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ORIGINAL ARTICLE

# Bornean orangutans (*Pongo pygmaeus*) show an attentional bias toward a male secondary sexual trait

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## Abstract

Visual attention mechanisms help organisms prioritize evolutionarily relevant stimuli, like threats and mating opportunities. Individuals may, therefore, attend to specific facial features. In humans, it has consistently been shown that secondary sexual traits and attractive faces capture and hold attention. By contrast, evidence for such biases in nonhuman primates, especially great apes, remains scarce. To address this gap, we conducted two eye-tracking experiments with four zoo-housed Bornean orangutans (*Pongo pygmaeus*), a species characterized by extreme sexual dimorphism. In both experiments, we found that orangutans exhibited an attentional bias toward fully flanged males, a sexually dimorphic trait of some adult males. They not only looked longer at flanged males but were also more likely to immediately fixate on them. This suggests that great ape cognition has been shaped by sexual selection in a similar fashion to humans, where attentional biases toward masculine and attractive faces are well-documented. At the same time, we cannot rule out the possibility that individuals attended more to flanged males due to their potential threat to both sexes. Nevertheless, by demonstrating attentional attunement to a secondary sexual trait, our findings contribute to the growing understanding of how sexually selected features influence cognition in nonhuman primates.

KEYWORDS
attentional bias, cognitive mechanisms, comparative psychology, preferential looking, primate, sexual dimorphism, sexual selection

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## INTRODUCTION

Individuals are constantly exposed to more information than they can process. Visual attention mechanisms help prioritize evolutionarily relevant stimuli, such as potential threats, mates, or socially salient cues, while filtering out less relevant input.[1–3] Accordingly, humans show attentional biases toward conspecifics' emotional expressions,[4,5] animate entities,[6] predators,[7] and potential partners.[8,9] Similar adaptive biases are found in nonhuman primates, who attend to predators (e.g., Refs. 10, 11), emotional expressions (e.g., Refs. 12, 13), and traits relevant to mate choice (e.g., Refs. 14–16). Here, we investigated whether Bornean orangutans, a species with pronounced sexual dimorphism,[17] show an attentional bias toward a secondary sexual characteristic.

Much of the existing literature on attentional biases has focused on emotionally valenced stimuli, particularly those associated with negative emotions, dominance, and competition. Both humans and nonhuman primates show attentional biases toward such stimuli. For example, humans immediately attend to angry faces (e.g., Refs. 18–20) and attend[21,22] and respond[23,24] immediately to cues of dominance. Similarly, nonhuman primates show attentional biases toward predators (chimpanzee, *Pan troglodytes*;[7,10] Japanese macaque, *Macaca fuscata*[11]), but also to stimuli of veterinarians or caretakers with a capture device (e.g., chimpanzee;[25] tufted capuchin, *Sapajus* spp.[26]). These biases extend to conspecific stimuli that are related to threat, such as threatening facial expressions and stimuli depicting conflict (rhesus macaque, *Macaca mulatta*;[27] long-tailed macaques, *Macaca fascicularis*;[28] bonobos, *Pan paniscus*[29]), or potentially threatening individuals (tufted capuchin;[30] brown tufted capuchin, *Sapajus apella*[31]). Overall, these attentional biases suggest that selection pressures have shaped both human and nonhuman primates to rapidly detect environmental and social threats, which has clear survival benefits. However, much less is known about other types of attentional biases, specifically those related to reproductive opportunities.

Visual attention may also be attuned to traits that signal reproductive fitness. In humans, many studies have found that heterosexual women and men have an attentional bias toward attractive members of the opposite sex.[8,9,32,33] Importantly, such attentional biases have been identified for both immediate, relatively involuntary (e.g., Ref. 8), and sustained, more voluntary, attention (e.g., Refs. 9, 32). In humans, attentional biases toward attractive faces also seem to extend to sexual dimorphism: both men and women seem to have a visual bias for more masculine male faces,[34–36] even though a female bias for masculine faces is not always apparent in studies of declared mate preferences.[37] Interestingly, attention toward sexually dimorphic traits seems to extend to nonhuman primates: rhesus macaque females look significantly longer at the more masculine faces of conspecifics.[38] This implies that attentional biases toward such sexually selected traits can also be found in nonhuman primates.

In the last two decades, an increasing number of studies have investigated attention and its relation to sexual selection in macaques using a preferential looking paradigm.[39] 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.[14,15] employing a preferential looking paradigm established that macaque females had an attentional bias toward bright red male faces when they were paired with paler faces, while males had an attentional bias toward 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.[40] found that macaques had a bias for red male faces, whereas Rosenfield et al.[38] 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.

To date, nonhuman primate studies that investigate adaptive attentional biases have mostly focused on macaques. However, to fully understand the evolutionary underpinnings of such attentional biases, it is important to test a wide range of species,[41] ideally with different social and mating systems.[42] Some primate species, such as orangutans (*Pongo* spp.), exhibit extreme forms of sexual dimorphism that are thought to be the result of both intense male–male competition and female choice.[17] In addition, these arboreal great apes are characterized by male bimaturism, meaning that there are two distinct types of male morphs: unflanged males and flanged males.[43] Unflanged males lack secondary sexual characteristics, but they are sexually mature and can produce offspring.[44] However, they are not preferred mates for adult females,[45] especially during ovulation.[46] 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.[44,45] Female choice for flanged males potentially reflects selection for good genes,[47] because the transition from unflanged to flanged males is energetically costly.[95]

At the same time, flanged males might also pose a threat to conspecific males and females. Regarding males, flanged males exhibit mutual aggression, and fights between flanged males can lead to serious bodily harm.[48] Unflanged males are to some extent tolerated by flanged males, but only from a distance.[45] Regarding females, it has been suggested that flanged males might pose an infanticide threat (e.g., Refs. 45, 46). While no definitive evidence of infanticide in orangutans has been found, females possess multiple behavioral and physiological counterstrategies that are often seen in infanticidal species.[45] However, it remains to be established whether male infanticide would actually be adaptive for flanged males.[45,49] Furthermore, the only report of an inferred case of infanticide in wild orangutans seems to implicate a new unflanged male as the cause of infanticide, and not a flanged male.[50] Nevertheless, even if the risk of infanticide is extremely low, the large costs associated with infanticide might cause females to avoid unfamiliar flanged males or unfamiliar males in general. Altogether, orangutans might benefit from closely monitoring flanged males, either to avoid risk, establish dominance, or to gain valuable social opportunities.

No attentional bias toward flanges was found in a recent study.[51] However, that study investigated only immediate attention. Moreover, this paradigm relied on manual reaction times, which are inherently noisy,[52] because reaction times are influenced by both speed of per-

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**TABLE 1** Overview of the Apenheul orangutans.

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

ception and motor output. In the current study, we, therefore, focus specifically on the perception of stimuli by using state-of-the-art eye-tracking techniques[53] to investigate whether Bornean orangutans have an immediate and sustained attentional bias toward 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 orangutans, we expected the participating orangutans to (1) gaze immediately at the portrait of the flanged male (immediate attention) and (2) spend relatively more time looking at the flanged male within each trial (sustained attention). 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 orangutans (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 orangutans 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 orangutans (*Pongo pygmaeus*; females: Samboja, Sandy, Wattana; flanged male: Amos) that lived in a fission-fusion enclosure with four other orangutans (one of which was transferred during the study period; Table 1) in Apenheul Primate Park (Apeldoorn, The Netherlands). The females, but not the males, had prior experience with touchscreen-based research. However, none of the individuals had experience with eye-tracking. All females were administered contraceptives. The four nonparticipating orangutans were initially allowed to participate in the study, but they showed a lack of motivation. Therefore, we could not collect data from them.

The orangutans were housed in a building consisting of four indoor enclosures that were each connected to outdoor islands. The orangutans were typically housed in 3–4 subgroups, and group composition was sometimes changed with the aim of mimicking the natural social structure of orangutans, 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.

### Experiment 1: Flanged versus unflanged stimuli

In Experiment 1, individuals were presented with combinations of flanged and unflanged male stimuli within each trial.

### Procedure

Participants were calibrated and tested using Tobii Pro Lab v. 1.194 and a Tobii Pro Spectrum with a sampling frequency of 1200 Hz that was attached to a 24″ monitor (16:9, 1920 × 1080). 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 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 orangutans, food, and mating orangutans. 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 orangutans completed a successful 2-point calibration, which is sufficient to produce accurate gaze data for this type of experimental design.[53]

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 orangutan 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 4 s. After the stimulus presentation, a gray screen was shown for 3 s. 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 (1) looked away from the center during trial onset because the start point of the trial would not be neutral, or (2) showed less than 1 s of fixation time on the stimuli during the trial because this could indicate a lack of attention and/or distraction during the trial. The total number of trials for which this was the case is reported in Table S1. During the fixation video and the stimulus presentation, the orangutans 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 orangutan reintroduction programs. These were supplemented with portrait pictures taken from semi-wild orangutans and pictures of zoo-housed orangutans within the orangutan EAZA Ex-situ Programme (EEP). The main criterion for the stimuli was that the full face of the male needed to be visible in the picture, including both eyes. Stimuli were collected by T.R. and discussed with J.O.P-G. in case of uncertainty about the inclusion of a stimulus. In total, we collected 54 stimuli of flanged males and 55 stimuli of unflanged males. These stimuli were then randomly paired and placed on the gray background via GIMP (v2.10.32). This resulted in 54 unique combinations. See Figure S1 for an example.

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.[54]

## Experiment 2: Combinations of both morphs

### 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. The total number of erroneous trials is reported in Table S1. Furthermore, the stimulus set differed from Experiment 1, as we also showed combinations of the same morph in this analysis (flanged–flanged, unflanged–unflanged).

### 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-gray 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 1.

For Experiment 2, we selected six naturalistic stimuli of four different orangutan males (two flanged: Bako & Sibu, two unflanged: Jingga & Wousan). Stimuli of Bako and Jingga were provided by Ouwehands Zoo, stimuli of Sibu were provided by Dublin Zoo, and stimuli of Wousan (housed in Paignton Zoo, UK) were kindly shared by Brian Lilly. All four males were part of the orangutan EEP and had not been previously housed with the subjects of the study. T.R. selected four portrait photos and two photos depicting both the face and (part of the) body, and consulted with J.O.P-G in case of uncertainty about the inclusion of a stimulus. For the body stimuli, our criterion was that we wanted at least one stimulus showing the full body, and one that at least showed the head and torso of the depicted individual. We realize that this is an unbalanced stimulus set, but we lacked sufficient good-quality pictures to include an equal number of portrait and body stimuli. Using GIMP (v2.10.32), we transformed each photo to grayscale and then applied the Equalize option to standardize 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. See Figure S2 for an example.

## Inter-rater reliability

All sessions of both experiments were scored by T.R. 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, T.R. and E.vB. 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 the 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.[55] For our analyses, we employed a Bayesian approach, which has become increasingly popular in recent years owing to its numerous advantages

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over frequentist analyses.[56,57] All models were created in the Stan computational framework and accessed using the *brms* package.[58,59] 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.[60] No divergence or excessive autocorrelation was found.

## Immediate attention

To investigate whether orangutans had an immediate attention bias toward flanged males when paired with unflanged males, we looked at the location of their first fixation. We used binary logistic regression with the location of the first fixation (1 = flanged male, 0 = unflanged male) as the dependent variable. We modeled 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 modeled 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[61] 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.[62] 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%.[57] We considered an effect to be robust if the credible interval did not overlap zero and the probability of direction was 0.975 or higher.

## Sustained attention

To investigate sustained attention, we used the total fixation duration on the stimuli per trial. We used a zero-one inflated beta model, which is suitable for continuous proportions containing zeros and ones.[63] 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., Ref. 64). 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 toward the flanged male stimulus. In Experiment 2, we also explored how the orangutans 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.[9] Hereafter, we tested whether this bias is affected by the stimulus category on the left side and right side of the screen.

To study whether orangutans had an attentional bias toward flanged males, we modeled *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 orangutan attention, we modeled 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 orangutans paid more attention to the screen had a larger weight in the analysis. In this manner, we avoided that trials where the orangutans were relatively distracted or disinterested would have a large influence on the outcome of our analysis.

To explore whether we could find attentional biases toward 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 orangutan fixated on stimuli depicting a specific individual. We constructed four separate models: one for each individual. Within each model, we modeled *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 the default Student's *t* prior with 3 degrees of freedom for the Intercept of *phi*.

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After running the models, we used the *emmeans* package[61] 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 noninvasive 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 orangutans adhered to the guidelines of the EAZA Ex-situ Program. Furthermore, our research complied with the ASAB guidelines,[65] 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: Bias toward flanged males

### First fixation (immediate attention)

The outcomes of the Bayesian binary logistic regression (Table S2) suggested that the orangutans had a first fixation bias toward 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 toward 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 orangutans 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 (sustained attention)

The outcomes of the Bayesian zero-one inflated beta regression (Table S3) suggested that the orangutans had an attentional bias toward 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 toward flanged males ($b_{left\text{-}right} = 0.033$ [0.045], 89% CrI [−0.036; 0.104], $pd = 0.773$).

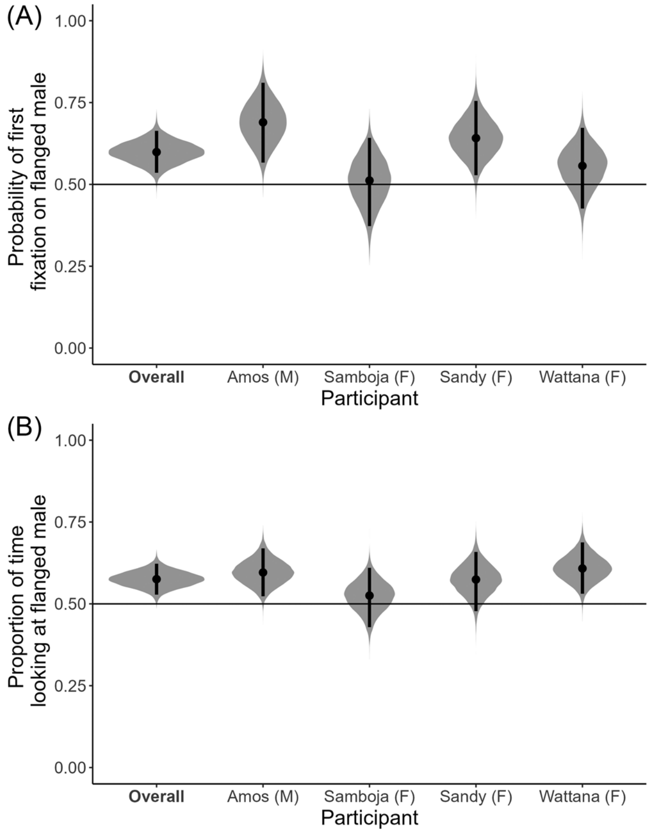

**FIGURE 1** Results of Experiment 1 depicting (A) predicted probability of fixating first on the flanged male stimulus and (B) predicted proportion of time spent fixating on the flanged male stimulus. We report the overall prediction and the predictions for each participant. Gray areas represent the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

## Experiment 2: Replication of Experiment 1

For this analysis, we included only the trials from Experiment 2 where we paired stimuli of an unflanged and flanged male. Thus, we excluded trials depicting the same male morph.

### First fixation (immediate attention)

Similar to Experiment 1, the outcomes of the Bayesian binary logistic regression (Table S2) suggested that the orangutans had a first fixation bias toward 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 orangutans (Figure 2A). Amos ($b_{Intercept} = 0.596$ [0.057], 89% CrI [0.504; 0.694], $pd$

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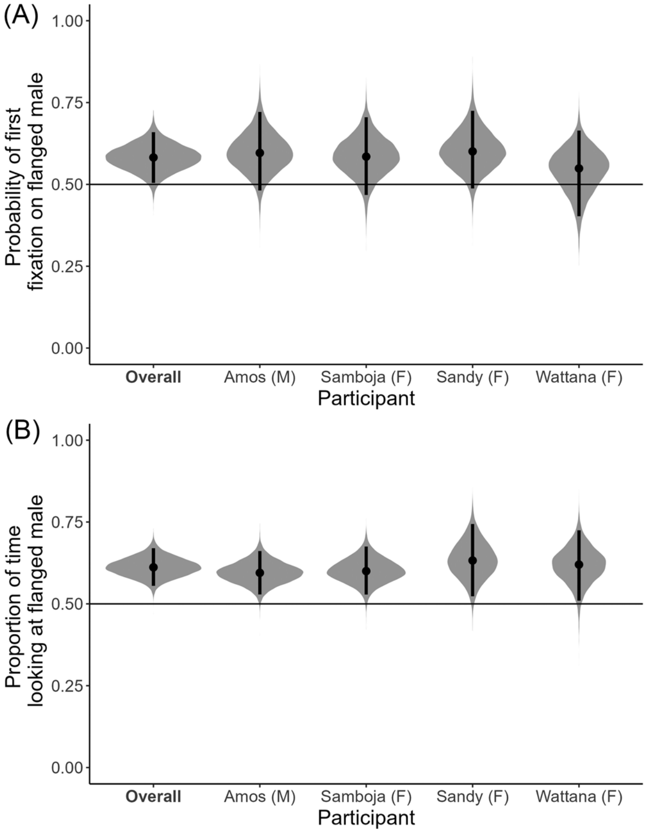

**FIGURE 2** Results of the replication of Experiment 1 in Experiment 2 depicting (A) predicted probability of fixating first on the flanged male stimulus and (B) predicted proportion of time spent fixating on the flanged male stimulus. We report the overall prediction and the predictions for each participant. Gray 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.

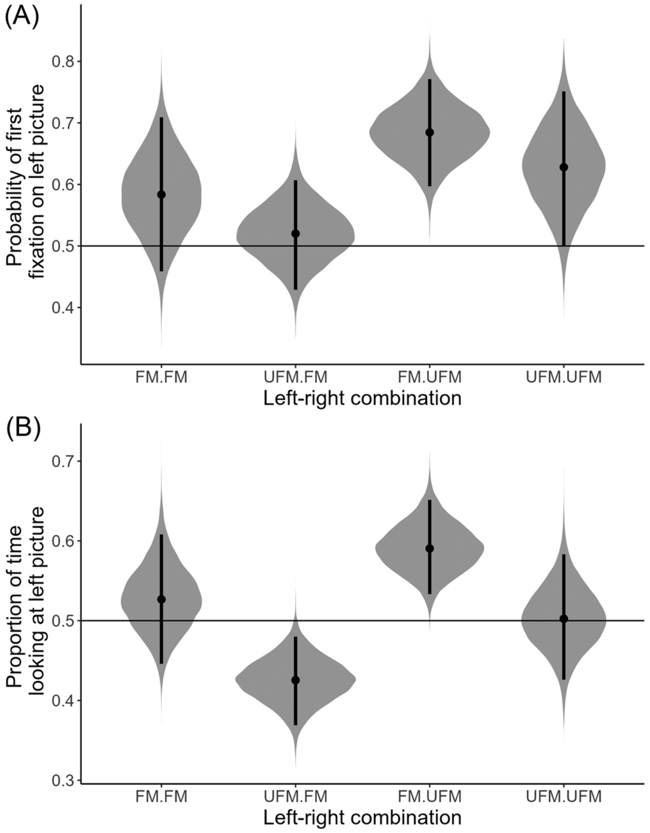

**FIGURE 3** Results of Experiment 2 depicting (A) predicted probability of fixating first on the left stimulus and (B) predicted proportion of time spent fixating on the left stimulus as a function of the morph depicted on the left and right side of the screen. We report the overall prediction and the predictions for each participant. Gray 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.

= 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 orangutans 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.

### Total fixation duration (sustained attention)

Similar to Experiment 1, the outcomes of the Bayesian zero-one inflated beta regression (Table S3) suggested that the orangutans had an attentional bias toward 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 orangutans had a robust bias toward 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).

## Experiment 2: Including same-morph combinations

### Bias toward flanges

With regard to the first fixation (immediate attention), we found that the probability of first fixation on the left stimulus depended on the combination of stimuli (Table S4 and Figure 3A). First, in line with our previous analyses, the orangutans 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%

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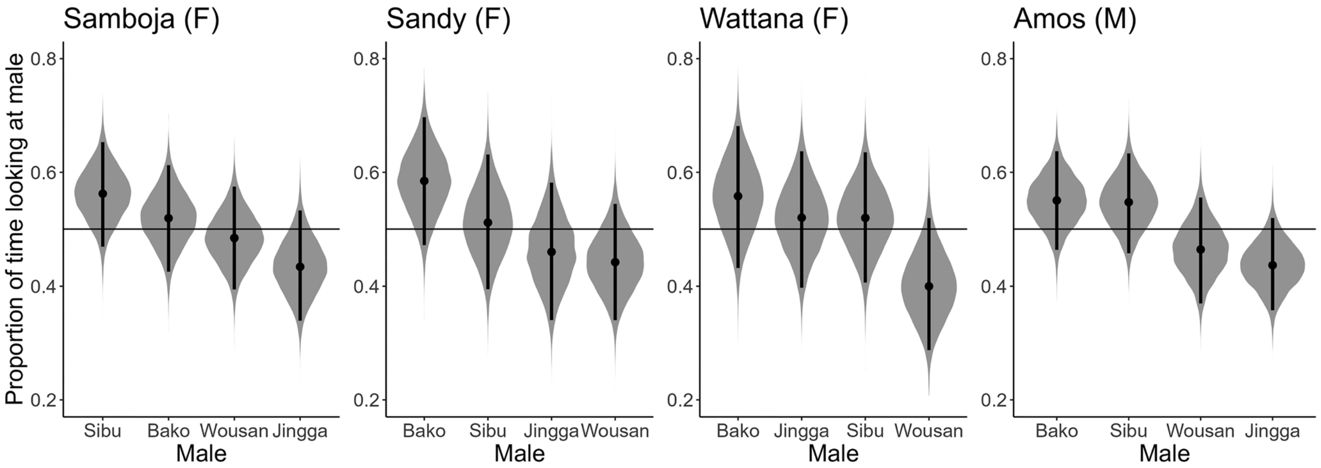

**FIGURE 4** Results of the individual preference models based on Experiment 2. The figures depict which male received most attention for each participant separately. Gray areas represent the posterior predictions for each iteration of the model, black dots indicate the median posterior prediction, and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

CrI [0.064; 0.263], $pd = 0.996$). However, the probability of fixating on the left stimulus first did not differ robustly between any of the other conditions (Table S6).

With regard to the total fixation duration (sustained attention), we found that the interaction between the morph of the left stimulus and the morph of the right stimulus predicted looking time bias toward the left stimulus (Table S5 and Figure 3B). If a flanged male and an 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 (Table S6).

## Individual preferences

For the three female participants, we constructed individual models to test whether they had robust attentional biases toward stimuli depicting specific males (Tables S6 and S7). 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 toward 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. For Sandy, we found that she tended to fixate more on Bako, a flanged male, while she spent the lowest amount of time fixating on Wousan, an unflanged male (Figure 4; $b_{Bako\text{-}Wousan} = 0.142$ [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. However, the credible interval slightly overlaps 0. 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 only a tendency to look more at Bako than 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, although the credible interval slightly overlaps 0. Lastly, Amos spent most time looking at both flanged males and tended to look more at both Bako ($b_{Bako\text{-}Jingga} = 0.113$ [0.059], 89% CrI [0.018; 0.207], $pd = 0.972$) and Sibu ($b_{Jingga\text{-}Sibu} = -0.110$ [0.060], 89% CrI [−0.205; −0.013], $pd = 0.965$) compared to Jingga (Figure 4).

## DISCUSSION

The effect of facial characteristics on attentional processes in the context of sexual selection has been extensively studied in humans.[8,9,32,36] 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 orangutans. This arboreal great ape species is an ideal model for studying the effect of secondary sexual characteristics on attention processes because they are characterized by male bimaturism, meaning that adult males exist in two distinct morphs: unflanged males, which 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.[43,46] Here, we presented four Bornean orangutans 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 noninvasively tracked their gaze. Across two experiments, we found that the orangutans were more likely to first fixate on stimuli depicting flanged males and spent longer fixating on flanged male stimuli. Fur-

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thermore, we found that orangutans 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 orangutans exhibited a higher likelihood of immediately fixating on stimuli depicting a male with flanges. This attentional bias toward flanges is in line with the general phenomenon of immediate attention toward 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.[4,6] Accordingly, humans have been found to immediately attend to the emotional expressions of conspecifics,[4,5,66,67] potential threats,[19] and attractive conspecifics.[8,9,68] Similarly, recent evidence suggests that primates also immediately attend to biologically salient stimuli such as emotional scenes;[67,69,70] but see Ref. 71.

At the same time, different methodologies might yield very different outcomes even when trying to probe the same underlying cognitive mechanism.[72] We recently published a study that found no immediate attention bias toward larger flanges using a dot-probe task,[51] which contrasts with our current results. This discrepancy may be explained by the fact that eye-tracking is a more sensitive method to investigate immediate attention in primates compared to manual response tasks. This has also been confirmed in previous research with humans: attentional biases based on eye movement data do not always replicate with manual response data.[73] Because manual response tasks involve both perceptual processing and motor execution, reaction time measures are susceptible to confounding effects related to motor output, rather than reflecting perceptual attention alone.[74] Consequently, manual reaction times can be relatively noisy.[52] Thus, methodological choices can critically affect the outcomes of studies on immediate attention, as illustrated by the discrepancy between our current and previous results.

Immediate attention is mostly driven by bottom-up processes and low-level stimulus properties.[75] 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 emphasize that differences in low-level properties, such as contrast, may provide a perceptual mechanism that makes specific traits stand out.[38] 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 favors traits that exploit the sensory system of receivers because a salient trait should stand out against environmental noise.[76] Orangutan 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 or competitors. This may explain why orangutans 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 orangutans exhibited a first fixation bias toward 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 toward the left face when two faces were paired.[32] Importantly, this bias does not appear to be restricted to humans. Guo et al.[77] 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 toward 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.[78] Overall, our findings regarding the first fixation of orangutans suggest that they also have a perceptual bias toward the left during their first fixation. It is essential to consider this when designing studies to explore immediate attention in primates.

With regard to sustained attention, we found that orangutans 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 orangutans could actively and voluntarily divide their attention during the 4 s that each trial lasted.[75] Therefore, it seems that the orangutans 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, orangutans pay attention to the flanges.[79] 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.[34,36] Additionally, a study in rhesus macaques showed that females prefer to look longer at a more masculine male face in a pair of two.[38] In humans,[80,81] and potentially also in rhesus macaques,[82] facial masculinity is linked to testosterone levels. In captivity, this also seems to be the case for orangutan flanges: males with higher testosterone levels developed flanges earlier than individuals with lower testosterone levels.[83] Altogether, our study is the first to describe an attentional bias toward 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 orangutans were more attentive to flanged males. They may have had more interest in flanged males because they are potential mating partners. Alternatively, their vigilance toward flanged males could be due to the potential threat they pose to infants due to infanticide risk.[49,50] Importantly, we also found a bias toward flanged males in the one male that participated in our study, suggesting that male competition could also underlie an attentional bias toward flanged males. Future studies could focus more on this specific aspect using meth-

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ods such as priming or testing at different points during the menstrual cycle of a fully cycling female orangutan. If an attentional bias toward flanged males is driven by a willingness to mate with them by female orangutans, 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,[46] thus showing concordance between cognition and behavior.

However, very few studies have investigated ovulatory shift effects in nonhuman 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, as in our study. To our knowledge, only one study has investigated the ovulatory shift effects in cognition in a nonhuman primate; Lacreuse et al.[84] found evidence for increased attention toward, 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[85] or a conclusive relationship between reproductive hormone levels and attention toward mate-relevant information such as facial masculinity.[34] Nonetheless, investigating the concordance between sexual motivation and attentional biases in orangutans might help further elucidate the link between mate choice-relevant stimuli and visual cognition in nonhuman primates.

In Experiment 2, we presented the orangutans with multiple unique stimuli of four Bornean orangutan males. Given that the topic of variation in individual preferences of females has received relatively little attention in the past,[86] we explored the individual attentional preferences of the three orangutan females that participated in our study. While we found some differences in attention toward 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. This may partly be due to the small sample size of our study. Alternatively, such individual preferences may be absent or cannot be extracted based on visual information alone. For example, orangutans also heavily rely on vocal communication. Specifically, flanged male long calls play an important role in facilitating male–female interactions.[87] Thus, females may use this information in combination with visual information to assess mate suitability in a hierarchical manner.[88]

In general, studies on primate attention have mostly focused on differential attention toward specific stimulus categories, such as emotional versus neutral stimuli,[12] familiar versus unfamiliar conspecifics,[89,90] same-sex versus other-sex stimuli,[31] 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 endeavor 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 interindividual differences in gaze patterns[91] and that individual preferences for salient traits such as attractiveness are predictive of attention.[9,32] 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[92,93] but has not yet been employed to study great ape cognition. Overall, while we found few individual differences in attention toward male orangutans, future research could benefit from a more individualized approach to examining primate attentional preferences.

The selection of appropriate stimuli was challenging for this study, especially for unflanged males. Photographic material of orangutans consists mostly of flanged males or mothers and their infants. Pictures of unflanged orangutan males are more difficult to find. Moreover, we used stimuli that were gathered mostly in a captive environment. In such environments, developmental arrest is usually shorter than in the wild.[83,94] Consequently, our stimuli of unflanged males potentially comprise relatively young individuals. One way to solve this is to create a dataset consisting of wild orangutan stimuli. This also offers the opportunity to include stimuli of the same male in flanged and unflanged status. In addition, we included a mix of portrait and full body stimuli in Experiment 2 to create a more naturalistic stimulus set. However, we presented fewer full body stimuli than face stimuli, which may have affected attentional patterns, as the full body stimuli were more novel. Because full body stimuli appeared in only one-third of the trials, individuals might have especially attended to the more novel/rare aspects of these stimuli, namely, the bodies and not the faces depicted in these stimuli. Even though it has previously been shown that orangutans show a strong attentional bias toward faces in full body stimuli,[79] future studies could investigate whether attentional biases toward male morphs differ depending on whether portraits or full body stimuli are shown in a fully balanced design.

To conclude, our study contributes to the understanding of how sexual selection shapes attentional processes by showing that Bornean orangutans allocate their attention to a conspicuous sexually dimorphic trait, namely, male flanges. We found this bias for both immediate and sustained attention, which suggests that both bottom-up and top-down attentional processes are attuned to this facial characteristic. It is important that we cannot conclude why the orangutans 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 toward 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 orangutans, which may have implications for our understanding of the interplay between cognition and sexual selection.

## AUTHOR CONTRIBUTIONS

Conceptualization: T.S.R. and M.E.K.; Methodology: T.S.R. and E.v.B.; Investigation: T.S.R.; Analysis: T.S.R. and E.v.B.; Visualization: T.S.R.;

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Writing—original draft: T.S.R.; Writing—reviewing and editing: E.v.B., J.O.P-G., and M.E.K.; Supervision: J.O.P-G. and M.E.K.

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## CONFLICT OF INTEREST STATEMENT

The authors report no conflicts of interest.

## DATA AVAILABILITY STATEMENT

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

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## PEER REVIEW

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