Chapter 7

Orang-utans like it cheeky: Attentional bias towards flanged males in Bornean orang-utans (*Pongo pygmaeus*)

Abstract

The selection of a mate is a decisive choice that carries substantial weight in an individual's fitness. As a result, individuals may employ various cognitive mechanisms to navigate the mate selection process effectively. These mechanisms, such as preferential attention towards attractive conspecifics or traits, have been widely studied in humans. However, only a few studies have investigated these mechanisms in non-human primates. To address this gap, we conducted two eye-tracking experiments with four zoo-housed Bornean orang-utans (*Pongo pygmaeus*), a species that is characterised by extreme sexual dimorphism. In both experiments, using naturalistic and controlled stimuli, we found that orang-utans exhibit an attentional bias towards males with fully developed flanges, a sexually dimorphic trait carried by some adult males. Importantly, this attentional bias was apparent in both immediate and voluntary attention. By revealing the presence of attunement towards mating-related traits in the attentional mechanisms of a great ape species, our findings not only contribute to the growing body of knowledge on the cognitive basis of mate choice but also open up avenues for future research into the interplay between mate choice and cognition in non-human primates.

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Data availability statement

The datasets and materials generated and/or analysed during the current study are available via Dataverse: https://doi.org/10.34894/BU1XYR

Introduction

Mate selection is a crucial process for sexually reproducing animals. The choice of a mate fundamentally defines an individual's biological fitness: picking a good partner can ensure that genes are well represented in the following generation, whereas picking a bad partner can cause genes to disappear from the population (Buss & Schmitt, 2019). Numerous species have evolved certain preferences that direct them when selecting a partner as a result of this significant motivation to do so (Rosenthal, 2017). Thus, these motivations influence cognition. In humans, for instance, various cognitive processes such as visual attention seem to be affected by sexual selection, and these processes can aid in identifying suitable mates or competitors (Maner & Ackerman, 2015). However, relatively little is known about the cognitive underpinnings of mate selection in other animals. In the current study, we investigated whether Bornean orang-utans, a species characterised by extreme sexual dimorphism (Utami Atmoko et al., 2008), showed an attentional bias towards fully developed flanged males.

The interplay between sexual selection and visual attention has been extensively studied in humans. Many studies have found that heterosexual women and men have an attentional bias towards attractive members of the opposite sex (Leder et al., 2016; Mitrovic et al., 2018; Roth et al., 2022, 2023). Similarly, humans also show vigilance toward attractive same-sex individuals (Maner et al., 2009). Importantly, such attentional biases have been identified for both immediate (e.g., Roth et al., 2022) and voluntary attention (e.g., Leder et al., 2016; Roth et al., 2023). Immediate attention constitutes automatic orienting towards relevant stimuli such as fear-inducing animals (Shibasaki & Kawai, 2009) or faces (Kawai et al., 2016). The typical measurement used to assess immediate attention is the time it takes for a participant to attend to any given stimulus after its onset. Voluntary attention reflects the deliberate and self-directed allocation of attentional resources to stimuli (Souto & Kerzel, 2021) and is typically measured as a function of the total time that participants spend looking at any given stimulus (Roth et al., 2023). In humans, attentional biases towards attractive faces also seem to extend to sexual dimorphism: both men and women seem to have a visual bias for more masculine male faces (Garza & Byrd-Craven, 2023; Yang et al., 2015). Interestingly, this is not only the case in humans: rhesus macaque (*Macaca mulatta*) females look significantly longer at the more masculine faces of conspecifics (Rosenfield et al., 2019). This implies that attentional biases towards such sexually selected traits can also be found in non-human primates.

In the last two decades, an increasing number of studies have investigated sustained attention and its relation to sexual selection in primates, mostly using a preferential looking paradigm (Winters et al., 2015). In this paradigm, individuals are confronted with different types of pictures presented simultaneously during each trial, and the relative attention to each stimulus is used as a proxy for interest. Many of the studies on this topic have been performed with rhesus macaques. Seminal work by Waitt et al. (2003, 2006) employing a preferential looking paradigm established that macaque females had an attentional bias towards bright red male faces when they were paired with paler faces, while males had an attentional bias towards bright red female hindquarters, but not faces. More recently, researchers have elaborated on these studies by testing free-roaming rhesus macaques. For instance, Dubuc et al. (2016) found that macaques had a bias for red male faces, whereas Rosenfield et al. (2019) identified an attentional bias for more masculine male faces. Thus, the preferential looking paradigm has been successfully used to study the interaction between sexual selection and attentional processes in primates.

The above-mentioned studies mostly relied on video recordings of participants combined with frame-by-frame analysis to determine gaze direction. Partly because this is an extremely time- and labour-intensive method, many recent studies on captive primates have used eye tracking. An eye tracker has infrared cameras specialized for the automatic and accurate detection of eye movements and gaze patterns to study primate social cognition (Hopper et al., 2021; Lewis & Krupenye, 2022). Recently, some studies have employed eye tracking to study the interaction between visual attention and sexual selection in primates. For example, Damon et al. (2019) used eye tracking to establish that rhesus macaques show an own-species bias for attractive faces similar to humans (Damon et al., 2019). Additionally, Lonsdorf et al. (2019) showed that brown-tufted capuchin monkeys (*Sapajus apella*), both male and female, were especially attentive towards pictures of same-sex individuals instead of opposite-sex individuals, suggesting that capuchin monkeys were more interested in potential competitors than potential mates. Thus, previous studies in primates have established that eye tracking can successfully elucidate attentional biases in the context of sexual selection.

To date, most studies have focused on macaques. However, to fully understand 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). Some primate species, such as orang-utans (*Pongo* spp.), exhibit extreme forms of sexual dimorphism that are thought to be the result of both intense male-male competition and female choice (Utami Atmoko et al., 2008). In addition, these arboreal great apes are characterised by male bimaturism, meaning that there are two distinct types of male morphs: unflanged males and flanged males (Utami et al., 2002). Unflanged males experience arrested development. They are sexually mature and produce offspring but are not preferred mates for adult females (Knott et al., 2009; Kunz et al., 2022). However, 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, ovulating females prefer mating with flanged males (Knott et al., 2009). Female choice for flanged males potentially reflects selection for good genes because the transition from unflanged to flanged males is energetically costly (Knott, 2009). Moreover, flanged males exhibit mutual aggression, and fights between flanged males can lead to serious bodily harm. Thus, by mating with flanged males, orang-utan females may select for males of good genetic quality.

In this study, we investigated whether Bornean orang-utans have an immediate and sustained attentional bias towards flanged males. In the first experiment, we presented unique paired portraits of one flanged male and one unflanged male. If flanges were indeed a source of information for orang-utans, we expected the participating orang-utans to (i) gaze immediately at the portrait of the flanged male and (ii) spend relatively more time looking at the flanged male within each trial. In our second experiment, we extended our first experiment by presenting naturalistic stimuli (i.e., different perspectives and natural poses, including other parts of the body in addition to the face) of four different male orang-utans (two flanged, two unflanged) in all possible combinations. This allowed us to investigate whether the results from Experiment 1, with more controlled stimuli, would hold for more naturalistic stimuli. Furthermore, it allowed us to explore how orang-utans divide their attention when presented with two stimuli of males of the same morph and whether they have looking biases for specific individuals over others.

Method

Subjects and housing

Our sample included four adult Bornean orang-utans (*Pongo pygmaeus*; females: Samboja, Sandy, Wattana; male: Amos) that lived in a fission-fusion enclosure with four other orang-utans (one of which was transferred during the study period; Table 1) in Apenheul Primate Park (Apeldoorn, The Netherlands). The females, but not the male, had prior experience with touchscreen-based research. However, none of the individuals had experience with eye tracking.

The orang-utans were housed in a building consisting of four indoor enclosures that were each connected to outdoor islands. The orang-utans were typically housed in 3-4 subgroups and group composition was sometimes changed with the aim of mimicking the natural social structure of orang-utans, in which they form temporary parties but no stable social groups. Some individuals never shared enclosures to avoid conflict (e.g., two adult males). The test setup was located in one of their night enclosures, out of view of the public. The setup was accessible from two of the indoor enclosures. Testing took place between March and August 2022 on Tuesdays and Fridays between 11.00 and 13.00.

Table 1. Overview of the Apenheul orang-utans.

Name	Sex	Date of birth	Origin	Participating?	Calibration accuracy (precision)
Kevin	M	~1982	Wild	No	
Sandy	F	29-4-1982	Captive	Yes	2.1mm (2.3mm)
Wattana	F	17-11-1995	Captive	Yes	0.5mm (2.3mm)
Amos	M	20-12-2000	Captive	Yes	0.4mm (5.0mm)
Samboja	F	9-6-2005	Captive	Yes	0.1mm (1.3mm)
Kawan (until 20-6-2022)	M	22-2-2010	Captive	No	
Baju	M	2-12-2015	Captive	No	
Indah	F	19-10-2017	Captive	No	

Experiment 1

Procedure

Participants were calibrated and tested using Tobii Pro Lab v. 1.194 and a Tobii Pro Spectrum with a sampling frequency of 1200Hz that was attached to a 24” monitor (16:9, 1920x1080). The monitor was placed behind a 1.2 cm thick polycarbonate panel with a drinking nozzle. Throughout calibration and testing, we used the great ape eye tracking mode on the eye tracker. On the top of the screen, we added a webcam to record the participants during the test sessions.

First, we calibrated the participants using a resizing video as a calibration target in Tobii Pro Lab. We used a range of different videos during the calibration process, depicting caretakers, baby orang-utans, food, and mating orang-utans. The calibration process was repeated until a successful calibration was obtained, and this calibration was reused during the experiment. With Sandy, we managed to obtain a successful 5-point calibration, whereas the other orang-utans completed a successful 2-point calibration, which is sufficient to produce accurate gaze data for this type of experimental design (Hopper et al., 2021).

After the calibration phase, data collection began. Each participant completed nine sessions of six trials (54 trials in total). Each session started with a 9-point grid to visually inspect calibration accuracy. Thereafter, six trials were started. Each trial started with a fixation video in the center of the screen (180 × 180 pixels) depicting one of the orang-utan caretakers. Stimulus presentation was started manually; when the eyetracker showed that the participant's gaze overlapped with the fixation video, the experimenter proceeded to the stimuli, which were presented for four seconds. After the stimulus presentation, a gray screen was shown for three seconds. After all six trials were completed, the experiment was automatically stopped. Participants completed a maximum of three sessions on testing days, and the order of the sessions was randomized between participants.

After the participants had completed all nine sessions, we repeated trials in which the participant (i) looked away from the center during trial onset because the start point of the trial would not be neutral, or (ii) showed less than 1s of fixation time on the stimuli during the trial because this could indicate a lack of attention and/or distraction during the trial. During the experiment, the orang-utans were rewarded with strongly diluted (±1:35) sugar-free raspberry lemonade.

Stimuli

In each trial, two stimuli, 690 × 500 pixels each, were presented: one flanged face and one unflanged face on a light-gray background (#808080). The stimuli were centered at 20% and 80% horizontally and 50% vertically on a dark-gray background (#626262). The stimuli were collected from the Internet, mainly from release reports published by Bornean orang-utan reintroduction programs. These were supplemented with portrait pictures taken from semi-wild orang-utans and pictures of zoo-housed orang-utans within the orang-utan EEP.

We checked for differences in luminance and contrast between stimuli using a custom MATLAB script to determine luminance and contrast for each stimulus, and then calculated the difference in luminance and contrast between the flanged and unflanged stimuli at the trial level. We found no robust differences in contrast (Bayesian intercept-only LM; 89% CrI [-0.08; 0.35], *pd* = 0.85) or luminance (Bayesian intercept-only LM; 89% CrI [-0.23; 0.21], *pd* = 0.53) between flanged and unflanged stimuli. This check ensured that gazing patterns were not driven mainly by low-level features at the stimulus level, which are known to capture visual attention (Theeuwes, 1995).

Experiment 2

Procedure

This procedure was identical to that used in Experiment 1. However, because of time pressure, we applied a maximum of four sessions per participant per test day instead of three. Experiment 2 consisted of 12 sessions of six trials in total, followed by repetition of erroneous trials, similar to Experiment 1.

Stimuli

Owing to an editing mistake, the dimensions of the stimuli for Experiment 2 were slightly different from those in Experiment 1. Each trial consisted of two stimuli of 600 × 450 pixels, centered at 22.5% and 77.5% horizontally and 50% vertically on a dark-grey background (#626262). While this meant that Experiments 1 and 2 were slightly different, the presentation of stimuli was administered in exactly the same way as in Experiment 2.

For Experiment 2, we selected six naturalistic stimuli of four different orang-utan males (two flanged: Bako & Sibu, two unflanged: Jingga & Wousan). Stimuli of Bako and Jingga were provided by Ouwehands Zoo (Rhenen, The Netherlands), stimuli of Sibu were provided by Dublin Zoo (Dublin, Ireland), and stimuli of Wousan (housed in Paignton Zoo, UK) were kindly shared by Brian Lilly. All four males were part of the orang-utan EEP and had not been previously housed with the subjects of the study. We selected four portrait photos and two photos depicting both the face and (part of the) body. Using GIMP (v2.10.32), we transformed each photo to grayscale and then applied the Equalize-option to standardise the luminance of all stimuli. We paired the stimuli such that participants were always presented with stimuli from the same category within a trial. Furthermore, we presented all possible combinations of males to the participants (four males, so six combinations) within one session.

Inter-rater reliability

All sessions of both experiments were scored by TR to check whether subjects looked away from the center of the screen during trial onset so that these trials could be repeated at the end. To test whether such trials could be reliably identified, TR and EvB coded eight sessions (48 trials) from Experiment 1 for looking away during trial onset. Of these 48 trials, they agreed to include 34 and excluded 10, but disagreed on inclusion of four trials, resulting in a Cohen's kappa of 0.78 (91.7% agreement), reflecting a good level of reliability between raters.

Statistical analysis

All analyses were performed using R Statistics Version 4.2.2 (R Core Team, 2023). For our analyses, we employed a Bayesian approach, which has become increasingly popular in recent years owing to its numerous advantages over frequentist analyses (Kruschke et al., 2012; Makowski et al., 2019). Whereas frequentist approaches, such as p-value null hypothesis testing, provide insight into the plausibility of the data under a particular hypothesis, Bayesian methods inform us about the credibility of our parameter values based on the observed data (Kruschke et al., 2012; McElreath, 2018). This difference is reflected in the contrasting interpretations of frequentist and Bayesian confidence intervals. While the former provides a range of values that contain the estimate over the long term, the latter identifies the most plausible parameter values given the data. Moreover, Bayesian methods allow the integration of prior expectations into the model, are less susceptible to Type I errors, and are more robust in small and noisy samples (Makowski et al., 2019). Taken together, these factors render Bayesian methods a valuable tool for data analysis.

All models were created in the Stan computational framework and accessed using the *brms*-package (Bürkner, 2017, 2018). All models were run with four chains and 6000 iterations, of which 1000 were warmup iterations. We checked model convergence by inspecting the trace plots, histograms of the posteriors, Gelman-Rubin diagnostics, and autocorrelation between iterations (Depaoli & van de Schoot, 2017). No divergence or excessive autocorrelation was found.

First fixation

To investigate whether orang-utans had a first fixation bias toward flanged males when paired with unflanged males, we used binary logistic regression with the location of the first fixation (1=flanged male, 0=unflanged male) as the dependent variable. We modelled the dependent variable as a function of the *Intercept* and the *Location of the flanged male stimulus* (left/right on the screen) to control for potential side biases. To investigate the effect of different combinations of male morphs on first fixation, we created a binary variable reflecting the location of the first fixation (1=left, 0=right). We modelled this dependent variable as a function of the interaction between *the left stimulus morph* (flanged/unflanged) and *the right stimulus morph* (flanged/unflanged). In all analyses, we allowed Intercepts to vary by Subject, and Session nested in Subject.

For binary logistic regressions, we specified regularizing Gaussian priors with M = 0 and SD = 1 for the Intercept and independent variables. We used the default Student's *t* priors with 3 degrees of freedom for variance parameters.

After running the models, we used the *emmeans*-package (Lenth, 2023) to provide estimates based on the posterior predictive distribution. Using these values, we calculated multiple quantitative measures to describe the effects. First, we report the median estimate *b* and the median absolute deviation of the estimate between square brackets. Second, we report an 89% credible interval for the estimate (89% CrI). We chose 89% instead of the conventional 95% to reduce the likelihood that the credible intervals would be interpreted as strict hypothesis tests. Instead, the main goal of credible intervals is to communicate the shape of posterior distributions (McElreath, 2018). Third, we report the probability of direction (*pd*), that is, the probability of a parameter being strictly positive or negative, which varies between 50% and 100% (Makowski et al., 2019).

Total fixation duration

To investigate total fixation duration, we used a zero-one inflated beta model, which is suitable for continuous proportions containing zeros and ones (Ospina & Ferrari, 2012). These models consist of multiple components: a beta component to describe the values between 0 and 1, and two binary components to predict the occurrence of zeros and ones. Zero-one-inflated beta regression has previously been employed in eye-tracking studies (e.g., Chiquet et al., 2021). For each trial, we calculated a *Looking time bias*-score. In Experiment 1 and the replication of this experiment in Experiment 2, we calculated this bias by dividing the fixation time on the flanged male stimulus by the sum of the fixation times on the flanged and unflanged stimuli.

Thus, the *Looking time bias*-score represents the proportion of the total fixation time on the stimuli directed towards the flanged male stimulus. In Experiment 2, we also explored how the orang-utans divided their attention when presented with two stimuli of males of the same morph compared to when presented with males of different morphs. Because we could not calculate a *Looking time bias*-score in the same way as described above, because in some trials there were either two flanged male- or no flanged male-stimuli, we calculated the score differently for this analysis. We used the location of the photos as a reference point to calculate the looking time bias by calculating the bias toward the left picture (Roth et al., 2023). Hereafter, we tested whether this bias is affected by the stimulus category on the left side and right side on the screen.

To study whether orang-utans had an attentional bias toward flanged males, we modelled *Looking time bias*-score as a function of the *Intercept* and the *Location of flanged male stimulus* (left/right on the screen) to control for potential side biases. To investigate the effect of different combinations of male morphs on orang-utan attention, we modelled the *Looking time bias*-score as a function of the interaction between *Left stimulus morph* (flanged/unflanged) and *Right stimulus morph* (flanged/unflanged). The same model formulas were specified for all four model components (*mu, phi, zoi, and coi*). In all analyses, we allowed Intercepts to vary by Subject, and Session nested in Subject. Furthermore, we weighed each trial by the total fixation duration on the stimuli combined in that trial relative to the subject's average. Thus, trials in which the orang-utans paid more attention to the screen had a larger weight in the analysis. In this manner, we avoided that trials where the orang-utans were relatively distracted or disinterested would have a large influence on the outcome of our analysis.

To explore whether we could find attentional biases towards specific males in Experiment 2, we calculated a *Looking time bias*-score for each stimulus in each trial, reflecting the proportion of total fixation duration that the orang-utan fixated on stimuli depicting a specific individual. We constructed three separate models: one for each female. Due to computational issues, we could not construe an individual preference-model for the male participant, Amos. Within each model, we modelled *Looking time bias* as a function of *Individual of interest* (Bako, Sibu, Jingga or Wousan) and *Other individual presented* (Bako, Sibu, Jingga or Wousan), to control for the effect of the second stimulus. We allowed the Intercept to vary by session.

For the zero-one inflated beta models, we used a Gaussian prior with M = 0 and SD = 1 for the Intercept of the beta component of the model and for all independent variables. This also applied to the independent variables in the formulas for *phi, coi*, and *zoi*. For all variance parameters, we kept the default Student's *t* priors with 3 degrees of freedom. Furthermore, we kept the default logistic priors for the Intercepts of *zoi* and *coi*, and default Student's *t* prior with 3 degrees of freedom for the Intercept of *phi*.

After running the models, we used the *emmeans*-package (Lenth, 2023) to integrate the different model components and to provide estimates based on the posterior predictive distribution. Using these values, we calculated multiple quantitative measures to describe the effects (see "First fixation").

Ethics statement

This study employed only non-invasive methods, and animals were not harmed or punished in any way during the study. Participation was voluntary, animals were tested in a social setting, and animals were never deprived of food or water. The care and housing of the orang-utans adhered to the guidelines of the EAZA Ex-situ Program (EEP). Furthermore, our research complied with the ASAB guidelines (ASAB Ethical Committee/ABS Animal Care Committee, 2023), was carried out in accordance with the national regulations, and was approved by the zoological management of Apenheul Primate Park (Apeldoorn, The Netherlands).

Results

Experiment 1

First fixation

The outcomes of the Bayesian binary logistic regression (Supplementary Table 1; see Appendix G for model stability checks) suggested that the orang-utans had a first fixation bias towards flanged male stimuli ($b_{Intercept}$ = 0.599 [0.033], 89% CrI [0.546; 0.651], *pd* = 0.998). However, this was not the case for all individuals (Figure 1A): Amos ($b_{Intercept}$ = 0.690 [0.066], 89% CrI [0.586; 0.787], *pd* = 0.999) and Sandy ($b_{Intercept}$ = 0.641 [0.059], 89% CrI [0.548; 0.733], *pd* = 0.994) showed a robust bias towards flanged male stimuli, while this was not the case for Samboja ($b_{Intercept}$ = 0.512 [0.073], 89% CrI [0.403; 0.627], *pd* = 0.565) and Wattana ($b_{Intercept}$ = 0.557 [0.064], 89% CrI [0.450; 0.650], *pd* = 0.800). Furthermore, we found that the orang-utans had a leftward bias: they were more likely to first fixate on the flanged male stimulus if it was on the left side of the screen ($b_{left\text{-}right}$ = 0.332 [0.064], 89% CrI [0.226; 0.433], *pd* = 1.00).

Total fixation duration

The outcomes of the Bayesian zero-one inflated beta regression (Supplementary Table 2; see Appendix G for model stability checks) suggested that the orang-utans had an attentional bias towards flanged male stimuli ($b_{Intercept}$ = 0.575 [0.024], 89% CrI [0.538; 0.615], *pd* = 0.999). Again, this was not the case for all individuals (Figure 1B): for Amos ($b_{Intercept}$ = 0.596 [0.038], 89% CrI [0.536; 0.656], *pd* = 0.996) and Wattana ($b_{Intercept}$ = 0.608 [0.040], 89% CrI [0.544; 0.671], *pd* = 0.997) we found a clear bias. For Sandy it was less pronounced ($b_{Intercept}$ = 0.574 [0.046], 89% CrI [0.498; 0.645], *pd* = 0.942), whereas Samboja showed no clear bias ($b_{Intercept}$ = 0.525 [0.046], 89% CrI [0.449; 0.596], *pd* = 0.700). Furthermore, we found no side bias, meaning that the location of the flanged male stimuli (left or right on the screen) did not modulate the bias towards flanged males ($b_{left\text{-}right}$ = 0.033 [0.045], 89% CrI [-0.036; 0.104], *pd* = 0.773).

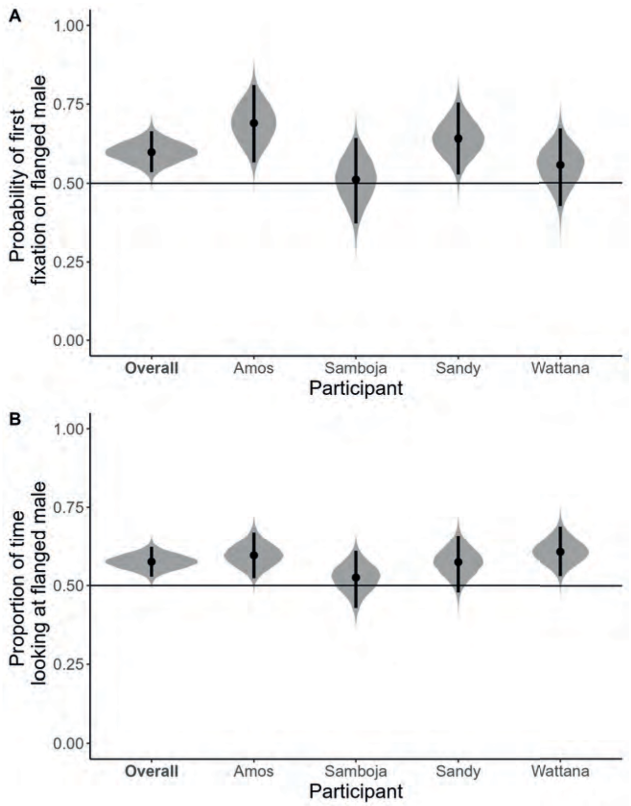

Figure 1. Results of Experiment 1 depicting (A) predicted probability of fixating first on the flanged male stimulus and (B) predicted proportion of time spent fixating on the flanged male stimulus. We report the overall prediction and the predictions for each participant. Grey areas represent the posterior predictions for each iteration of the model, black dots indicate the median posterior prediction, and black lines indicate the 95% credible interval.

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Experiment 2

Replication first fixation

Similar to Experiment 1, the outcomes of the Bayesian binary logistic regression (Supplementary Table 1) suggested that the orang-utans had a first fixation bias towards flanged male stimuli ($b_{Intercept}$ = 0.582 [0.039], 89% CrI [0.520; 0.645], *pd* = 0.981). Although all individuals showed a bias in the expected direction, the finding was not robust for all four orang-utans (Figure 2A) Amos ($b_{Intercept}$ = 0.596 [0.057], 89% CrI [0.504; 0.694], *pd* = 0.955) and Sandy ($b_{Intercept}$ = 0.601 [0.057], 89% CrI [0.509; 0.698], *pd* = 0.963) showed a more robust first fixation bias than Samboja ($b_{Intercept}$ = 0.585 [0.056], 89% CrI [0.489; 0.678], *pd* = 0.925) and especially Wattana ($b_{Intercept}$ = 0.549 [0.064], 89% CrI [0.436; 0.648], *pd* = 0.756). In addition, we again found that the orang-utans had a leftward bias ($b_{left\text{-}right}$ = 0.195 [0.072], 89% CrI [-0.079; 0.309], *pd* = 0.997), although it was less pronounced than in Experiment 1.

Replication total fixation duration

Similar to Experiment 1, the outcomes of the Bayesian zero-one inflated beta regression (Supplementary Table 2) suggested that the orang-utans had an attentional bias towards flanged male stimuli ($b_{Intercept}$ = 0.607 [0.028], 89% CrI [0.564; 0.653], *pd* = 1.000). However, in contrast to Experiment 1, all four orang-utans had a robust bias towards flanged males (Figure 2B): Amos ($b_{Intercept}$ = 0.593 [0.032], 89% CrI [0.541; 0.645], *pd* = 0.997), Samboja ($b_{Intercept}$ = 0.597 [0.036], 89% CrI [0.540; 0.656], *pd* = 0.995), Sandy ($b_{Intercept}$ = 0.625 [0.054], 89% CrI [0.542; 0.715], *pd* = 0.991), and Wattana ($b_{Intercept}$ = 0.613 [0.048], 89% CrI [0.526; 0.690], *pd* = 0.978). Furthermore, similar to Experiment 1, we found no side bias ($b_{Intercept}$ = 0.002 [0.049], 89% CrI [-0.073; 0.085], *pd* = 0.519).

Full dataset

With regard to the first fixation duration, we found that probability of first fixation on the left stimulus depended on the combination of stimuli (Supplementary Table 3; Figure 3A; see Appendix G for model stability checks). First, in line with our previous analyses, the orang-utans had an overall left bias for first fixation (*b* = 0.604 [0.029], 89% CrI [0.558; 0.651], *pd* = 1.000). Second, we found a difference in probability of first fixation on the left stimulus between trials where a flanged male was presented on the left with an unflanged male on the right, and an unflanged male on the left with a flanged male on the right ($b_{FM.UFM\text{-}UFM.FM}$ = 0.164 [0.063], 89% CrI [0.064; 0.263], *pd* = 0.996). However, probability of fixating on the left stimulus first did not differ robustly between any of the other conditions (Supplementary Table 5).

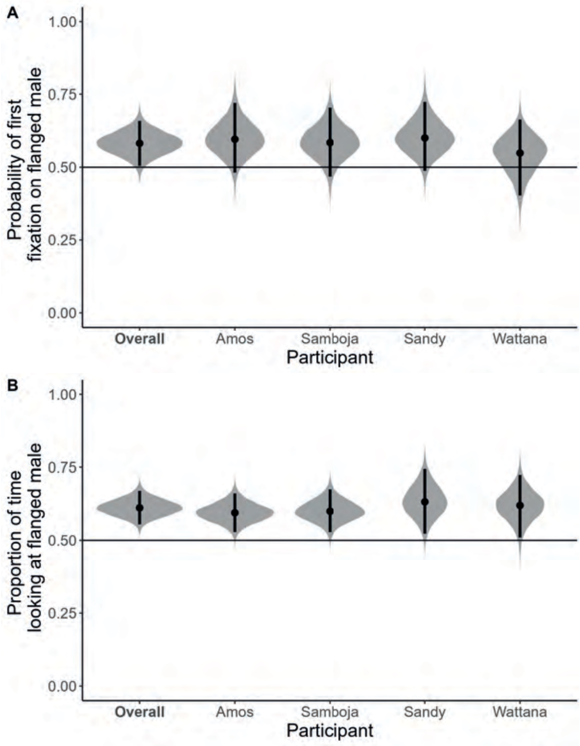

Figure 2. Results of the replication of Experiment 1 in Experiment 2 depicting (A) predicted probability of fixating first on the flanged male stimulus and (B) predicted proportion of time spent fixating on the flanged male stimulus. We report the overall prediction and the predictions for each participant. Grey areas represent the posterior predictions for each iteration of the model, black dots indicate the median posterior prediction, and black lines indicate the 95% credible interval.

With regard to the total fixation duration, we found that the interaction between morph of the left stimulus and morph of the right stimulus predicted looking time bias towards the left stimulus (Supplementary Table 4; Figure 3B; see Appendix G for model stability checks). If a flanged male and unflanged male stimulus were paired, the bias deviated robustly from 0.5 (flanged left-unflanged right: *b* = 0.588 [0.030], 89% CrI [0.540; 0.636], *pd* = 1.000; unflanged left-flanged right: *b* = 0.427 [0.028], 89% CrI [0.382; 0.473], *pd* = 0.996). However, this was not the case when two males of the same morph were shown (flanged-flanged: *b* = 0.521 [0.041], 89% CrI [0.455; 0.585], *pd* = 0.702; unflanged-unflanged: *b* = 0.505 [0.039], 89% CrI [0.440; 0.567], *pd* = 0.556). The pairwise contrasts confirmed this pattern, although not all of them were robust (Supplementary Table 5).

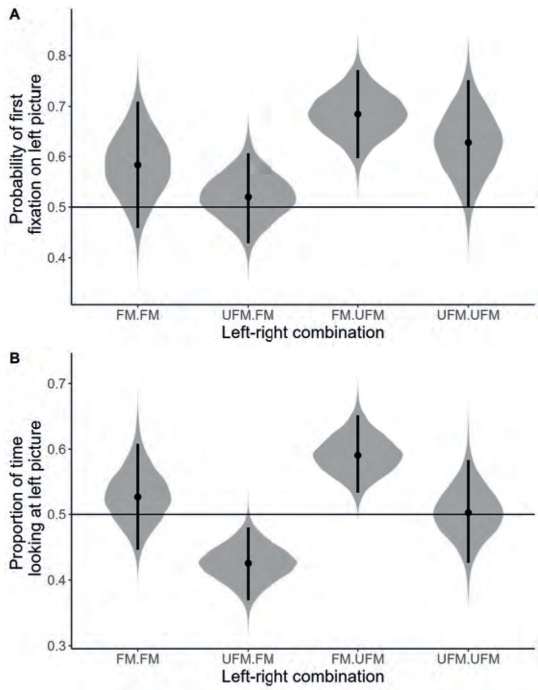

Figure 3. Results of Experiment 2 depicting (A) predicted probability of fixating first on the left stimulus and (B) predicted proportion of time spent fixating on the left stimulus as a function of the morph depicted on the left and right side of the screen. We report the overall prediction and the predictions for each participant. Grey areas represent the posterior predictions for each iteration of the model, black dots indicate the median posterior prediction, and black lines indicate the 95% credible interval.

Individual preferences

For the three female participants, we constructed individual models to test whether they had robust attentional biases towards stimuli depicting specific males (Supplementary Table 6). For Samboja, we found that she spent the largest proportion of time fixating on pictures of Sibu, a flanged male, and the lowest proportion of time fixating on Jingga, an unflanged male (Figure 4). Pairwise contrasts revealed that the difference in attention towards Sibu and Jingga was robust ($b_{Jingga\text{-}Sibu}$ = -0.127 [0.064], 89% CrI [-0.228; -0.024], *pd* = 0.976). Other contrasts revealed no robust differences, although Samboja tended to prefer Bako over Jingga (Supplementary Table 7). For Sandy, we found that she spent the largest proportion of time fixating on Bako, a flanged male, while she spent the lowest amount of time fixating on Wousan, an unflanged male (Figure 4). Pairwise contrasts revealed that this difference was robust ($b_{Bako\text{-}Wousan}$ = 0.142 [0.078], 89%

CrI [0.015; 0.265], *pd* = 0.964). While other contrasts revealed no robust differences, Sandy tended to prefer Bako to Jingga (Supplementary Table 7). Lastly, Wattana had no clear preference: she spent most time fixating on Bako, closely followed by Jingga and Sibu. Interestingly, she spent the least amount of time fixating on Wousan compared with the other three males (Figure 4). However, pairwise contrasts revealed a clear difference only between Bako and Wousan ($b_{Bako\text{-}Wousan}$ = 0.156 [0.090], 89% CrI [0.011; 0.294], *pd* = 0.960). Furthermore, Wattana tended to prefer both Sibu and Jingga over Wousan (Supplementary Table 7).

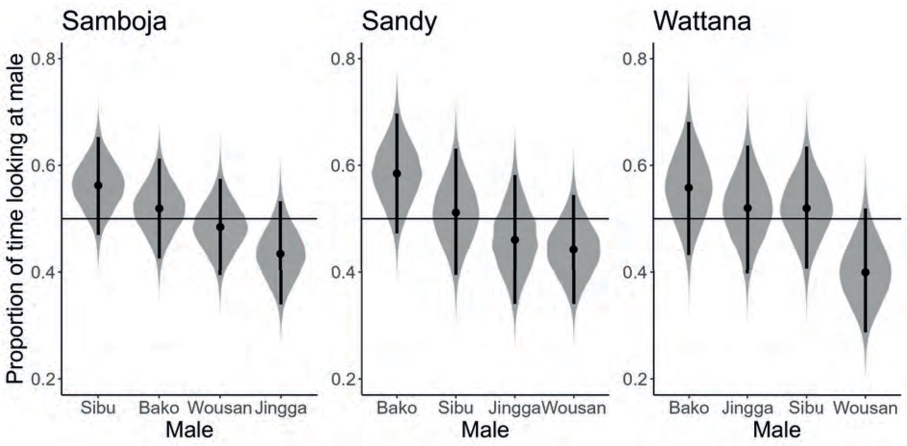

Figure 4. Results of the individual preference-models based on Experiment 2. The figures depict which male received most attention for each female participant separately. Grey areas represent the posterior predictions for each iteration of the model, black dots indicate the median posterior prediction, and black lines indicate the 95% credible interval.

Discussion

The effect of facial characteristics on attentional processes in a mate choice context has been extensively studied in humans (Leder et al., 2016; Roth et al., 2022, 2023; Yang et al., 2015). However, relatively few studies have explored this topic in primates. In this study, we investigated how fully developed secondary sexual characteristics affect attentional processes in Bornean orang-utans. This arboreal great ape species is an ideal model for studying the effect of secondary sexual characteristics on attention processes because they are characterised by male bimaturism, meaning that adult males exist in two distinct morphs: unflanged males, who are reproductively active but not fully developed, and flanged males, which are morphologically distinct from adult females and unflanged males, and are preferred partners of females (Knott et al., 2009; Utami et al., 2002). Here, we presented four Bornean orang-utans with flanged and unflanged stimuli (Experiment 1) or combinations of different morphs, that is, flanged-flanged, unflanged-unflanged, or flanged-unflanged (Experiment 2), while we non-invasively tracked their gaze. Across two experiments, we found that the orang-utans were more likely to first fixate on stimuli depicting flanged males, and spent longer fixating on flanged male stimuli. Furthermore, we found that orang-utans had an immediate attentional bias toward the left side of the screen. Below, we discuss our findings in the context of human and primate literature on attention and provide suggestions for future research.

In two separate experiments, we discovered that orang-utans exhibited a higher likelihood of immediately fixating on stimuli depicting a male with flanges. This attentional bias towards flanges is in line with the general phenomenon of immediate attention towards evolutionarily relevant stimuli. By immediately detecting and processing biologically salient stimuli, an individual can effectively cope with situations that are relevant to their biological fitness (Carretié, 2014; New et al., 2007). Accordingly, humans have been found to immediately attend to the emotional expressions of conspecifics (Carretié, 2014; Kret & van Berlo, 2021; van Berlo et al., 2023), potential threats (Öhman et al., 2001), and attractive conspecifics (Lindell & Lindell, 2014; Roth et al., 2022, 2023). Similarly, recent evidence suggests that primates also immediately attend to biologically salient stimuli such as emotional scenes (King et al., 2012; Kret et al., 2016; van Berlo et al., 2023; but see Laméris et al., 2022). Our results suggest that immediate attentional bias may also be present for stimuli that are relevant to mate choice in primates.

Immediate attention is mostly driven by bottom-up processes and low-level stimulus properties (Theeuwes, 2010). We attempted to control for luminance and contrast at the stimulus level by comparing the luminance and contrast of flanged and unflanged stimuli in Experiment 1 and standardizing the stimuli in Experiment 2. However, local differences in contrast and luminance within stimuli may have affected immediate attention and influenced our results. Nonetheless, it is important to emphasise that differences in low-level properties, such as contrast, may provide a perceptual mechanism that makes specific traits stand out (Rosenfield et al., 2019). Therefore, rather than an alternative explanation, low-level properties may be the mechanism by which attention is attracted to biologically meaningful traits. In general, sexual selection favours traits that exploit the sensory system of receivers because a salient trait should stand out against environmental noise (Ryan & Cummings, 2013). Orang-utan flanges may be an example of a trait that exploits the sensory system of receivers for sexual selection purposes. Their unique flanged features may stand out, making them more salient to their potential mates. This may explain why orang-utans fixated first on stimuli depicting a male with flanges in our experiments, as these stimuli stood out against background noise due to their distinct low-level properties.

We also found that the orang-utans exhibited a first fixation bias towards the left stimulus in both experiments irrespective of the type of stimulus that was shown on the left. These results are consistent with those of previous human experiments. For instance, a study on attractiveness bias in humans found that 82% of the first fixations were directed towards the left face when two faces were paired (Leder et al., 2016). Importantly, this bias does not appear to be restricted to humans. Guo et al. (2009) presented facial stimuli to humans, dogs (*Canis lupus familiaris*), and rhesus macaques, and found that these species have a strong left bias in their first fixation when presented with faces. However, this bias may extend beyond the faces. In humans, it seems that an initial attentional bias towards the left visual field can be found across contexts, which suggests a more general perceptual bias driven by asymmetries in the attentional system between the two brain hemispheres (Ossandón et al., 2014). Overall, our findings regarding the first fixation of orang-utans suggest that they also have a perceptual bias towards the left during their first fixation. It is essential to consider this when designing studies to explore immediate attention in primates.

With regard to voluntary attention, we found that orang-utans fixated on flanged male faces for a larger proportion of each trial than on unflanged male faces across the two experiments. While immediate attention is mainly driven by automatic bottom-up attentional processes, the results for the total fixation duration were probably more reflective of top-down attention because the orang-utans could actively and voluntarily divide their attention during the four seconds that each trial lasted (Theeuwes, 2010). Therefore, it seems that the orang-utans volitionally fixated more on the flanged male faces than on the unflanged males. These results complement those of a previous study where it was shown that when scanning faces, orang-utans pay attention to the flanges (Kano et al., 2012). Furthermore, these results are in line with those of previous studies in humans and macaques. Previous research has shown an attentional bias for masculinity in male faces in humans (Garza & Byrd-Craven, 2023; Yang et al., 2015). Additionally, a study in rhesus macaques showed that females prefer to look longer at a more masculine male face in a pair of two (Rosenfield et al., 2019). In humans (Penton-Voak & Chen, 2004; Pound et al., 2009), and potentially also in rhesus macaques (Rhodes et al., 1997), facial masculinity is linked to testosterone levels. This is also seems to be the case for orang-utan flanges: males with higher testosterone levels developed flanges earlier than individuals with lower testosterone levels (Emery Thompson et al., 2012). Altogether, our study is the first to describe a voluntary attentional bias towards a masculine trait in a great ape species, suggesting that a preference for masculine traits that are under the control of testosterone is shared across different primate species. Furthermore, we show that this preference appears to be expressed at both early stages of visual processing as well as at later stages that involve volitional control.

One important caveat of our study is that we could not determine why orang-utans were more attentive to flanged males. They may have had more interest in flanged males because they are potential mating partners. Alternatively, their vigilance towards flanged males could be due to the potential threat they pose to infants due to infanticide risk (Beaudrot et al., 2009; Knott et al., 2019). Importantly, we also found a bias towards flanged males in the one male that participated in our study, suggesting that male competition could also cause an attentional bias towards flanged males. Future studies could focus more on this specific aspect using methods such as priming or testing at different points during the menstrual cycle of a fully cycling female orang-utan. If an attentional bias towards flanged males is driven by a willingness to mate with them by female orang-utans, we would expect to see a stronger bias during ovulation. This would be in line with previous research suggesting that females actively approach flanged males to mate with them during ovulation (Knott et al., 2009), thus showing concordance between cognition and behaviour.

However, very few studies have investigated ovulatory shift effects in non-human primates from a cognitive perspective, as such studies are difficult to conduct. In general, female primates in zoos and sanctuaries do not always have an active menstrual cycle as they are on birth control or have a dependent infant. To our knowledge, only one study has investigated the ovulatory shift effects in cognition in a non-human primate; Lacreuse et al. (2007)found evidence for increased attention towards, but not enhanced recognition of, male faces over female faces during the periovulatory period of rhesus macaques. Furthermore, recent studies in humans have also cast doubt on previously reported ovulatory shift effects in women because they have failed to find changes in mate attraction across the menstrual cycle (Stern et al., 2021) or a conclusive relationship between reproductive hormone levels and attention towards mate-relevant information such as facial masculinity (Garza & Byrd-Craven, 2023). Nonetheless, investigating the concordance between sexual motivation and attentional biases in orang-utans might help further elucidate the link between mate choice-relevant stimuli and visual cognition in non-human primates.

In Experiment 2, we presented the orang-utans with multiple unique stimuli of four Bornean orang-utan males. Given that the topic of variation in individual preferences of females has received relatively little attention in the past (Jennions & Petrie, 1997), we explored the individual attentional preferences of the three orang-utan females that participated in our study. While we found some robust differences in attention towards the four males at the individual level, all of these differences concerned pairs of flanged and unflanged males. Thus, we did not observe subtle attentional preferences, such as a preference for one flanged male over another. In general, studies on primate attention have mostly focused on differential attention towards specific stimulus categories, such as emotional versus neutral stimuli (Pritsch et al., 2017), familiar versus unfamiliar conspecifics (Hanazuka et al., 2013; Lewis et al., 2021), same-sex versus other-sex stimuli (Lonsdorf et al., 2019), or presence versus absence of facial characteristics (this study). However, we believe that it would be interesting for future studies to move beyond such classifications and look more into individual preferences. Admittedly, this would be a challenging endeavour that might require larger samples and more diverse stimulus sets. Nevertheless, it is relevant to explore such preferences, as studies in humans have already shown that humans exhibit considerable inter-individual differences in gaze patterns (Rogers et al., 2018) and that individual preferences for salient traits such as attractiveness are predictive of attention (Leder et al., 2016; Roth et al., 2023). One potential approach would be to employ reverse correlation techniques to create classification images per participant, which represent the face that attracts their attention. This technique has been widely applied to study human face perception (Dotsch & Todorov, 2012; Karremans et al., 2011) but has not yet been employed to study great ape cognition. Overall, while we found some individual differences in female attention towards male orang-utans, future research could benefit from a more individualized approach to examining primate attentional preferences.

To conclude, our study contributes to the understanding of how sexual selection shapes attentional processes by showing that Bornean orang-utans allocate their attention to a conspicuous sexually dimorphic trait, namely male flanges. We found this bias for both immediate and voluntary attention, which suggests that both bottom-up and top-down attentional processes are attuned to this facial characteristic. Thus, it seems that the visual system of great apes may be attuned towards stimuli that are relevant in the context of mate choice, as has been previously shown for humans. It is important that we cannot conclude why the orang-utans preferentially attended to flanged males: they might either be attracted to them or be vigilant. Therefore, we suggest that future work could make use of the natural fluctuations in mating motivation during the menstrual cycle. This would allow us to investigate whether the attentional bias towards flanged males increases as a function of mating motivation, which would suggest that the bias is driven by attraction. Overall, this study highlights the importance of understanding the role of sexual selection in shaping attentional processes, not just in humans but also in other great apes such as orang-utans, which may have implications for our understanding of the interplay between cognition and sexual selection.