate species (King et al., 2012; Kret et al., 2016; Lacreuse et al., 2013; Schino et al., 2020; van Berlo et al., 2023), inconsistencies remain as well, as both chimpanzees (Kret et al., 2018; Wilson & Tomonaga, 2018) and Bornean orang-utans (Laméris et al., 2022) do not seem to show the expected attentional bias towards emotions in the dot-probe task. One important methodological explanation for these inconsistencies is that the dot-probe paradigm relies on reaction times as a measure of attention. However, reaction times are inherently noisy (Morís Fernández & Vadillo, 2020) and may involve trade-offs with accuracy (Draheim et al., 2019). Especially in species with reduced manual dexterity compared to humans, this may obfuscate existing biases. Some of these issues can be resolved by employing non-invasive eye-tracking, as I did in Chapter 7. These methods allow disentangling different attentional processes (Clauss et al., 2022), and, speaking from own experience, seem to yield less noisy data compared to reaction time tasks.

Thus, even though the dot-probe paradigm has helped to gain insight into attentional processes of primates, I consider eye-tracking a better alternative, because it yields more reliable and less noisy data, thereby allowing for a more fine-scaled analysis of different attentional processes. It is important to note that eye-tracking is especially suitable for investigating overt attentional processes, because it relies on eye movements. However, attention also operates *without* eye movements, a process referred to as covert attention. Covert attention refers to a shift in focus, that precedes eye movements (Weierich et al., 2008). Nonetheless, employing eye-tracking in combination with cuing tasks allows one to distinguish between covert and overt attention by investigating whether attentional biases are present in the absence of eye movements (e.g., Petrova et al., 2013), although such study designs might be too complex for non-restraint experiments in primates. Concluding, eye-tracking seems a more suitable method to investigate *overt* attentional processes in primates, but cannot give insight into *covert* attention in primates.

Practical implications

In Chapter 5, I showed that initial attraction during a speed-date predicts fixation duration in an eye-tracking task. This result establishes a link between attentional

biases and subsequent behaviour. While previous research has established such a link at trait level (Eastwick et al., 2011), I demonstrated that cognitive tasks might be predictive of differential behaviour towards potential mates instead of a general tendency to evaluate potential mates as suitable or not. In other words, this finding suggests that attraction to another is reflected in implicit cognitive processes. Dating apps or websites could therefore consider a more cognitive-based approach to identifying preferred partners. Currently, dating websites mostly rely on self-reported personality information and attitudes, and explicitly stated preferences. Dating apps like Tinder, on the other hand, rely on sequential presentation of potential partners. Both of these have important shortcomings. First, several studies have shown that explicitly stated preferences for personality traits in potential partners fail to predict initial mate choice (Eastwick & Finkel, 2008; Joel et al., 2017; Tidwell et al., 2013). Second, in sequential presentation paradigms of faces, people tend to develop suboptimal sampling heuristics (Furl et al., 2019; Lee & Courey, 2020).

To solve these issues, dating websites and apps could try to implement a more implicit first filter by using eye-tracking tasks for example. Recent developments in webcam- (Semmelmann & Weigelt, 2018) or even smartphone-based eye-tracking (Valliappan et al., 2020) allow for measuring attentional preferences by presenting a grid of pictures of potential partners. These attentional preferences could be considered the first filter, after which people can further explore the profiles of the potential partners that they attended to. The benefit of such an approach is that it fits more closely with the human mate choice process: it allows participants to implicitly sample different options based on visual cues, without inducing decision-making biases that are characteristic of dating apps like Tinder. After applying such a first filter, users could be allowed to further explore the profiles and pictures of potential mates that attracted their attention, so that there is still room for exercising explicit preferences.

Another practical goal of this thesis was to explore methods to identify mate preferences of zoo-housed orang-utans. Reproductive success of zoo-housed orang-utans is relatively low compared to other great ape species (Kaumanns et al., 2004). Developing methods to identify individual mate preferences could potentially help to solve this, as it would allow for better matching of individuals across zoos (Asa et al., 2011). However, based on the results presented in this thesis, such methods do not yet seem feasible for application within the orang-utan breeding programme. Apart from the methodological considerations (see

section above), there are some other caveats that should be addressed before such an approach can be considered useful.

First, while I found a robust bias towards flanged male stimuli in the eye-tracking experiments described in Chapter 7, I did not find clear indications of subtle individual attentional preferences in Experiment 2, where individuals were presented with multiple stimuli of four different males. While I found a few robust biases towards one specific flanged male compared to the unflanged males, none of the females seemed to attend more to one specific flanged male compared to another flanged male. This is not to say that it would be impossible to identify such preferences via eye-tracking. However, it would require larger samples than studies that investigate attentional biases towards a specific stimulus category. This may not be feasible in zoos, because it would be a time-consuming endeavour. Instead, it might be more promising to develop methods that require little time investment and are intrinsically rewarding for participants. For example, one could explore designs in which individuals self-expose to stimuli or can trigger video calls with or video fragments of different conspecifics. For example, a recent study in parrots (order *Psittaciformes*) employed a free-choice paradigm where individuals could trigger video calls with other parrots and interact with them (Kleinberger et al., 2023). Given that such methods rely on intrinsic motivation, they may be better suited to investigate individual preferences compared to extrinsically rewarded tasks.

Second, it will be important to establish a link between performance or biases in cognitive tasks and later behaviour. For example, if we assume that we can reliably measure a cognitive preference towards one specific individual over another, would this also translate into more affiliation or even a higher probability of successful reproduction with this individual? This thesis suggests that such a link may exist in humans, at least when considering the eye-tracking results. However, a similar link has, to my knowledge, not yet been established in non-human primates.

A final practical implication from this thesis concerns the ovulatory shift in female preferences. In Chapter 8, I reported two cases of Bornean orang-utan females who were especially sensitive to flanged male signals (auditory or visual) in their peri-ovulatory period. This corroborates findings from wild Bornean orang-utans (Knott et al., 2009), and may also be relevant for the future development of test paradigms to identify mate preferences. As I argued in the “Theoretical implications”-section, it could be the case that the attraction-filter is especially

sensitive during ovulation. Unfortunately, I could not control for ovulation status during the cognitive tasks. Female primates in zoos and sanctuaries are often on birth control or have a dependent infant, which makes it difficult to control for ovulation status during experiments. However, the results of Chapter 8 suggest that investigating cognitive biases towards potential mates would ideally be performed when a female is ovulating. At this point, her biases are most likely to reflect mating motivation, thereby probably making them a more reliable predictor of actual mate choice.

Future directions

Based on the implications and considerations outlined above, I will now suggest some future directions for research on mate choice and sexually selective cognition.

First, research on cognition and mate choice would benefit from more ecologically valid paradigms to establish links between ratings of attractiveness, cognitive biases, and proxies of mate choice. Chapter 3 and 5 of this thesis provide examples of such an approach in humans, employing speed-dating as a proxy of mate choice (Finkel & Eastwick, 2008). In general, researchers have typically examined the role of attractiveness in human mate choice through isolated experiments where participants rated various samples in terms of attractiveness. Subsequently, these ratings are frequently associated with sample characteristics that are thought to reflect mate quality, such as masculinity and femininity (e.g., Collins & Missing, 2003; Little, Connely, et al., 2011). I see two main issues with this approach, the first of which concerns the fact that this approach lacks ecological validity due to the isolated setting in which the stimuli are presented. For example, subtle differences in isolated olfactory cues might indeed be correlated with attractiveness ratings. However, this does not mean that in a natural setting these subtle differences can be perceived at all, let alone have an effect on human mate choice. Secondly, the traditional approach does not help to establish a link between cues and mate choice behaviour. This link is often implicitly assumed to be there when certain cues are considered attractive. Thus, finding a link between cues that play a role in mate choice and actual mate choice should be a priority in future work.

This last point also applies to future work on animal cognition in general. While researchers often investigate cognitive biases using computerized experiments in animals, they are hardly ever linked to behaviour. One exception in non-human primates comes to mind. Ryan et al. (2020) performed an eye-tracking task with infant rhesus macaques, where they measured how long each individual fixated on eyes in facial stimuli. They correlated this to actual social behaviour, and found that individuals that spent more time fixating on eyes during the eye-tracking task were also more likely to initiate social interactions. Even though this study shows a trait-level association between looking behaviour and actual social behaviour, and not a link between attentional preferences to social preferences per se, similar studies could help to gain a better understanding of the link between social cognition and social behaviour. While such studies have not yet been performed with regard to mate choice in non-human primates, there are examples from other species. For example, in zebra finches (*Taeniopygia guttata*), female preferences in an operant and playback experiment that exposes females to male calls corresponds with female preferences in a live mate choice context (Holbeck & Riebel, 2007). Other work has shown that allowing females to exert their preferences is associated with higher reproductive success (Ihle et al., 2015). More work on this topic in non-human primates is essential to understand whether preference tasks can be used to predict mate preferences.

Furthermore, future studies could consider a more physiological approach to studying mate choice. Measurement of physiological information has already been used to study initial attraction in speed-date studies (Prochazkova et al., 2022; Zeevi et al., 2022). However, these measures could also be combined with cognitive tasks. In the context of mate choice, this has recently been done by Pronk et al. (2021), who presented participants with multiple dating profiles and measured pupil diameter while participants were scanning these profiles. Participants who showed pupil dilation while scanning a profile, were more likely to select this profile as a suitable partner. Similarly, evidence indicates that heart rate variability concurs with sexual arousal (Lorenz et al., 2012). Another physiological measure, facial temperature, has recently been shown to vary as a function of emotional valence in humans (Aristizabal-Tique et al., 2023), although some studies argue that facial temperature provides only information about arousal (Kosonogov et al., 2017). Conveniently, most of these physiological measures can also be assessed to some extent in non-human primates non-invasively (pupil: Kret et al., 2014; facial temperature: Kuraoka & Nakamura, 2022;

heart rate: Unakafov et al., 2018; Wang et al., 2023), although heart rate variability cannot yet be estimated non-invasively (Madan et al., 2018). Thus, combining these measures with cognitive tasks can potentially help to determine whether cognitive biases are the result of positive or negative valence. In the end, this is an essential step for establishing a link between motivational state and cognitive biases.

One further line of research that deserves attention in future research is measurement of individual preferences in primates. Currently employed cognitive tasks, including the ones described in this thesis, mostly rely on categorical designs, aiming to identify a preference or bias for one category over another *across individuals*. However, when considering mate choice, it is well-known that individuals can vary in their mate preferences (Jennions & Petrie, 1997). To capture such inter-individual variation in preferences, it will be necessary to develop suitable test designs. One example comes from systematic investigations of individual food preference in primates (Hopper et al., 2019; Huskisson et al., 2020, 2021). This line of research has shown that simple computerised paired presentation tasks can be used to identify individual preferences for food, and that these preferences are consistent across tasks. I suggest future studies should employ this approach beyond food preferences to gain a better insight into individual preferences for specific stimuli or, in the case of sexually selective cognition, specific potential mates.

Conclusion

Recent psychological research has suggested an important role for cognitive processes in human mate choice. In this dissertation, I have taken a closer look at these processes in humans, and investigated whether these are also present in Bornean orang-utans by running a set of comparative studies. The thesis has shown that attractiveness-based attentional biases are clearly present in humans, and that such biases might also be related to actual mate choice. When it comes to Bornean orang-utans, the findings are mixed: they did not show any biases in touchscreen tasks, but did have an attentional bias towards flanged males across two eye-tracking experiments. Furthermore, auditory signals may play a more important role in orang-utan compared to human mate choice. Even though the results of this thesis suggest that both humans and orang-utans have an

attraction-filter that is reflected in cognitive biases towards mate-relevant traits, a better understanding of the link between such biases and actual mate choice remains of pivotal importance. Furthermore, future studies should employ test paradigms that tap into different cognitive processes, and consider incorporating non-invasive measures of physiology. This could help to elucidate the valence underlying cognitive biases that might be functional in a mate choice context. Finally, although current paradigms might not yet be suitable for testing attraction on an individual basis, future studies can use the findings and recommendations from this thesis to work toward the goal of identifying individual mate preferences.