Bonobos and chimpanzees preferentially attend to familiar members of the dominant sex

Abstract:

Social animals must carefully track consequential events and opportunities for social learning. However, the competing demands of the social world produce tradeoffs in *social attention*, defined as directed visual attention toward conspecifics. A key question is how socioecology shapes these biases in social attention over evolution and development. Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) provide ideal models for addressing this question because they have large communities with fission-fusion grouping, divergent sex-based dominance hierarchies, and occasional intergroup encounters. Using non-invasive eye-tracking measures, we recorded captive apes' attention to side-by-side images of familiar and unfamiliar conspecifics of the same sex. We tested four competing hypotheses about the influence of taxonomically-widespread socioecological pressures on social attention, including intergroup conflict, dominance, dispersal, and mating competition. Both species preferentially attended to familiar over unfamiliar conspecifics when viewing the sex that typically occupies the highest ranks in the group: females for bonobos, and males for chimpanzees. However, they did not demonstrate attentional biases between familiar and unfamiliar members of the subordinate sex. Findings were consistent across species despite differences in which sex tends to be more dominant. These results suggest that sex-based dominance patterns guide social attention across *Pan*. Our findings reveal how socioecological pressures shape social attention in apes and likely contribute to the evolution of social cognition across primates.

Keywords:

social attention, great apes, eye-tracking, preferential looking, familiarity, dominance

Introduction

The demands of sociality have shaped the behavior and cognition of diverse taxa, on both proximate and ultimate levels. For example, the capacity to recognize individuals—and to discriminate familiar from unfamiliar conspecifics—is widespread among social animals, from mammals to fishes and even some insects[1–4]. This skill has evolved independently, in at least several lineages, in instances where the benefits of tracking individual relationships outweigh the cognitive costs[5,6]. Individual recognition allows animals to (1) cultivate long-term affiliative relationships that can impact fitness; (2) establish dominance hierarchies that minimize the need for repeated contest aggression; and (3) identify potentially threatening unfamiliar or outgroup individuals[6–9]. It is therefore considered fundamental to the emergence and elaboration of complex societies, including the evolution of the particularly sophisticated social dynamics and social cognition seen in humans and other primates[7,10–13].

Living in large communities with intricate and differentiated social relationships demands tradeoffs, or biases, in *social attention*, defined as directed visual attention toward conspecifics[14–16]. In a dynamic social landscape, organisms must prioritize how they allocate social attention to ensure that they keep track of the most important individuals and social events, and identify potentially ephemeral opportunities to mate or to learn socially[17]. A growing literature has demonstrated that such biases in social attention exist across many taxa, such as early infant preferences for female faces, and presumed indicators of fitness in rhesus macaques and other primate species[18–21]. However, a key question remains: how are biases in social attention shaped by the demands of a species' socioecology?

Bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) provide an ideal model for addressing this question because they live in large multi-female, multi-male communities that sometimes encounter other groups, foster highly differentiated social relationships that have been linked to fitness, and exhibit fission-fusion grouping patterns; animals are familiar with dozens of individuals within their community but they often range in smaller foraging parties that change in social composition throughout the day[22–30]. The variability of the social environment has likely attuned apes’ social attention to the most functionally relevant individuals and events. Even more critically, bonobos and chimpanzees demonstrate many similarities and key differences in their socioecology that might account for adaptive variation in their social attention toward both groupmates and unfamiliar individuals. Finally, as humans’ two closest extant relatives, they provide unique insights into the evolutionary pressures that have driven the attentional patterns of our own species.

The social lives of chimpanzees and bonobos, like those of many species, are most fundamentally shaped by at least four principal forces: intergroup interactions, social dominance hierarchies, dispersal patterns, and mating competition (in addition to predation and feeding ecology, which we did not address in the present study as these are less relevant to patterns of conspecific social attention). Chimpanzees are notoriously xenophobic and engage in hostile, sometimes lethal, intergroup encounters—in stark contrast to bonobos, who often interact prosocially with members of other groups[31–34]. With regard to social dominance, chimpanzees exhibit linear hierarchies in which adult males almost universally outrank adult females[35,36]. Bonobos, conversely, have been variously characterized as female dominant or female-male codominant, with females forming coalitions to curtail male aggression and maintain predominant control of group decisions[37–41]. Bonobos do not display reverse sexual dimorphism nor are female bonobos masculinized as they are in other typical female dominant species, like hyenas and some lemurs[42,43]. However, male bonobos seldom form coalitions and have weaker affiliative relationships with one another, whereas female bonobos engage in many affiliative interactions (like genito-genital rubbing and grooming), maintain feeding priority within the group, and often occupy the highest positions within the dominance hierarchy[44–46]. Thus, intersexual dominance in bonobos is complex and nuanced: while adult females are not uniformly dominant to adult males (as adults males are to adult females in chimpanzees) and there is instead a mixed-sex hierarchy, the several highest-ranking members of the group tend to be females. Despite this nuance, we can safely characterize these species as differing in the sense that males are dominant in chimpanzees but not in bonobos and the highest-ranking individuals tend to be male chimpanzees and female bonobos. In contrast to their divergent systems of intergroup aggression and social dominance, bonobos and chimpanzees exhibit similar dispersal patterns: most pubertal females immigrate to new communities before reproducing, whereas males remain in their natal community for their entire lives[47,48]. Both species are also highly promiscuous, with each sex exhibiting various forms of intrasexual competition (e.g., [49–51]). These similarities and key differences in socioecology may drive adaptive variation of social attention in these species.

The present study capitalized on this unique constellation of both shared and, critically, differing socioecological traits in order to investigate the socioecological pressures that have shaped social attention across bonobos and chimpanzees. While being non-invasively eye-tracked, captive apes viewed static images of faces of a familiar groupmate alongside a second unfamiliar conspecific of the same sex, following a standard two-image preferential looking design. We decided to contrast a familiar and unfamiliar conspecific within each trial (as opposed to a different factor relevant to our hypotheses) because familiarity is central to all of our hypotheses and, if apes showed a familiarity bias, this contrast would allow us to detect recognition of known conspecifics. We then tested four hypotheses, stemming from the variables outlined above, to determine which features of bonobo and chimpanzee socioecology likely account for their observed biases of social attention (see **Fig. S1** for more details). These hypotheses were developed based on the existing literature on *Pan* socioecology, and formed the basis for our study design. We grounded these hypotheses firmly in prior research that has identified the importance of intergroup interactions, dominance hierarchies, dispersal patterns, and both intersexual attraction and intrasexual competition in the social lives of these species. We developed and named these hypotheses for ease of referencing and for potential future use.

The **Intergroup Conflict Differentiation hypothesis** argues that the degree of intergroup conflict modulates patterns of social attention and predicts, accordingly, that as chimpanzees are more xenophobic, they will show greater differentiation of familiar versus unfamiliar conspecifics than will the more xenophilic bonobos. Some research provides support for this hypothesis. Tan, Ariely, and Hare (2017) demonstrated that on the first day of their experiment, bonobos were more willing to pay a cost to watch a video of a stranger over a video of a known groupmate, consistent with the more xenophilic preferences of bonobos over chimpanzees[33].

The **Dominance Differentiation hypothesis** argues instead that social dominance has the greatest impact on social attention. This hypothesis predicts that both species will show greater differentiation in social attention between members of the more dominant sex (i.e., chimpanzees will discriminate more between familiar and unfamiliar males, whereas bonobos will discriminate more between females). Previous work has identified some support for the influence of dominance on social attention in primates. Macaque infants who were not mother-reared are still able to discriminate the faces of adult macaques, which represent a primary and dominating threat to infant macaques[52]. Male infant macaques of high-ranking mothers also look more at faces as compared to sons of low-ranking mothers[18]. Finally, previous work indicates that in some primate species, lower ranking individuals devote more social attention to higher ranking individuals than vice versa[53–55] (but see [56]).

The **Dispersal Differentiation hypothesis** proposes that dispersal patterns moderate biases in social attention. This hypothesis predicts that both chimpanzees and bonobos will demonstrate greater differentiation in social attention between familiar and unfamiliar females. Although experimental research has not yet directly tested this hypothesis, data from the wild suggest that dispersing female apes garner significant amounts of attention from both males and females in the resident group. Specifically, female immigrant chimpanzees face heightened female competition and aggression when attempting to join a new group; resident males often intervene in female conflicts involving immigrants, almost always supporting immigrant females over resident females[57]. In contrast, female immigrant bonobos engage in affiliative behaviors with at least one resident female (sometimes termed the ‘specific senior female’) which helps to facilitate the immigrant’s integration into her new group[58,59]. These strongly affiliative and aggressive behaviors towards immigrant females in bonobos and chimpanzees, respectively, imply that dispersing females likely attract heightened social attention from both resident male and female conspecifics.

Finally, the **Mating Competition Differentiation hypothesis** suggests that mating competition differently impacts social attention in males compared to females. This hypothesis thus generates two sets of predictions: 1) Intersexual attraction predicts greater differentiation between members of the opposite sex, whereas 2) Intrasexual competition predicts greater differentiation between members of the same sex. Some research offers support for this hypothesis and its predictions. Deaner and colleagues (2005) found that male rhesus macaques were willing to forgo fruit juice for the opportunity to view female perinea, which suggests that male-male competition creates high value on visual access to female genitalia[53]. In addition, both male and female adult rhesus macaques looked longer at male conspecifics with dark red faces as compared to those with lighter red faces in a looking time field experiment[60]. The authors propose that these attentional preferences may be influenced both by female mate choice and male-male competition in these species. Finally, female rhesus macaques have been shown to preferentially attend to more masculine male conspecific faces when they are paired with less masculine faces, and this attentional bias increased with more pronounced within-pair difference in masculinity[61]. The authors suggest that these attentional biases likely result from intersexual selection. By examining attention to familiar versus unfamiliar conspecifics in bonobos and chimpanzees, this study allowed us to investigate how social attention may be impacted by four of the fundamental socioecological factors that likely drive the evolution of social cognition across most taxa.

Methods

A) Participants

Twenty-nine apes participated in this study: 11 chimpanzees (4 females, 7 males) living at the Edinburgh Zoo in Scotland; 6 chimpanzees (5 females, 1 male) and 6 bonobos (4 females, 2 males) living at the Kumamoto Sanctuary in Japan; and 6 bonobos (3 females, 3 males) living at the Planckendael Zoo in Belgium. Subjects ranged in age from 2 to 46 years (bonobo mean = 21.9 years, SD = 13.8; chimpanzee mean = 27.5 years, SD = 10.2; see supplementary materials for ethical notes and **Tables S1 - S2** for details).

B) Apparatus

Experiments utilized established eye-tracking procedures and comparable set-ups across facilities[62–64]. Apes viewed images through a transparent polycarbonate or acrylic panel on a 23” LCD monitor just outside of their enclosures at a distance of approximately 60cm. We non-invasively recorded their eye movements via an infrared eye-tracker (X120 in Edinburgh and Planckendael, X300 in Kumamoto, Tobii Technology AB, Stockholm, Sweden), positioned below the monitor, which mapped their gaze onto the stimuli. Stimulus presentation and data collection were controlled using Tobii Studio. To encourage minimal head movements and optimize corneal reflection measurements, apes had access to a small amount of diluted fruit juice (provided irrespective of viewing patterns) that was delivered through a plastic nozzle positioned on the transparent panel, directly in front of the eye-tracker (see **Fig. 1a**).

Before testing, we conducted a two-point automated calibration for each ape participant by presenting a small video clip (and often a piece of real fruit) on each reference point. We adopted this small number of reference points for apes because they tend to view these reference points only briefly as compared to human subjects. This two-point calibration procedure is regularly used in eye-tracking studies with great apes because it is sufficient to provide high quality data and minimize the loss of subjects who would not reliably attend to a greater number of calibration points[64–66]. After each calibration was obtained, we manually checked the accuracy of the calibration using 9 points on the screen and repeated the calibration process if necessary. The same calibration file was used for each individual throughout testing, and before the start of every session the accuracy was checked with at least one of the 9 points. Using this procedure, calibration errors are typically less than a degree, and any error of this size should not impact the ability to determine preferential looking to images[62].

C) Stimuli

Our stimuli consisted of static images of adult conspecific faces exhibiting neutral expressions (hereafter referred to as “avatars”). These were 600 x 600 pixel close-up color photographs of forward-facing conspecifics surrounded by a gray background (see **Fig. 1b)**. Each trial featured two images, one of a familiar groupmate and another of an unfamiliar conspecific, on the center left and center right regions of a black 1920 x 1080 pixel screen (locations counterbalanced across trials). Conspecifics deemed ‘unfamiliar’ have never been housed at the same institution as the subject, according to institutional and studbook data. Images were sex-matched within trials, and the brightness, blurriness, and contrast of photographs were kept as consistent as possible across stimuli. For each participant population, the stimulus set included three images of familiar conspecifics and three images of unfamiliar conspecifics, with one set for female images and one set for male images. Each familiar image was paired with each unfamiliar image, and this pair was shown twice: once with the familiar image on the left, and once with the familiar image on the right. In total, subjects therefore experienced 18 trials involving male stimuli and 18 trials involving female stimuli. Within each group, the majority of individuals received identical stimuli. If, however, a participant was included in the standard stimulus set for their group, for their stimulus set, their own image was replaced with that of a different member of their group. As a control, the unfamiliar conspecific images used for the Kumamoto chimpanzees and bonobos were those used as familiar images for the Edinburgh chimpanzees and Planckendael bonobos, respectively. The apes at Kumamoto Sanctuary live in social groups that have only one (chimpanzees) or two (bonobos) resident males. Therefore, we could only present one or two images of familiar males to these populations (respectively), and then filled the remaining "familiar" trials with images of unfamiliar males in order to maintain even counterbalancing of image presentation and equal degrees of novelty across stimuli (i.e., these fewer familiar conspecific images did not appear more frequently than the unfamiliar conspecific images they were paired with). These populations, therefore, saw some "fake" trials that contained two images of unfamiliar males, which were excluded from the final analyses.

D) Procedure

Directly before first presenting the test trials, we habituated the Edinburgh and Planckendael apes to the experimental set-up by showing each individual at least one set of three images of non-primate animals with neutral expressions in their natural environments. Kumamoto chimpanzees and bonobos did not require habituation as they had already participated in other eye-tracking studies.

The 36 test trials were administered in clusters of three (twelve clusters total). Each trial lasted three seconds and was preceded by a 0.5 second presentation of a black screen with a fixation cross in the center (in an effort to attract apes to the center of the screen before the trial began). Within a cluster, trials progressed one immediately following the other for a total duration of 10.5 seconds per cluster. Each cluster featured only same-sex images (male or female trials), and within a cluster all 6 images of that sex were shown once (three familiar individuals paired with three unfamiliar individuals). The side on which the familiar individual was presented alternated in a cluster (either one or two times) and was counterbalanced across clusters: for each sex, familiar individuals were presented 9 times on the left side, and 9 times on the right side across clusters. Clusters alternated between male trials and female trials, and the order of cluster presentation was counterbalanced between subjects such that half of the participants started with female clusters (n

= 14), and half started with male clusters (n = 15). There were four variations of cluster order (2 beginning with male clusters, and 2 beginning with female clusters), and these were counterbalanced across participants. Because participation was voluntary (i.e., apes could walk away at any time), the number of clusters administered within a day varied between one to twelve, depending on duration of apes' attendance and attention at the testing set-up. After administering all trials via the pre-determined order, we checked that subjects had at least one fixation to either the familiar or unfamiliar image (see AOI procedure below). After the completion of the original trial order, trials that yielded zero fixations to either image were repeated until we had data for a full set of 36 trials per subject. In total, we tested 1040 trials; all but 1 of 29 subjects completed their entire set of 36 trials (4 missing trials due to persistent lack of interest). We excluded 132 "fake" trials. All 908 available trials were included in our analyses. On average, apes fixated to one or both of the AOIs for 1.22 seconds (SD = 0.84) of each 3s trial.

E) Data Scoring and Analysis

In Tobii Studio, we defined 700 x 700 pixel areas of interest (AOI) around the two images in each trial (i.e., including a 50 pixel buffer on each side of the images). We used the statistical software R (version 3.2.3; R Core Team 2020) to sum total fixation duration within each AOI (i.e., Familiar and Unfamiliar) for the entire 3s trial duration. Fixations were calculated using Tobii Studio's I-VT Filter (additional information provided in Supplemental Materials). To measure apes' biases in looking toward the familiar versus unfamiliar conspecific, we then calculated raw difference scores (i.e., looking to Familiar minus looking to Unfamiliar) as well as a proportional Differential Looking Score (DLS; i.e., [Familiar minus Unfamiliar] divided by [Familiar plus Unfamiliar]) as dependent variables for each trial. We conducted two planned, confirmatory analyses and one exploratory analysis. First, we planned to analyze the predictors of biases in social attention (**Model 1**). Second, we planned to analyze whether apes showed above-chance discrimination of familiar and unfamiliar conspecific faces, taking into account any relevant predictors identified in Model 1 (**Model 2**). Finally, we pursued an exploratory analysis which examined predictors of biases across populations (**Model 3**).

General Modeling Approach:

To investigate which of our hypotheses accounted for variation in apes' biases in social attention, we fitted linear mixed effects models in R for both dependent variables. The raw difference score was modelled using the *lmer* function from the 'lme4' package. The DLS was modelled using the *glmmTMB* function with a beta distribution from the 'glmm' package, as this distribution best models proportional scores (Bates et al. 2014; McCulloch and Neuhaus, 2005). We used a significance threshold of 0.05 when reporting p-values, and report p-values between 0.05 and 0.1 as "trends" for all models. We have chosen to designate trends in this study because *P*-values are continuous variables that convey meaningful variation; a significance test that is based simply on a binary 'accept/reject' decision cannot accurately depict whether an effect or correlation is biologically meaningful[69]. The DLS was standardized from its original [-1,1] interval to a (0,1) interval so that it could be correctly modeled by the beta distribution model, which specifically models proportional scores and requires a continuous distribution that is bounded on this interval. We modeled both measures because raw difference scores give a direct measure of the difference in looking time to the familiar individual versus the unfamiliar individual that captures variation in overall looking duration but can be weakened by differences in raw looking times between individuals or sexes (see [16]). Therefore, to control for these potential differences in raw looking time, we also used the DLS, noting that this proportional score, in contrast, amplifies strongly biased looks even on trials when overall looking duration is low.

For every model in our analyses, we first used likelihood ratio tests to compare the fit of the full model against the null model, which included only the random effects (see supplementary materials for full model sets and comparisons). We then used the *Anova* function with Type III sum of squares provided in the 'car' package to generate *p*-values for individual factors within each model, which produces p-values by running a series of model reductions that tests for the presence of a main effect after testing for the presence of an interaction and other main effects (Fox, John et al., 2012). Before running each model, we first ran the *vif* function to determine whether any model effects had collinearity. The *vif* function calculates the Variance Inflation Factors of all predictors in the models. The *vif* function indicated that none of the models' effects were collinear. Finally, we visually inspected plots of residual values against fitted values and qq-plots to confirm that the models met the assumptions of normally distributed and homogenous residuals.

Model 1: Predictors of biases in social attention

To investigate the influence of the four socioecological drivers on biases in ape social attention, we generated two full models that differed only in the dependent measure (raw difference scores vs DLS). These models included species as a categorical fixed effect to test the prediction of the **Intergroup Conflict Differentiation** hypothesis that looking biases will be greater in chimpanzees than bonobos. The second fixed effect included was sex of the individuals in the images (avatars) to test the prediction of the **Dispersal Differentiation** hypothesis that, across species, looking biases will be greater when looking at images of females than those of males. We also included the interaction between avatar sex and species to test the **Dominance Differentiation** hypothesis, which predicts that chimpanzees demonstrate heightened discrimination between familiar and unfamiliar males, while bonobos demonstrate heightened discrimination between females. Finally, the interaction between avatar sex and sex of the participant was included as a fixed effect to test the **Mating Competition Differentiation** hypothesis, which suggests that biases in social attention are shaped by intrasexual competition or intersexual attraction. We included trial number as a continuous fixed effect to account for a potential habitual effect with an increasing number of trials. We included subject ID (to account for repeated measures from each individual), ID of familiar avatar, and ID of unfamiliar avatar (to account for potential random variability in preferences for specific individuals) as random intercepts.

Model 2: Discrimination of familiar and unfamiliar conspecific faces

After determining which factors shape variation in apes' social attention, we then investigated whether apes show a significant bias in attention toward familiar or unfamiliar avatars. To do so, we performed a post-hoc linear mixed effects **Model 2** using the *lmer* function in 'lme4'. In this model we only used DLS as our dependent measure, as results from **Model 1** suggested DLS to be most consistent. Here we used DLS with its original [-1,1] interval, so that it was possible to determine if these scores were significantly different from zero (a score of zero signifies no bias toward familiar or unfamiliar images). **Model 2** included the same random effects that were included in the main analyses (subject, ID of familiar avatar, and ID of unfamiliar avatar). By including a single fixed effect (identified as a driver of variation in **Model 1**), we were able to determine whether data from each level of this factor differs from zero (indicated by a significant model intercept, see details below). Here, an intercept that is significantly different from zero denotes a significant bias in attention toward familiar (positive intercept values) or unfamiliar avatars (negative intercept values).

Model 3: Patterns of biases across conspecific populations

Finally, data visualization indicated potential differences in patterns of social attention between conspecific populations, and therefore we pursued a final exploratory analysis, **Model 3**, to probe these potential population differences. **Model 3** was fitted for both the raw difference score and the DLS, and included the same test predictors as **Model 1,** but included a population term to test a three-way interaction between avatar sex, species, and population. In this model, population was dummy-coded as European apes (Edinburgh chimpanzees and Planckendael bonobos) and Japanese apes (Kumamoto chimpanzees and bonobos), so that it could be included in the interaction with species as a crossed, rather than nested, variable. **Model 3** also included trial number as a fixed effect to control for a potential habituation effect with an increasing number of trials and the same random effects as **Model 1** (subject ID, ID of familiar avatar, and ID of unfamiliar avatar). This **Model 3** therefore allowed us to directly examine the stability of these attentional patterns across conspecific populations.

F) Results:

Model 1:Predictors of biases in social attention

The full-null model comparison for **Model 1** was not significant for either the difference score ($\chi2 = 7.093$, p = 0.312) or DLS ($\chi2 = 5.721$, p = 0.455), suggesting that the results of the full models should be interpreted cautiously [71]. Although no factors significantly predicted variation in difference scores, the model based on the DLS measure identified a significant interaction between species and avatar sex ($\chi 2 = 5.526$, p = 0.019; see **Tables S3 - S4**). Consistent with the Dominance Differentiation Hypothesis, chimpanzees demonstrated a relatively stronger bias toward familiar individuals when viewing images of males as compared to females, while bonobos exhibited a relatively stronger bias toward familiar individuals when viewing images of females (see **Fig. 2**).

Post-Hoc Model 2: Discrimination of familiar and unfamiliar conspecific faces

Model 1 revealed that bonobos and chimpanzees likely differ in their social attention to each sex, providing support for the Dominance Differentiation Hypothesis. This may reflect species differences in the dominance of each sex; namely, chimpanzee males and bonobo females are generally more dominant than individuals of the other sex. In chimpanzees, males occupy the highest positions in the dominance hierarchy, have close social bonds, and almost universally outrank females. In bonobos, the dominance hierarchy is more nuanced and difficult to characterize; however, females often outrank males, form close social bonds and coalitions, and maintain feeding priority within their groups. Therefore, here, we operationally defined male chimpanzees and female bonobos as the dominant sex. To clarify this point, in post-hoc **Model 2** we recoded avatar sex as 'the dominant sex for each species' and 'the subordinate sex for each species.' Trials depicting male chimpanzees or female bonobos were coded as *dominant*, whereas those depicting female chimpanzees or male bonobos were coded as *subordinate*. **Model 2** included the same random effects as **Model 1** and just the one fixed effect – sex-based dominance status of avatar – to investigate whether apes showed a significant bias in attention toward the familiar or unfamiliar avatar when viewing members of the dominant or subordinate sex. **Model 2** allowed us to directly test the effect of dominance on biases in social attention, and the intercept measured whether apes overall showed a significant bias in attention toward familiar or unfamiliar individuals. By releveling the reference category of the dominance status term, we were able to determine whether apes' attention was significantly biased toward familiar or unfamiliar individuals when those individuals were members of the dominant or subordinate sex.

First, however, we confirmed that the effect of dominance did not differ across species by running **Model 2a**, which included an interaction between 'sex-based dominance status of avatar' and species. The full-null model comparison was not significant for **Model 2a**, and therefore the results of the full models should again be interpreted cautiously (likelihood ratio test: $\chi2 = 5.264$, p = 0.153) However, this model did identify a significant effect of 'dominance status of avatar sex' ($\chi2 = 5.347$, p = 0.021 ; see **Table S5**) but, critically, no significant interaction between dominance status and species ($\chi2 = 1.368$, p = 0.242). Thus, the effect of dominance status does not differ across species. We therefore proceeded to **Model 2b**, which only included a main effect of dominance status.

Model 2b trended towards being significantly better than the null model ($\chi2 = 3.783$, p = 0.052) and again revealed a significant effect of 'dominance status of avatar sex' ($\chi2 = 5.465$, p = 0.019; see **Table S6**). Most interestingly, we found that, when viewing the dominant sex, apes' attention was significantly biased toward familiar individuals over unfamiliar individuals (estimate = 0.102, $\chi2 = 5.478$, p = 0.019; see **Fig. 3**). In contrast, we found no significant biases in attention when apes viewed members of the subordinate sex (estimate = -0.026, $\chi2 = 0.372$, p = 0.542, see **Tables S5-6**).

Exploratory Model 3: Patterns of biases across conspecific populations

Exploratory **Model 3** was developed to probe potential population differences in biases of social attention. The full-null model comparison was significant for the difference score **Model 3** (likelihood ratio test: $\chi 2$ = 20.642, p = 0.024) but not the DLS **Model 3** (likelihood ratio test: $\chi 2$ = 10.459, p = 0.401). For both the difference score and DLS **Model 3,** the three-way interaction between species, dummy-coded population, and avatar sex trended towards being significant (**Difference score:** $\chi 2$ = 3.472, p = 0.062; **DLS:** $\chi 2$ = 3.153, p = 0.076, see **Tables S7 – S8**), and therefore we did not reduce this interaction further. Instead, we subset the data by species and re-ran **Model 3** on the chimpanzee and bonobo datasets separately. These models included the interaction between avatar sex and dummy-coded population and the interaction between subject sex and avatar sex, along with the control term, trial number, and the same random effects.

For the **Chimpanzee Model 3**, the full-null model comparison was not significant for the raw difference score nor DLS (**Difference Score:** $\chi 2$ = 8.315, p = 0.139; **DLS** $\chi 2$ = 6.862, p = 0.334). For the raw difference score **Chimp Model 3** the two-way interaction between population and avatar sex was significant, and it trended towards significant in the DLS **Chimp Model 3** (**Difference Score:** $\chi 2$ = 5.323, p = 0.021; **DLS:** $\chi 2$ = 3.697, p = 0.055). Edinburgh chimpanzees exhibited a relatively stronger bias toward familiar individuals when viewing males relative to females, whereas Kumamoto chimpanzees exhibited a relatively stronger bias toward unfamiliar individuals when viewing males relative to females (see **Fig. 4**). The two-way interaction between subject sex and avatar sex was not significant in either model (**Difference Score:** $\chi 2$ = 1.172, p = 0.279; **DLS:** $\chi 2$ = 2.226, p = 0.136, see **Tables S9 – S10**).

For the **Bonobo Model 3**, the full-null model comparison was not significant for the raw difference score nor DLS (**Difference Score:** $\chi 2$ = 4.459, p = 0.485; **DLS:** $\chi 2$ = 4.604, p = 0.466). For both the raw difference score and DLS**,** the two-way interaction between population and avatar sex was not significant (**Difference Score:** $\chi 2$ = 0.0991, p = 0.753; **DLS:** $\chi 2$ = 0.880, p = 0.348), nor was the two-way interaction between subject sex and avatar sex (**Difference Score:** $\chi 2$ = 0.271, p = 0.603; **DLS:** $\chi 2$ = 1.440, p = 0.230). However, the effect of avatar sex was significant for the DLS **Bonobo Model 3** ($\chi 2$ = 4.353, p = 0.037), although not for the difference score **Bonobo Model 3** ($\chi 2$ = 1.491, p = 0.222, see **Tables S11 – S12**). Bonobos exhibited a stronger bias toward familiar individuals when viewing females as compared to males (see **Fig. 4**).

G) Discussion

In this study, we set out to characterize biases in social attention among chimpanzees and bonobos, and to identify the socioecological factors that shape them. Our findings indicate that both species successfully discriminate familiar from unfamiliar conspecifics based on images of faces alone (Model 2b) and several lines of evidence suggest that their biases in attention are best explained by the **Dominance Differentiation hypothesis**. First, the only significant predictor of DLS in Model 1 was the interaction between species and avatar sex. This interaction reflected chimpanzees' relatively greater attention toward familiar individuals when viewing males than when viewing females, and bonobos' relatively greater attention toward familiar individuals when viewing females than when viewing males. Second, Models 2a and 2b directly demonstrated that sex-based dominance status of the avatars shaped DLS, and that this effect did not differ across species: both chimpanzees and bonobos showed more biased attention toward familiar individuals over unfamiliar ones when viewing members of the more dominant sex than when viewing members of the more subordinate sex. Indeed, this bias toward familiar conspecifics was significantly different from chance only for trials depicting members of the more dominant sex

(Model 2b). These results are among the first experimental evidence that biases in great ape social attention are driven by the demands of their socioecology.

Our findings are consistent with other reports that document effects of social status on patterns of social attention in other primate species. For example, Micheletta and colleagues (2015) used a match-to-sample task and found that crested macaques were better able to discriminate higher ranking familiar individuals as compared to higher ranking unfamiliar individuals[52]. Grampp and colleagues (2019) report that wild juvenile vervet monkeys observed the highest-ranking conspecifics more frequently than low-ranking individuals[73]. Similarly, others have found that both male and female rhesus macaques prefer to attend to faces of high-ranking conspecifics as compared to low-ranking individuals[17],[21]. In addition, high-ranking rhesus macaques selectively gaze-followed other high-ranking macaques as compared to low-ranking conspecifics[74]. Overall, these results suggest that hierarchical dominance patterns drive biases in social attention in primates, and that this mechanism is conserved across primate species. In our study, unlike in previous work, status was reflected only by the sex of the avatar. These findings thus contribute new evidence that, in some species, attention is preferentially allocated not just to the very highest-ranking individuals, but also to any known individuals of whichever sex plays the greatest role in governing group behavior.

While in chimpanzees males almost universally outrank females, in bonobos there is more nuance in the relationship between sex and dominance. Given that bonobos have mixed-sex hierarchies where females typically occupy the highest and sometimes also the lowest ranks, future work should attempt to disentangle the influence of sex and rank on social attention and broader social behavior. One important question is whether the differences we observed in the present study owe specifically to differences in agonistic dominance between the sexes or other related traits like centrality in coalitionary networks or in networks of group decision-making.

Another crucial question is whether the patterns documented in this study stem from selection on mechanisms of attention or from species differences in socialization (in which male chimpanzees and female bonobos play dominant roles in their societies). Based on the results from Model 3, we suspect that both drivers play a role. Model 3 identified an interaction between population and avatar sex for chimpanzees, but not for bonobos, suggesting that the chimpanzee populations differed in their patterns of social attention based on avatar sex (**Figure 4**). Edinburgh Zoo is home to a typical multi-male multi-female group, while the chimpanzee group at Kumamoto Sanctuary has a single male. Although both populations showed stronger biases when viewing male stimuli as compared to female stimuli, these biases favored familiar individuals only for Edinburgh chimpanzees. With only one resident male (and therefore no dominance displays or agonistic conflicts among males), females of the Kumamoto group may reasonably show more interest in outgroup males. Thus, socialization may contribute to biases in social attention, perhaps in concert with selective pressures on mechanisms of attention. Previous work has also identified connections between social experience and social attention patterns in primates. Parr and colleagues (2016) found that, from birth, infant rhesus macaques prefer to look at conspecific faces as compared to heterospecific faces, but that this effect reverses as they age. The authors propose that this may be the result of a rapid experience-dependent preference, as after a few weeks of exposure to many conspecific faces in their natal groups, the infants began to prefer attending to heterospecific faces[75]. In addition, recent work demonstrates that there is a positive relationship between time spent viewing the eyes of faces and number of initiations made for social interactions with peers in infant male rhesus macaques[76]. The combination of these results suggests a link between social attention and social experience in infancy in rhesus macaques. Future work should attempt to expand upon these recent investigations to clarify the relationships between social experience and social attention across species and social environments.

We note several important limitations of our study. First, although our findings were consistent across a number of analyses, we must remain cautious in our interpretation of the results given that some full models did not differ significantly from null models. We find reassuring, however, that Model 2b directly replicated the findings of these models with a full-null model comparison on the verge of significance ($p = 0.052$). Second, although the sample size for this study is on the larger end within great ape research (n = 29) and, unusually, involves multiple populations of each species, our results may be limited by the low numbers of individuals within each population. A larger number of individuals within each population and an even greater number of populations would allow for a stronger survey of variance in patterns of social attention between populations. Additionally, although the participants in this study varied widely in age (2.5 – 46 years), there were only a few individuals within the younger age classes. Future studies that more evenly sample across ages would permit investigation into developmental patterns. Finally, we used both raw difference scores and DLS as dependent measures in Models 1 and 3, given the different strengths of each metric. Only DLS revealed predictors of variation in Model 1, and this finding suggests that DLS, which amplifies biases even on trials with brief attention times, may better capture meaningful variation. Indeed, this measure further demonstrated significant biases in social attention in Model 2 (although we did not attempt to run this model with raw difference scores).

A final question raised by our work is what consequences may arise from attention biases that favor dominant individuals or members of the dominant sex. Consistent with the patterns documented in our study, an independent line of research has shown that chimpanzees contagiously yawn more in response to yawning males than females, and bonobos exhibit greater yawn contagion in response to females than males[77,78]. Such results suggest that attention likely shapes the behavior of observers in meaningful ways. More functionally, third-party interactions among dominant individuals (e.g., conflicts and rank reversals) can have profound impacts on group dynamics and therefore convey particularly important social information[63,79,80]. Bonobos have been shown to make social decisions based on such observations, preferentially associating with novel partners who behave dominantly in third-party contexts[12]. Finally, dominant individuals may have preferential access to ecological or social knowledge and may therefore be particularly valuable targets for social learning[81]. Accordingly, wild vervet monkeys display a rank transmission bias in which they favor learning from high-ranking individuals in a foraging context[82]. Similarly, chimpanzees preferentially copy high-ranking individuals when presented with novel foraging tasks, also demonstrating a dominance transmission bias[83,84]. Research with humans suggests that children develop culturally-influenced expectations about how high-ranking individuals may behave, and begin to make a distinction between prestigious and dominant individuals around age five[85]. The early development of knowledge and expectations of dominant group members in humans further suggests that we may share these cognitive abilities with our closest living phylogenetic relatives. Overall, our findings demonstrate that patterns of social attention across *Pan* are consistently shaped by species differences in the dominance of the sexes. These socioecological factors may well have contributed to the evolution and development of social and cultural cognition across apes, including humans, and to patterns of social behavior across a much wider array of taxa.

H) Ethics

These non-invasive experimental protocols adhered to the School of Psychology and Neuroscience Animal Ethics Committee at the University of St. Andrews. Animal husbandry and research protocol complied with international standards (the Weatherall report "The use of non-human primates in research") and institutional guidelines (see Supplementary Materials for more information).

I) Data accessibility

Data and R code available in the electronic supplementary material data file.

J) Competing Interests

We declare no competing interests.

K) References

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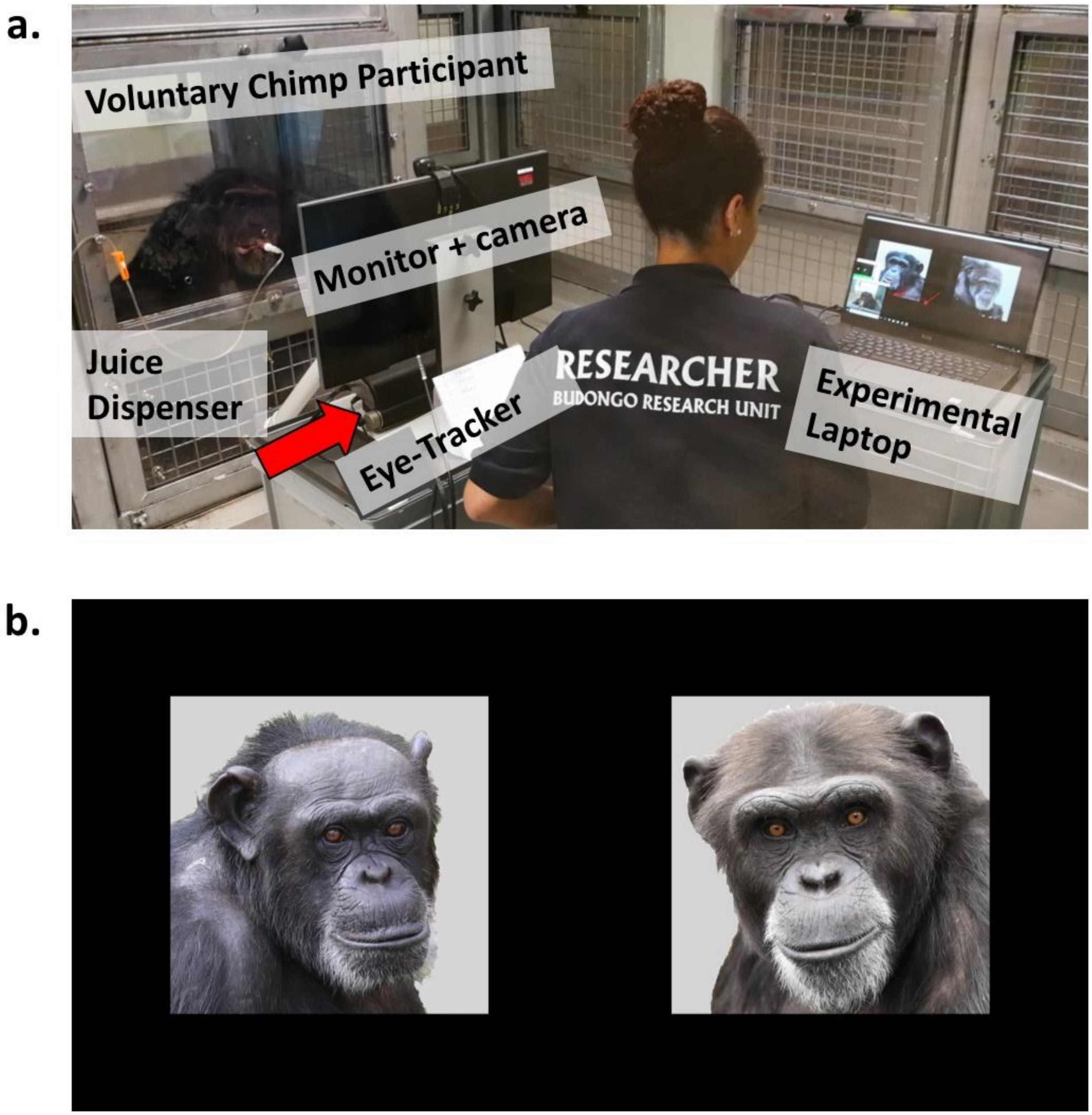

Fig. 1: Experimental set-up at Edinburgh Zoo (a) and example of a single trial for the Kumamoto Sanctuary chimpanzees (b). Here, unfamiliar individual is presented on the left, while familiar individual is presented on the right.

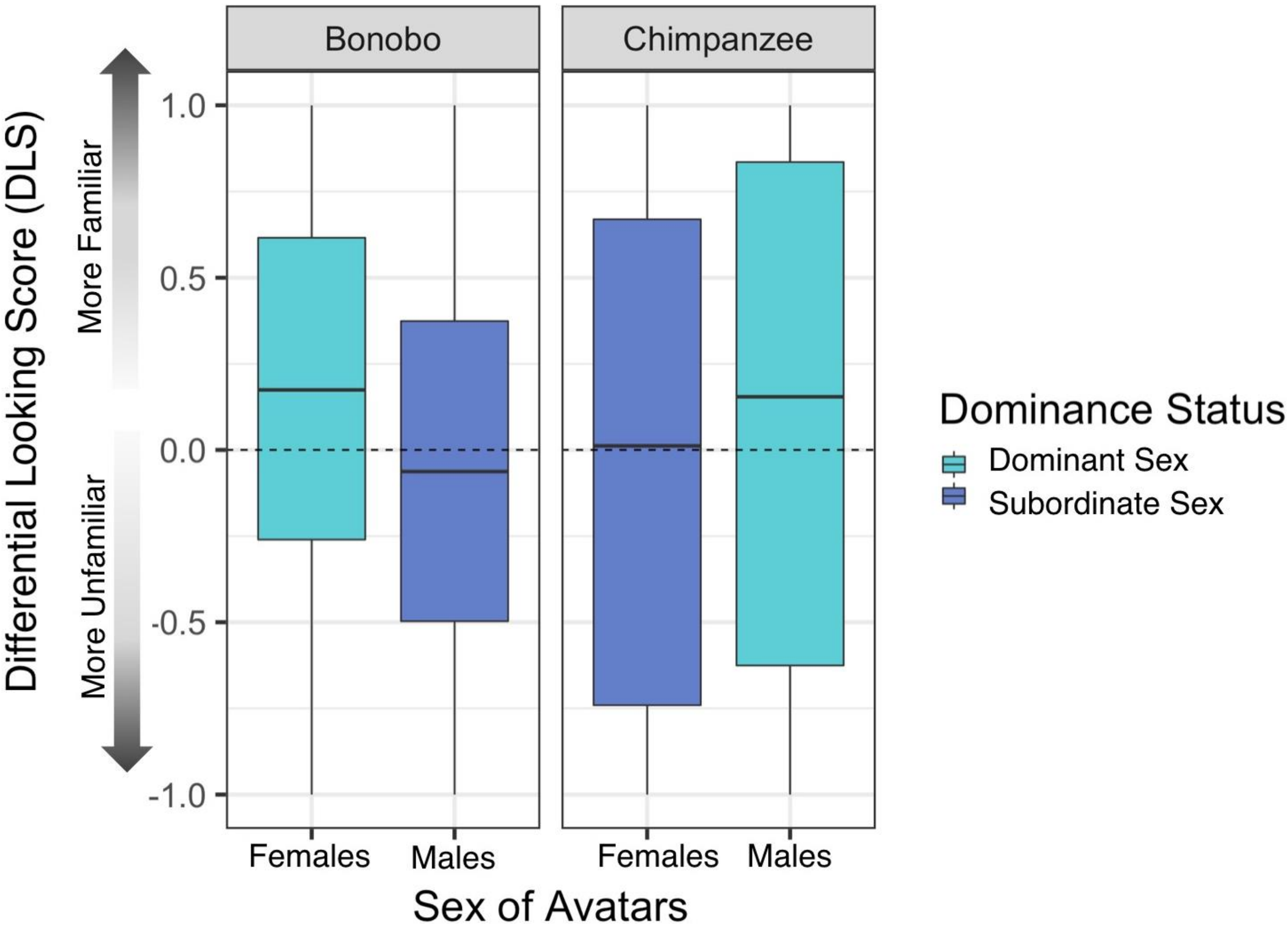

Fig. 2: Species' biases in attention toward familiar versus unfamiliar conspecific faces. Positive and negative values indicate biases toward familiar and unfamiliar individuals, respectively. Both species demonstrate stronger biases in attention while viewing images of the dominant sex (males for chimpanzees, females for bonobos) as compared to when viewing images of the subordinate sex. Boxes denote the interquartile range (IQR, from 25th percentile to 75th percentile), middle lines denote medians, and whiskers denote 95% confidence intervals.

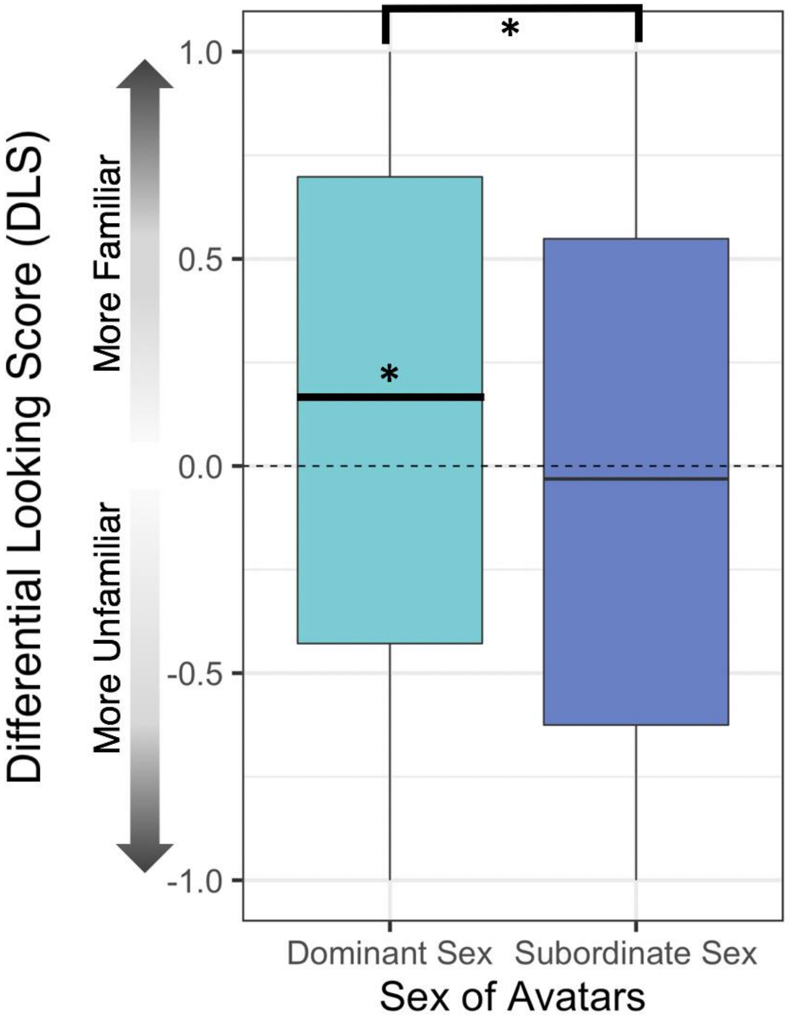

Fig. 3: *Pan* biases in attention toward familiar versus unfamiliar conspecific faces, when viewing members of the dominant versus subordinate sex. Positive and negative values indicate biases toward familiar and unfamiliar individuals, respectively. The dominant sex refers to female bonobos and male chimpanzees, whereas the subordinate sex refers to male bonobos and female chimpanzees. Boxes denote the interquartile range (IQR, from 25th percentile to 75th percentile), middle lines denote medians, and whiskers denote 95% confidence intervals. Asterisks denote $p < 0.05$.

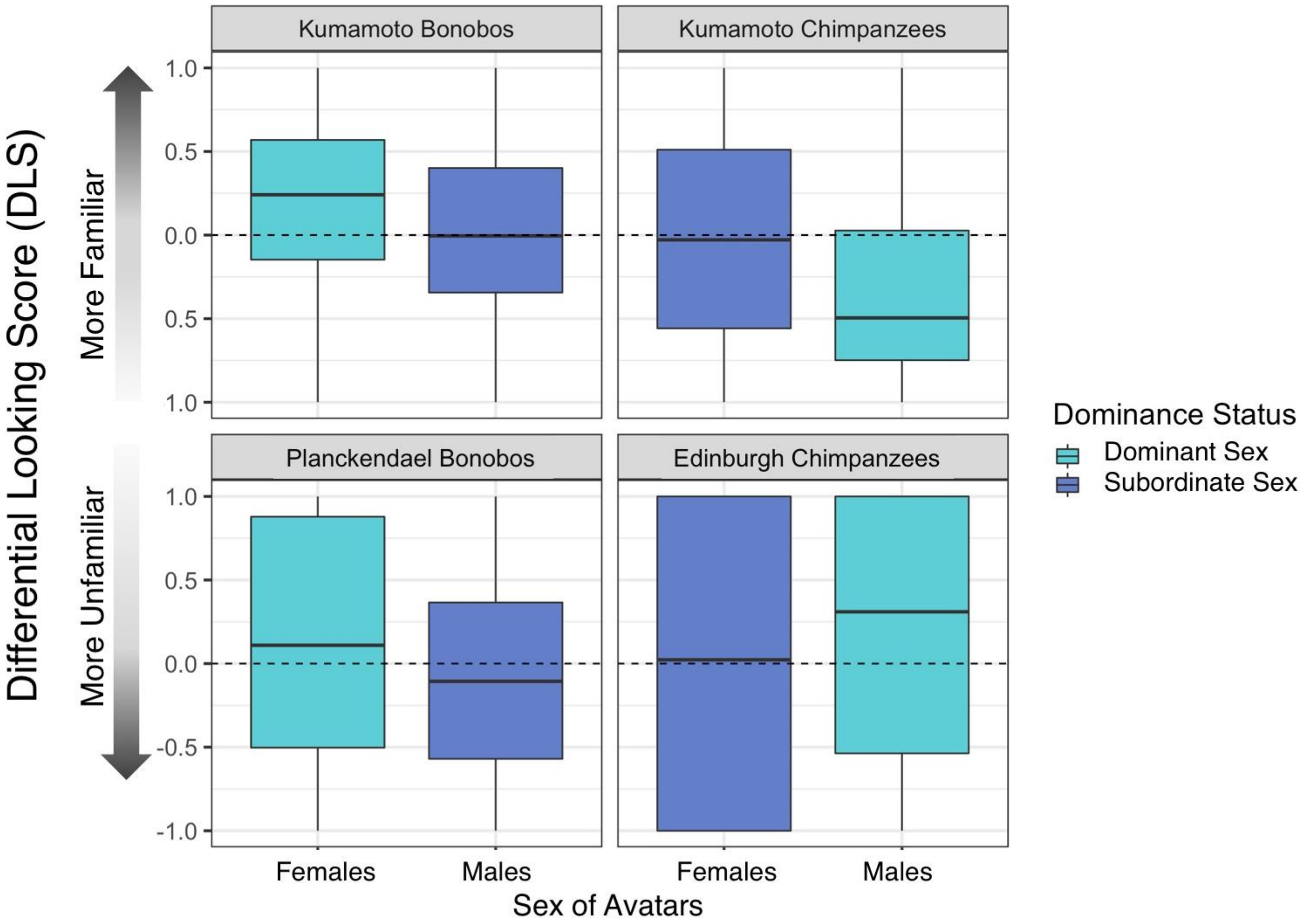

Fig. 4: Ape population biases in attention toward familiar versus unfamiliar conspecific faces. Positive and negative values indicate biases toward familiar and unfamiliar individuals, respectively. Chimpanzees demonstrate stronger biases in attention while viewing images of males, while bonobos demonstrate stronger biases when viewing images of females. Boxes denote the interquartile range (IQR, from 25th percentile to 75th percentile), middle lines denote medians, and whiskers denote 95% confidence intervals.