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

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4 Laura S. Lewis^{a, b, *}, Fumihiro Kano^{c, d}, Jeroen M. G. Stevens^{e, f}, Jamie G. DuBois^{b, g}, Josep
5 Call^b, Christopher Krupenye^{b, h}

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7 ^a *Department of Human Evolutionary Biology, Harvard University, Cambridge, MA, U.S.A.*8 ^b *School of Psychology & Neuroscience, University of St Andrews, St Andrews, U.K.*9 ^c *Kumamoto Sanctuary, Wildlife Research Center, Kyoto University, Kumamoto, Japan*10 ^d *Center for the Advanced Study of Collective Behavior, University of Konstanz, Konstanz,*
11 *Germany*12 ^d *Behavioural Ecology and Ecophysiology, Department of Biology, University of Antwerp,*
13 *Belgium*14 ^e *Centre for Research and Conservation, Royal Zoological Society of Antwerp, Antwerp, Belgium*15 ^f *Department of Psychology, University of Cambridge, Cambridge, U.K.*16 ^g *Department of Psychological & Brain Sciences, Johns Hopkins University, Baltimore,*
17 *MD, U.S.A.*

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26 * Corresponding author.

27 *E-mail address:* Laura.lewis889@gmail.com (L. S. Lewis).

28

29 **Abstract:**

30

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

49

50 **Keywords:**51 **social attention, great apes, eye-tracking, preferential looking, familiarity, dominance**

52

53 **Introduction**

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

65 Living in large communities with intricate and differentiated social relationships demands
66 tradeoffs, or biases, in *social attention*, defined as directed visual attention toward
67 conspecifics[14–16]. In a dynamic social landscape, organisms must prioritize how they allocate
68 social attention to ensure that they keep track of the most important individuals and social events,
69 and identify potentially ephemeral opportunities to mate or to learn socially[17]. A growing
70 literature has demonstrated that such biases in social attention exist across many taxa, such as early
71 infant preferences for female faces, and presumed indicators of fitness in rhesus macaques and

72 other primate species[18–21]. However, a key question remains: how are biases in social attention
73 shaped by the demands of a species' socioecology?

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

86 The social lives of chimpanzees and bonobos, like those of many species, are most
87 fundamentally shaped by at least four principal forces: intergroup interactions, social dominance
88 hierarchies, dispersal patterns, and mating competition (in addition to predation and feeding
89 ecology, which we did not address in the present study as these are less relevant to patterns of
90 conspecific social attention). Chimpanzees are notoriously xenophobic and engage in hostile,
91 sometimes lethal, intergroup encounters—in stark contrast to bonobos, who often interact
92 prosocially with members of other groups[31–34]. With regard to social dominance, chimpanzees
93 exhibit linear hierarchies in which adult males almost universally outrank adult females[35,36].
94 Bonobos, conversely, have been variously characterized as female dominant or female-male

95 codominant, with females forming coalitions to curtail male aggression and maintain predominant
96 control of group decisions[37–41]. Bonobos do not display reverse sexual dimorphism nor are
97 female bonobos masculinized as they are in other typical female dominant species, like hyenas and
98 some lemurs[42,43]. However, male bonobos seldom form coalitions and have weaker affiliative
99 relationships with one another, whereas female bonobos engage in many affiliative interactions
100 (like genito-genital rubbing and grooming), maintain feeding priority within the group, and often
101 occupy the highest positions within the dominance hierarchy[44–46]. Thus, intersexual dominance
102 in bonobos is complex and nuanced: while adult females are not uniformly dominant to adult males
103 (as adults males are to adult females in chimpanzees) and there is instead a mixed-sex hierarchy,
104 the several highest-ranking members of the group tend to be females. Despite this nuance, we can
105 safely characterize these species as differing in the sense that males are dominant in chimpanzees
106 but not in bonobos and the highest-ranking individuals tend to be male chimpanzees and female
107 bonobos. In contrast to their divergent systems of intergroup aggression and social dominance,
108 bonobos and chimpanzees exhibit similar dispersal patterns: most pubertal females immigrate to
109 new communities before reproducing, whereas males remain in their natal community for their
110 entire lives[47,48]. Both species are also highly promiscuous, with each sex exhibiting various
111 forms of intrasexual competition (e.g., [49–51]). These similarities and key differences in
112 socioecology may drive adaptive variation of social attention in these species.

113 The present study capitalized on this unique constellation of both shared and, critically,
114 differing socioecological traits in order to investigate the socioecological pressures that have
115 shaped social attention across bonobos and chimpanzees. While being non-invasively eye-tracked,
116 captive apes viewed static images of faces of a familiar groupmate alongside a second unfamiliar
117 conspecific of the same sex, following a standard two-image preferential looking design. We

118 decided to contrast a familiar and unfamiliar conspecific within each trial (as opposed to a different
119 factor relevant to our hypotheses) because familiarity is central to all of our hypotheses and, if apes
120 showed a familiarity bias, this contrast would allow us to detect recognition of known conspecifics.
121 We then tested four hypotheses, stemming from the variables outlined above, to determine which
122 features of bonobo and chimpanzee socioecology likely account for their observed biases of social
123 attention (see **Fig. S1** for more details). These hypotheses were developed based on the existing
124 literature on *Pan* socioecology, and formed the basis for our study design. We grounded these
125 hypotheses firmly in prior research that has identified the importance of intergroup interactions,
126 dominance hierarchies, dispersal patterns, and both intersexual attraction and intrasexual
127 competition in the social lives of these species. We developed and named these hypotheses for
128 ease of referencing and for potential future use.

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

136 The **Dominance Differentiation hypothesis** argues instead that social dominance has the
137 greatest impact on social attention. This hypothesis predicts that both species will show greater
138 differentiation in social attention between members of the more dominant sex (i.e., chimpanzees
139 will discriminate more between familiar and unfamiliar males, whereas bonobos will discriminate
140 more between females). Previous work has identified some support for the influence of dominance

141 on social attention in primates. Macaque infants who were not mother-reared are still able to
142 discriminate the faces of adult macaques, which represent a primary and dominating threat to infant
143 macaques[52]. Male infant macaques of high-ranking mothers also look more at faces as compared
144 to sons of low-ranking mothers[18]. Finally, previous work indicates that in some primate species,
145 lower ranking individuals devote more social attention to higher ranking individuals than vice
146 versa[53–55] (but see [56]).

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

161 Finally, the **Mating Competition Differentiation hypothesis** suggests that mating
162 competition differently impacts social attention in males compared to females. This hypothesis
163 thus generates two sets of predictions: 1) Intersexual attraction predicts greater differentiation

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

179

180 **Methods**

181

182 **A) Participants**

183 Twenty-nine apes participated in this study: 11 chimpanzees (4 females, 7 males) living at the
184 Edinburgh Zoo in Scotland; 6 chimpanzees (5 females, 1 male) and 6 bonobos (4 females, 2 males)
185 living at the Kumamoto Sanctuary in Japan; and 6 bonobos (3 females, 3 males) living at the
186 Planckendael Zoo in Belgium. Subjects ranged in age from 2 to 46 years (bonobo mean = 21.9

187 years, SD = 13.8; chimpanzee mean = 27.5 years, SD = 10.2; see supplementary materials for
188 ethical notes and **Tables S1 - S2** for details).

189

190

191 **B) Apparatus**

192 Experiments utilized established eye-tracking procedures and comparable set-ups across
193 facilities[62–64]. Apes viewed images through a transparent polycarbonate or acrylic panel on a
194 23” LCD monitor just outside of their enclosures at a distance of approximately 60cm. We non-
195 invasively recorded their eye movements via an infrared eye-tracker (X120 in Edinburgh and
196 Planckendael, X300 in Kumamoto, Tobii Technology AB, Stockholm, Sweden), positioned below
197 the monitor, which mapped their gaze onto the stimuli. Stimulus presentation and data collection
198 were controlled using Tobii Studio. To encourage minimal head movements and optimize corneal
199 reflection measurements, apes had access to a small amount of diluted fruit juice (provided
200 irrespective of viewing patterns) that was delivered through a plastic nozzle positioned on the
201 transparent panel, directly in front of the eye-tracker (see **Fig. 1a**).

202 Before testing, we conducted a two-point automated calibration for each ape participant by
203 presenting a small video clip (and often a piece of real fruit) on each reference point. We adopted
204 this small number of reference points for apes because they tend to view these reference points
205 only briefly as compared to human subjects. This two-point calibration procedure is regularly used
206 in eye-tracking studies with great apes because it is sufficient to provide high quality data and
207 minimize the loss of subjects who would not reliably attend to a greater number of calibration
208 points[64–66]. After each calibration was obtained, we manually checked the accuracy of the
209 calibration using 9 points on the screen and repeated the calibration process if necessary. The same

210 calibration file was used for each individual throughout testing, and before the start of every
211 session the accuracy was checked with at least one of the 9 points. Using this procedure,
212 calibration errors are typically less than a degree, and any error of this size should not impact the
213 ability to determine preferential looking to images[62].

214

215 C) Stimuli

216 Our stimuli consisted of static images of adult conspecific faces exhibiting neutral expressions
217 (hereafter referred to as “avatars”). These were 600 x 600 pixel close-up color photographs of
218 forward-facing conspecifics surrounded by a gray background (see **Fig. 1b**). Each trial featured
219 two images, one of a familiar groupmate and another of an unfamiliar conspecific, on the center
220 left and center right regions of a black 1920 x 1080 pixel screen (locations counterbalanced across
221 trials). Conspecifics deemed ‘unfamiliar’ have never been housed at the same institution as the
222 subject, according to institutional and studbook data. Images were sex-matched within trials, and
223 the brightness, blurriness, and contrast of photographs were kept as consistent as possible across
224 stimuli. For each participant population, the stimulus set included three images of familiar
225 conspecifics and three images of unfamiliar conspecifics, with one set for female images and one
226 set for male images. Each familiar image was paired with each unfamiliar image, and this pair was
227 shown twice: once with the familiar image on the left, and once with the familiar image on the
228 right. In total, subjects therefore experienced 18 trials involving male stimuli and 18 trials
229 involving female stimuli. Within each group, the majority of individuals received identical stimuli.
230 If, however, a participant was included in the standard stimulus set for their group, for their
231 stimulus set, their own image was replaced with that of a different member of their group. As a
232 control, the unfamiliar conspecific images used for the Kumamoto chimpanzees and bonobos were

233 those used as familiar images for the Edinburgh chimpanzees and Planckendael bonobos,
234 respectively. The apes at Kumamoto Sanctuary live in social groups that have only one
235 (chimpanzees) or two (bonobos) resident males. Therefore, we could only present one or two
236 images of familiar males to these populations (respectively), and then filled the remaining
237 “familiar” trials with images of unfamiliar males in order to maintain even counterbalancing of
238 image presentation and equal degrees of novelty across stimuli (i.e., these fewer familiar
239 conspecific images did not appear more frequently than the unfamiliar conspecific images they
240 were paired with). These populations, therefore, saw some “fake” trials that contained two images
241 of unfamiliar males, which were excluded from the final analyses.

242

243 **D) Procedure**

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

249 The 36 test trials were administered in clusters of three (twelve clusters total). Each trial
250 lasted three seconds and was preceded by a 0.5 second presentation of a black screen with a fixation
251 cross in the center (in an effort to attract apes to the center of the screen before the trial began).
252 Within a cluster, trials progressed one immediately following the other for a total duration of 10.5
253 seconds per cluster. Each cluster featured only same-sex images (male or female trials), and within
254 a cluster all 6 images of that sex were shown once (three familiar individuals paired with three
255 unfamiliar individuals). The side on which the familiar individual was presented alternated in a

256 cluster (either one or two times) and was counterbalanced across clusters: for each sex, familiar
257 individuals were presented 9 times on the left side, and 9 times on the right side across clusters.
258 Clusters alternated between male trials and female trials, and the order of cluster presentation was
259 counterbalanced between subjects such that half of the participants started with female clusters (n
260 = 14), and half started with male clusters ($n = 15$). There were four variations of cluster order (2
261 beginning with male clusters, and 2 beginning with female clusters), and these were
262 counterbalanced across participants. Because participation was voluntary (i.e., apes could walk
263 away at any time), the number of clusters administered within a day varied between one to twelve,
264 depending on duration of apes' attendance and attention at the testing set-up. After administering
265 all trials via the pre-determined order, we checked that subjects had at least one fixation to either
266 the familiar or unfamiliar image (see AOI procedure below). After the completion of the original
267 trial order, trials that yielded zero fixations to either image were repeated until we had data for a
268 full set of 36 trials per subject. In total, we tested 1040 trials; all but 1 of 29 subjects completed
269 their entire set of 36 trials (4 missing trials due to persistent lack of interest). We excluded 132
270 "fake" trials. All 908 available trials were included in our analyses. On average, apes fixated to
271 one or both of the AOIs for 1.22 seconds ($SD = 0.84$) of each 3s trial.

272

273 **E) Data Scoring and Analysis**

274 In Tobii Studio, we defined 700 x 700 pixel areas of interest (AOI) around the two images in
275 each trial (i.e., including a 50 pixel buffer on each side of the images). We used the statistical
276 software R (version 3.2.3; R Core Team 2020) to sum total fixation duration within each AOI (i.e.,
277 Familiar and Unfamiliar) for the entire 3s trial duration. Fixations were calculated using Tobii
278 Studio's I-VT Filter (additional information provided in Supplemental Materials). To measure

279 apes' biases in looking toward the familiar versus unfamiliar conspecific, we then calculated raw
280 difference scores (i.e., looking to Familiar minus looking to Unfamiliar) as well as a proportional
281 Differential Looking Score (DLS; i.e., [Familiar minus Unfamiliar] divided by [Familiar plus
282 Unfamiliar]) as dependent variables for each trial. We conducted two planned, confirmatory
283 analyses and one exploratory analysis. First, we planned to analyze the predictors of biases in
284 social attention (**Model 1**). Second, we planned to analyze whether apes showed above-chance
285 discrimination of familiar and unfamiliar conspecific faces, taking into account any relevant
286 predictors identified in Model 1 (**Model 2**). Finally, we pursued an exploratory analysis which
287 examined predictors of biases across populations (**Model 3**).

288

289 *General Modeling Approach:*

290

291 To investigate which of our hypotheses accounted for variation in apes' biases in social
292 attention, we fitted linear mixed effects models in R for both dependent variables. The raw
293 difference score was modelled using the *lmer* function from the 'lme4' package. The DLS was
294 modelled using the *glmmTMB* function with a beta distribution from the 'glmm' package, as this
295 distribution best models proportional scores (Bates et al. 2014; McCulloch and Neuhaus, 2005).
296 We used a significance threshold of 0.05 when reporting p-values, and report p-values between
297 0.05 and 0.1 as "trends" for all models. We have chosen to designate trends in this study because
298 *P*-values are continuous variables that convey meaningful variation; a significance test that is
299 based simply on a binary 'accept/reject' decision cannot accurately depict whether an effect or
300 correlation is biologically meaningful[69]. The DLS was standardized from its original [-1,1]
301 interval to a (0,1) interval so that it could be correctly modeled by the beta distribution model,
302 which specifically models proportional scores and requires a continuous distribution that is

303 bounded on this interval. We modeled both measures because raw difference scores give a direct
304 measure of the difference in looking time to the familiar individual versus the unfamiliar individual
305 that captures variation in overall looking duration but can be weakened by differences in raw
306 looking times between individuals or sexes (see [16]). Therefore, to control for these potential
307 differences in raw looking time, we also used the DLS, noting that this proportional score, in
308 contrast, amplifies strongly biased looks even on trials when overall looking duration is low.

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

321

322 *Model 1: Predictors of biases in social attention*

323 To investigate the influence of the four socioecological drivers on biases in ape social attention,
324 we generated two full models that differed only in the dependent measure (raw difference scores
325 vs DLS). These models included species as a categorical fixed effect to test the prediction of the

326 **Intergroup Conflict Differentiation** hypothesis that looking biases will be greater in
327 chimpanzees than bonobos. The second fixed effect included was sex of the individuals in the
328 images (avatars) to test the prediction of the **Dispersal Differentiation** hypothesis that, across
329 species, looking biases will be greater when looking at images of females than those of males. We
330 also included the interaction between avatar sex and species to test the **Dominance Differentiation**
331 hypothesis, which predicts that chimpanzees demonstrate heightened discrimination between
332 familiar and unfamiliar males, while bonobos demonstrate heightened discrimination between
333 females. Finally, the interaction between avatar sex and sex of the participant was included as a
334 fixed effect to test the **Mating Competition Differentiation** hypothesis, which suggests that
335 biases in social attention are shaped by intrasexual competition or intersexual attraction. We
336 included trial number as a continuous fixed effect to account for a potential habitual effect with an
337 increasing number of trials. We included subject ID (to account for repeated measures from each
338 individual), ID of familiar avatar, and ID of unfamiliar avatar (to account for potential random
339 variability in preferences for specific individuals) as random intercepts.

340

341 *Model 2: Discrimination of familiar and unfamiliar conspecific faces*

342 After determining which factors shape variation in apes' social attention, we then
343 investigated whether apes show a significant bias in attention toward familiar or unfamiliar avatars.
344 To do so, we performed a post-hoc linear mixed effects **Model 2** using the *lmer* function in 'lme4'.
345 In this model we only used DLS as our dependent measure, as results from **Model 1** suggested
346 DLS to be most consistent. Here we used DLS with its original [-1,1] interval, so that it was
347 possible to determine if these scores were significantly different from zero (a score of zero signifies
348 no bias toward familiar or unfamiliar images). **Model 2** included the same random effects that

349 were included in the main analyses (subject, ID of familiar avatar, and ID of unfamiliar avatar).
350 By including a single fixed effect (identified as a driver of variation in **Model 1**), we were able to
351 determine whether data from each level of this factor differs from zero (indicated by a significant
352 model intercept, see details below). Here, an intercept that is significantly different from zero
353 denotes a significant bias in attention toward familiar (positive intercept values) or unfamiliar
354 avatars (negative intercept values).

355

356 *Model 3: Patterns of biases across conspecific populations*

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

369

370 **F) Results:**

371 *Model 1: Predictors of biases in social attention*

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

381

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

383 **Model 1** revealed that bonobos and chimpanzees likely differ in their social attention to
384 each sex, providing support for the Dominance Differentiation Hypothesis. This may reflect
385 species differences in the dominance of each sex; namely, chimpanzee males and bonobo females
386 are generally more dominant than individuals of the other sex. In chimpanzees, males occupy the
387 highest positions in the dominance hierarchy, have close social bonds, and almost universally
388 outrank females. In bonobos, the dominance hierarchy is more nuanced and difficult to
389 characterize; however, females often outrank males, form close social bonds and coalitions, and
390 maintain feeding priority within their groups. Therefore, here, we operationally defined male
391 chimpanzees and female bonobos as the dominant sex. To clarify this point, in post-hoc **Model 2**
392 we recoded avatar sex as ‘the dominant sex for each species’ and ‘the subordinate sex for each
393 species.’ Trials depicting male chimpanzees or female bonobos were coded as *dominant*, whereas
394 those depicting female chimpanzees or male bonobos were coded as *subordinate*. **Model 2**

395 included the same random effects as **Model 1** and just the one fixed effect – sex-based dominance
396 status of avatar – to investigate whether apes showed a significant bias in attention toward the
397 familiar or unfamiliar avatar when viewing members of the dominant or subordinate sex. **Model**
398 **2** allowed us to directly test the effect of dominance on biases in social attention, and the intercept
399 measured whether apes overall showed a significant bias in attention toward familiar or unfamiliar
400 individuals. By releveling the reference category of the dominance status term, we were able to
401 determine whether apes’ attention was significantly biased toward familiar or unfamiliar
402 individuals when those individuals were members of the dominant or subordinate sex.

403 First, however, we confirmed that the effect of dominance did not differ across species by
404 running **Model 2a**, which included an interaction between ‘sex-based dominance status of avatar’
405 and species. The full-null model comparison was not significant for **Model 2a**, and therefore the
406 results of the full models should again be interpreted cautiously (likelihood ratio test: $\chi^2 = 5.264$,
407 $p = 0.153$) However, this model did identify a significant effect of ‘dominance status of avatar sex’
408 ($\chi^2 = 5.347$, $p = 0.021$; see **Table S5**) but, critically, no significant interaction between dominance
409 status and species ($\chi^2 = 1.368$, $p = 0.242$). Thus, the effect of dominance status does not differ
410 across species. We therefore proceeded to **Model 2b**, which only included a main effect of
411 dominance status.

412 **Model 2b** trended towards being significantly better than the null model ($\chi^2 = 3.783$, $p =$
413 0.052) and again revealed a significant effect of ‘dominance status of avatar sex’ ($\chi^2 = 5.465$, $p =$
414 0.019 ; see **Table S6**). Most interestingly, we found that, when viewing the dominant sex, apes’
415 attention was significantly biased toward familiar individuals over unfamiliar individuals (estimate
416 $= 0.102$, $\chi^2 = 5.478$, $p = 0.019$; see **Fig. 3**). In contrast, we found no significant biases in attention

417 when apes viewed members of the subordinate sex (estimate = -0.026, $\chi^2 = 0.372$, $p = 0.542$, see
418 **Tables S5-6**).

419

420

421 *Exploratory Model 3: Patterns of biases across conspecific populations*

422 Exploratory **Model 3** was developed to probe potential population differences in biases of
423 social attention. The full-null model comparison was significant for the difference score **Model 3**
424 (likelihood ratio test: $\chi^2 = 20.642$, $p = 0.024$) but not the DLS **Model 3** (likelihood ratio test: χ^2
425 = 10.459, $p = 0.401$). For both the difference score and DLS **Model 3**, the three-way interaction
426 between species, dummy-coded population, and avatar sex trended towards being significant
427 (**Difference score:** $\chi^2 = 3.472$, $p = 0.062$; **DLS:** $\chi^2 = 3.153$, $p = 0.076$, see **Tables S7 – S8**), and
428 therefore we did not reduce this interaction further. Instead, we subset the data by species and re-
429 ran **Model 3** on the chimpanzee and bonobo datasets separately. These models included the
430 interaction between avatar sex and dummy-coded population and the interaction between subject
431 sex and avatar sex, along with the control term, trial number, and the same random effects.

432 For the **Chimpanzee Model 3**, the full-null model comparison was not significant for the
433 raw difference score nor DLS (**Difference Score:** $\chi^2 = 8.315$, $p = 0.139$; **DLS** $\chi^2 = 6.862$, $p =$
434 0.334). For the raw difference score **Chimp Model 3** the two-way interaction between population
435 and avatar sex was significant, and it trended towards significant in the DLS **Chimp Model 3**
436 (**Difference Score:** $\chi^2 = 5.323$, $p = 0.021$; **DLS:** $\chi^2 = 3.697$, $p = 0.055$). Edinburgh chimpanzees
437 exhibited a relatively stronger bias toward familiar individuals when viewing males relative to
438 females, whereas Kumamoto chimpanzees exhibited a relatively stronger bias toward unfamiliar
439 individuals when viewing males relative to females (see **Fig. 4**). The two-way interaction between

440 subject sex and avatar sex was not significant in either model (**Difference Score:** $\chi^2 = 1.172$, $p =$
441 0.279 ; **DLS:** $\chi^2 = 2.226$, $p = 0.136$, see **Tables S9 – S10**).

442 For the **Bonobo Model 3**, the full-null model comparison was not significant for the raw
443 difference score nor DLS (**Difference Score:** $\chi^2 = 4.459$, $p = 0.485$; **DLS:** $\chi^2 = 4.604$, $p = 0.466$).
444 For both the raw difference score and DLS, the two-way interaction between population and avatar
445 sex was not significant (**Difference Score:** $\chi^2 = 0.0991$, $p = 0.753$; **DLS:** $\chi^2 = 0.880$, $p = 0.348$),
446 nor was the two-way interaction between subject sex and avatar sex (**Difference Score:** $\chi^2 =$
447 0.271 , $p = 0.603$; **DLS:** $\chi^2 = 1.440$, $p = 0.230$). However, the effect of avatar sex was significant
448 for the DLS **Bonobo Model 3** ($\chi^2 = 4.353$, $p = 0.037$), although not for the difference score
449 **Bonobo Model 3** ($\chi^2 = 1.491$, $p = 0.222$, see **Tables S11 – S12**). Bonobos exhibited a stronger
450 bias toward familiar individuals when viewing females as compared to males (see **Fig. 4**).

451

452 **G) Discussion**

453 In this study, we set out to characterize biases in social attention among chimpanzees and
454 bonobos, and to identify the socioecological factors that shape them. Our findings indicate that
455 both species successfully discriminate familiar from unfamiliar conspecifics based on images of
456 faces alone (Model 2b) and several lines of evidence suggest that their biases in attention are best
457 explained by the **Dominance Differentiation hypothesis**. First, the only significant predictor of
458 DLS in Model 1 was the interaction between species and avatar sex. This interaction reflected
459 chimpanzees' relatively greater attention toward familiar individuals when viewing males than
460 when viewing females, and bonobos' relatively greater attention toward familiar individuals when
461 viewing females than when viewing males. Second, Models 2a and 2b directly demonstrated that
462 sex-based dominance status of the avatars shaped DLS, and that this effect did not differ across

463 species: both chimpanzees and bonobos showed more biased attention toward familiar individuals
464 over unfamiliar ones when viewing members of the more dominant sex than when viewing
465 members of the more subordinate sex. Indeed, this bias toward familiar conspecifics was
466 significantly different from chance only for trials depicting members of the more dominant sex
467 (Model 2b). These results are among the first experimental evidence that biases in great ape social
468 attention are driven by the demands of their socioecology.

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

484 While in chimpanzees males almost universally outrank females, in bonobos there is more
485 nuance in the relationship between sex and dominance. Given that bonobos have mixed-sex

486 hierarchies where females typically occupy the highest and sometimes also the lowest ranks,
487 future work should attempt to disentangle the influence of sex and rank on social attention and
488 broader social behavior. One important question is whether the differences we observed in the
489 present study owe specifically to differences in agonistic dominance between the sexes or other
490 related traits like centrality in coalitionary networks or in networks of group decision-making.

491 Another crucial question is whether the patterns documented in this study stem from selection
492 on mechanisms of attention or from species differences in socialization (in which male
493 chimpanzees and female bonobos play dominant roles in their societies). Based on the results from
494 Model 3, we suspect that both drivers play a role. Model 3 identified an interaction between
495 population and avatar sex for chimpanzees, but not for bonobos, suggesting that the chimpanzee
496 populations differed in their patterns of social attention based on avatar sex (**Figure 4**). Edinburgh
497 Zoo is home to a typical multi-male multi-female group, while the chimpanzee group at Kumamoto
498 Sanctuary has a single male. Although both populations showed stronger biases when viewing
499 male stimuli as compared to female stimuli, these biases favored familiar individuals only for
500 Edinburgh chimpanzees. With only one resident male (and therefore no dominance displays or
501 agonistic conflicts among males), females of the Kumamoto group may reasonably show more
502 interest in outgroup males. Thus, socialization may contribute to biases in social attention, perhaps
503 in concert with selective pressures on mechanisms of attention. Previous work has also identified
504 connections between social experience and social attention patterns in primates. Parr and
505 colleagues (2016) found that, from birth, infant rhesus macaques prefer to look at conspecific faces
506 as compared to heterospecific faces, but that this effect reverses as they age. The authors propose
507 that this may be the result of a rapid experience-dependent preference, as after a few weeks of
508 exposure to many conspecific faces in their natal groups, the infants began to prefer attending to

509 heterospecific faces[75]. In addition, recent work demonstrates that there is a positive relationship
510 between time spent viewing the eyes of faces and number of initiations made for social interactions
511 with peers in infant male rhesus macaques[76]. The combination of these results suggests a link
512 between social attention and social experience in infancy in rhesus macaques. Future work should
513 attempt to expand upon these recent investigations to clarify the relationships between social
514 experience and social attention across species and social environments.

515 We note several important limitations of our study. First, although our findings were
516 consistent across a number of analyses, we must remain cautious in our interpretation of the results
517 given that some full models did not differ significantly from null models. We find reassuring,
518 however, that Model 2b directly replicated the findings of these models with a full-null model
519 comparison on the verge of significance ($p = 0.052$). Second, although the sample size for this
520 study is on the larger end within great ape research ($n = 29$) and, unusually, involves multiple
521 populations of each species, our results may be limited by the low numbers of individuals within
522 each population. A larger number of individuals within each population and an even greater
523 number of populations would allow for a stronger survey of variance in patterns of social attention
524 between populations. Additionally, although the participants in this study varied widely in age (2.5
525 – 46 years), there were only a few individuals within the younger age classes. Future studies that
526 more evenly sample across ages would permit investigation into developmental patterns. Finally,
527 we used both raw difference scores and DLS as dependent measures in Models 1 and 3, given the
528 different strengths of each metric. Only DLS revealed predictors of variation in Model 1, and this
529 finding suggests that DLS, which amplifies biases even on trials with brief attention times, may
530 better capture meaningful variation. Indeed, this measure further demonstrated significant biases

531 in social attention in Model 2 (although we did not attempt to run this model with raw difference
532 scores).

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

554 shaped by species differences in the dominance of the sexes. These socioecological factors may
555 well have contributed to the evolution and development of social and cultural cognition across
556 apes, including humans, and to patterns of social behavior across a much wider array of taxa.

557

558 **H) Ethics**

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

564 **I) Data accessibility**

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

566

567 **J) Competing Interests**

568 We declare no competing interests.

569

570

571 **K) References**

572

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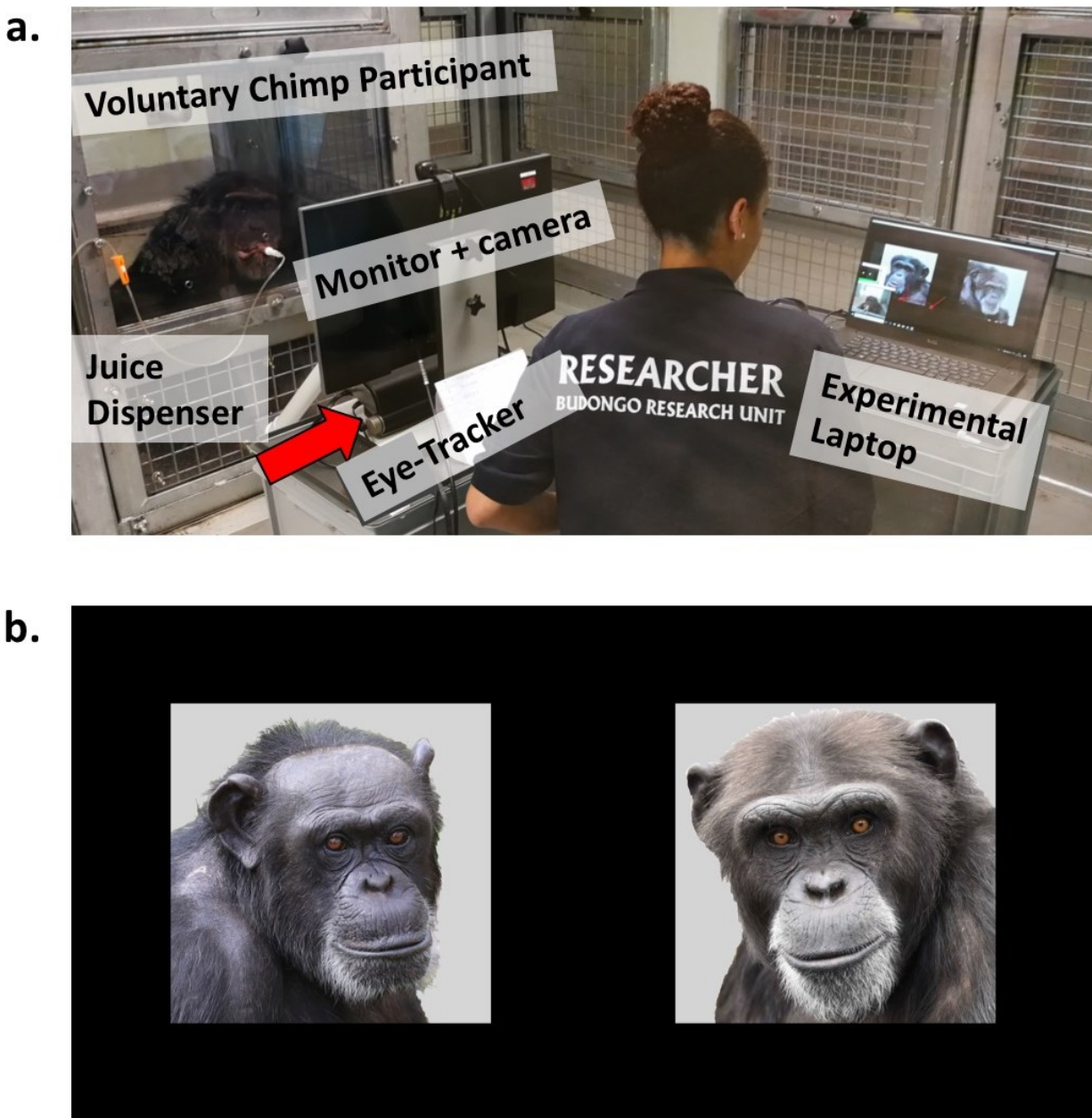
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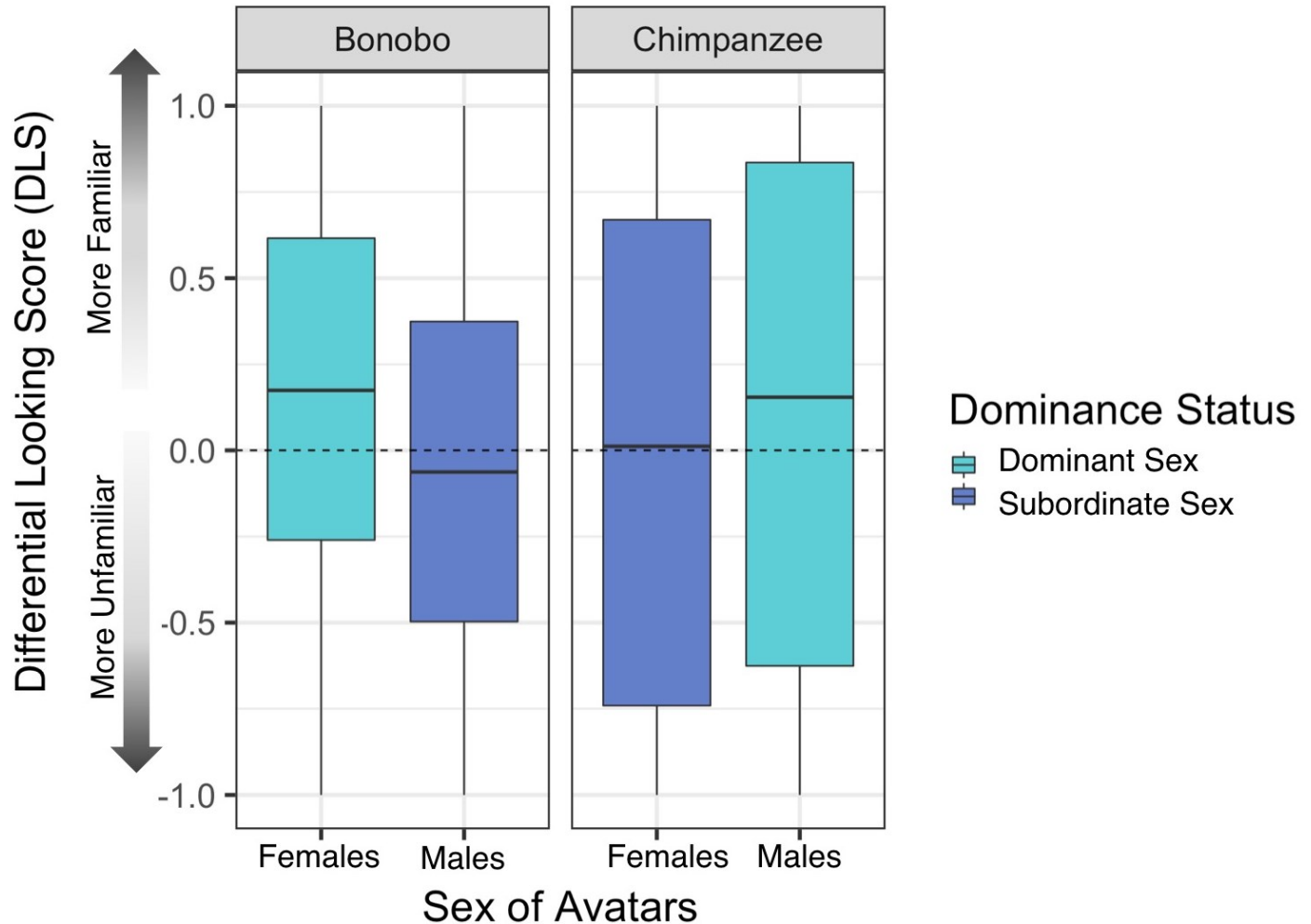
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 794 **Fig. 1:** Experimental set-up at Edinburgh Zoo (a) and example of a single trial for the Kumamoto
 795 Sanctuary chimpanzees (b). Here, unfamiliar individual is presented on the left, while familiar
 796 individual is presented on the right.
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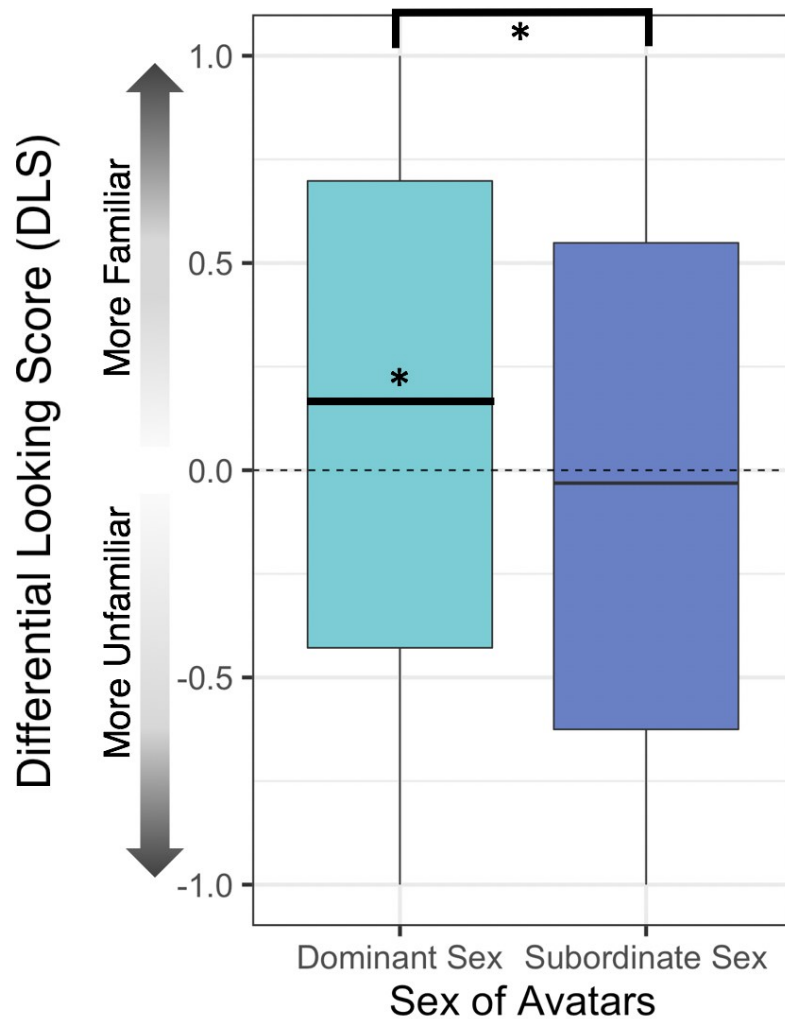
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800 **Fig. 2: Species' biases in attention toward familiar versus unfamiliar conspecific faces.**

801 Positive and negative values indicate biases toward familiar and unfamiliar individuals,
 802 respectively. Both species demonstrate stronger biases in attention while viewing images of the
 803 dominant sex (males for chimpanzees, females for bonobos) as compared to when viewing
 804 images of the subordinate sex. Boxes denote the interquartile range (IQR, from 25th percentile to
 805 75th percentile), middle lines denote medians, and whiskers denote 95% confidence intervals.

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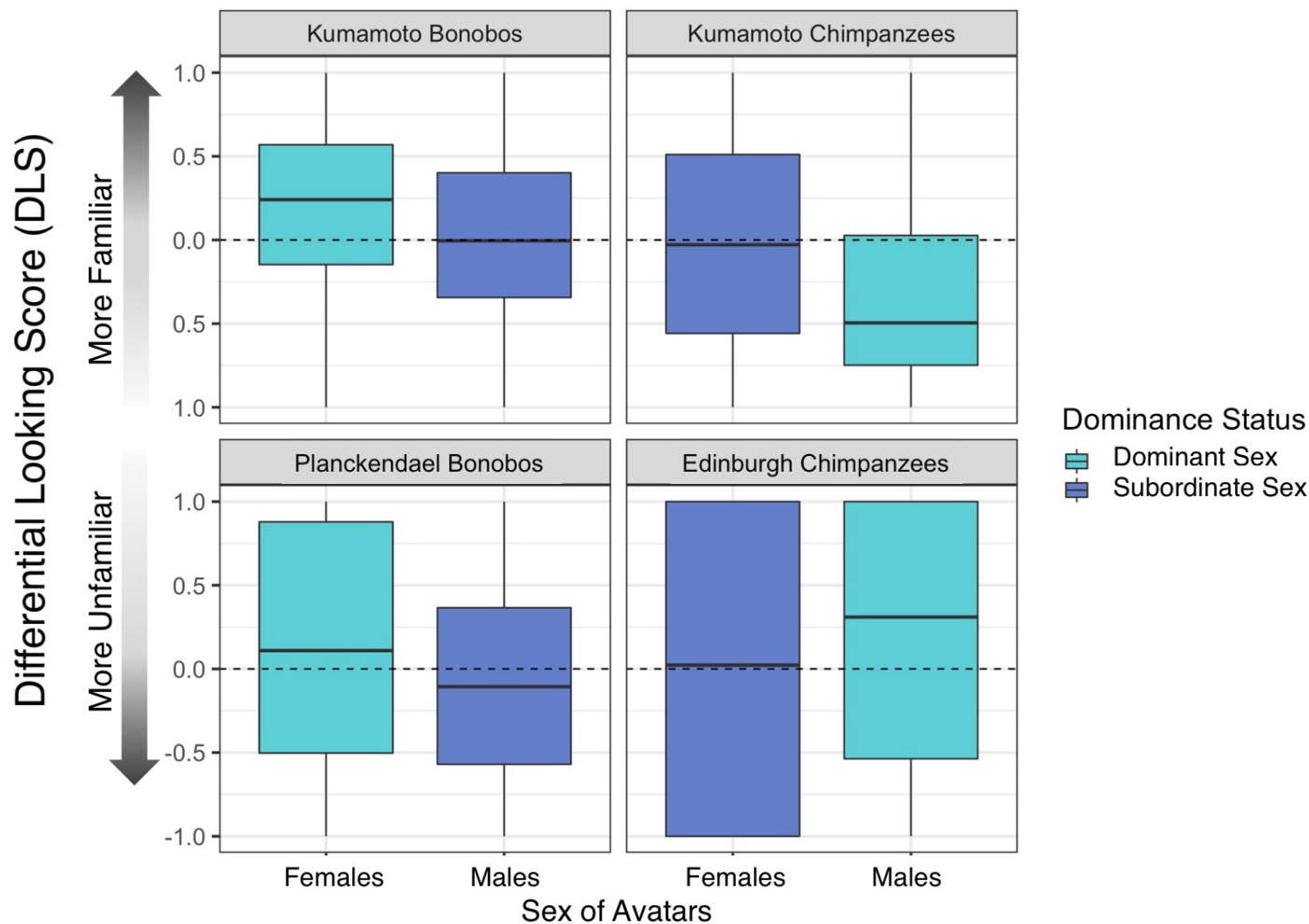


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809 **Fig. 3: *Pan* biases in attention toward familiar versus unfamiliar conspecific faces, when**
 810 **viewing members of the dominant versus subordinate sex.** Positive and negative values
 811 indicate biases toward familiar and unfamiliar individuals,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

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

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