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1 **Does male mate choice select for female colouration in a promiscuous primate species?**

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5

6 **Abstract**

7 The traditional view of sex roles and sexual selection emphasises the evolution of male
8 ornaments as a result of female mate choice and male-male competition. Female ornaments are
9 now receiving more attention, although their roles in mating decision are still less well
10 understood, especially considering cases in which colourful ornaments are expressed by both
11 sexes. In this study, we analysed whether female skin colouration (luminance and redness of
12 the face and hindquarters) influenced male mate choice and sexual behaviours in relation to
13 intra-cycle (cycle phase), inter-cycle (number of consecutive cycles, conceptive nature of the
14 cycle), and inter-individual (age, social rank, weight, and parity) variation in a captive
15 population of Japanese macaques (*Macaca fuscata*). Males did not preferentially choose
16 darker/redder females. Moreover, males did not appear to use female skin colouration to
17 apportion their mating efforts on the most fertile period of the menstrual cycle or during cycles
18 that lead to conception, or to discriminate between females. To our knowledge, our study is
19 among the few to report a lack of male choice for female colouration in a species where both
20 sexes potentially display ornamentation. While female colouration appeared to contain
21 information about intra-cycle, inter-cycle, and inter-individual variation in fecundity, this study
22 further demonstrates that this trait may not have been sexually selected and that males mated
23 regardless of such variation across females. This study adds to the growing research on the role
24 and evolution of female colouration in the context of sexual signalling and mate attraction.

25

26 **Keywords:** male mate choice, female ornament, colourful trait, sexual signalling, Japanese
27 macaques

28

29 **Introduction**

30 Mate choice is a crucial process in reproduction. Individuals have to simultaneously choose and
31 avoid potential mates based on the expected benefits (e.g., good genes, social support,
32 reproductive success) and costs (e.g., disease transmission, energy costs, intra-sexual
33 competition) associated with mating (Beltran-Bech & Richard, 2014; Møller et al., 1999; Thrall
34 et al., 2000; Trivers, 1972). The traditional view of sex roles and sexual selection has
35 emphasised the importance of female mate choice and male competition, and, as a consequence,
36 the function of male ornaments has been well studied across taxa (Andersson & Simmons, 2006,
37 2006; Cunningham & Birkhead, 1998; Fitzpatrick & Servedio, 2017). Perhaps partly as a result,
38 the role of male mate choice on the evolution of female traits has been relatively less
39 investigated. However, males can also face costs associated with mating in the form of
40 energetically demanding courtship displays, mate guarding, and the production of ejaculates
41 (Balshine et al., 2002; Dewsbury, 1982; Harshman & Zera, 2007; Lukas & Clutton-Brock,
42 2014). Similarly, female competition can also arise when females vary in reproductive quality
43 or when the number of females exceeds male mating or mate-guarding capacities such as in
44 cases with a high ovarian cycle synchrony or with a female-biased operational sex ratio, i.e.,
45 the ratio of the number of fertile adult males to the number of potentially fertile females in a
46 group at a given time (Amundsen, 2000; Bonduriansky, 2001; Edward & Chapman, 2011;
47 Kvarnemo & Ahnesjo, 1996). Thus, male mate choice or mutual mate choice can evolve in
48 some species to balance the ratio of costs/benefits inherent in mating (Clutton-Brock, 2007;
49 Fitzpatrick & Servedio, 2018; Johnstone et al., 1996; Kokko et al., 2003).

50 There is increasing evidence that males discriminate among possible mates in species
51 with traditional and reversed-sex roles and with different mating systems (from monogamy to
52 polygynandry). Males may choose older females that have already successfully reproduced and
53 raised offspring (spiny-footed lizards, *Acanthodactylus erythrurus*: Belliure et al., 2018;
54 chimpanzees, *Pan troglodytes*: Muller et al., 2006; brown widow spiders, *Latrodectus*
55 *geometricus*: Waner et al., 2018). Males may also choose females of higher social ranks
56 compared with lower-ranking ones. This may be particularly adaptative in species where social
57 rank is maternally inherited: higher-ranking offspring may achieve better condition and higher
58 survival than lower-ranking offspring (e.g., mandrills, *Mandrillus sphinx*: Setchell & Wickings,
59 2006). Males may also choose to mate with unmated vs. mated females to reduce sperm
60 competition and increase their reproductive success (house crickets, *Acheta domesticus*: Assis
61 et al., 2017; wolf spiders, *Schizocosa ocreata*: Roberts & Uetz, 2005). To mate selectively,
62 males may thus rely on female signals and/or express preferences for female traits that correlate
63 with reproductive quality, such as pheromones (widow spiders, *Lactrodectus hesperus*:
64 Baruffaldi & Andrade, 2015; humans, *Homo sapiens*: Gildersleeve et al., 2012; wolf spiders:
65 Roberts & Uetz, 2005), body size (long-tailed dance flies, *Rhamphomyia longicauda*: Funk &
66 Tallamy, 2000; LeBas et al., 2003; stalk-eyed flies, *Diasemopsis meigenii*: Harley et al., 2013;
67 rainbow darters, *Etheostoma caeruleum*: Soudry et al., 2020; hermit crabs, *Pagurus*
68 *middendorffii*: Wada et al., 2011), or vocal pitch (humans: Pisanski et al., 2018).

69 Among female traits, colourful ornaments have received more attention than others. In
70 some species, females express sex-specific colourful ornaments whose colour and/or size are
71 attractive to males. Such colourful ornaments are likely to be sexually selected traits as they
72 correlate with indices of fecundity, such as sexual or egg maturity, readiness to spawn, brood
73 size, or offspring condition (two-spotted gobies, *Gobiusculus flavescens*: Amundsen &
74 Forsgren, 2001; collared lizards, *Crotaphytus collaris*: Baird, 2004; cichlid fishes,

75 *Pelvicachromis taeniatus*: Baldauf et al., 2011; blue crabs, *Calinectes sapidus*: Baldwin &
76 Johnsen, 2012; spiny-footed lizards: Belliure et al., 2018; cichlid fishes, *Mikrogeophagus*
77 *ramizeri*: LaPlante & Delaney, 2020; pygmy halbeaks, *Dermogenys collettei*: Ogden et al.,
78 2020; striped plateau lizards, *Sceloporus virgatus*: Weiss, 2002, 2016). Comparatively, studies
79 on the role of non-sex-specific colourful ornaments (i.e., ornaments expressed by both sexes)
80 have yielded a contrasting picture of the extent to which these ornaments modulate mate choice.
81 Female colouration may indeed represent a genetically correlated response of selection for male
82 traits with no clear adaptive value in females. Males may thus express no preference for such
83 traits (three spined sticklebacks, *Gasterosteus aculeatus*: Wright et al., 2015) or preference may
84 be merely explained by sensory exploitation rather than sexual selection (sockeye salmon,
85 *Oncorhynchus nerka*: Foote et al., 2004). However, there is some evidence that males can show
86 preferences toward non-sex-specific colourful ornaments that reflect female reproductive state
87 (rhesus macaque, *Macaca mulatta*: Dubuc et al., 2009; Higham et al., 2010, 2011; agamid
88 lizards, *Ctenophorus ornatus*: LeBas & Marshall, 2000) or reproductive success (blue tits,
89 *Cyanistes caeruleus*: Doutrelant et al., 2008, 2012; Mahr et al., 2012; rhesus macaques: Dubuc,
90 Winters, et al., 2014; rock sparrows, *Petronia petronia*: Pilastro et al., 2003; Griggio et al., 2009,
91 2005; brown boobies, *Sula leucogaster*: Montoya et al., 2018; blue-footed boobies, *Sula*
92 *nebouxii*: Torres & Velando, 2005). Therefore, in these species, female colourful ornaments
93 can have a crucial impact on the mating strategies and reproductive success of both males and
94 females.

95 Here, we investigate the potential role of female colouration on male mate choice in a
96 promiscuous primate species, the Japanese macaque (*Macaca fuscata*). Female mate choice has
97 been suggested as an important process modulating mating strategies in this species (Fujita,
98 2010). However, this does not mean that males should not choose or discriminate among
99 potential mates. While their parental investment is mostly restricted to gamete contribution,

100 male Japanese macaques deal with high costs associated with mating. Japanese macaques are
101 seasonal breeders and multi-mount ejaculators and thus invest a non-negligible portion of their
102 daily energy expenditure for somatic maintenance and mating itself (Fooden & Aimi, 2005;
103 Matsubara, 2003; Thomsen et al., 2006). Like males of other species, male Japanese macaques
104 also face physical and physiological costs associated with extended consortships and mate-
105 guarding, reduced feeding activity, and male-male aggression leading to increased vigilance,
106 injuries, or chronic stress (e.g., in several mammal species including primates: Alberts et al.,
107 1996; Girard-Buttoz et al., 2014; Higham & Maestriperi, 2014; Lukas & Clutton-Brock, 2014;
108 Thompson & Georgiev, 2014). Males would thus benefit from discriminating among females
109 to focus their mating effort on mates that are fertile and of “good quality”. In Japanese macaques,
110 both sexes express red skin colouration (luminance: how light/dark the skin appears, redness:
111 at least partially reflecting the colour of the blood itself) of the face and hindquarters that peaks
112 during the mating season with sex hormones (Fooden & Aimi, 2005). Recent studies provided
113 more insight into the potential signalling function of female colouration in this species and
114 characteristics that males may be selecting for. Hindquarter colouration may signal the intra-
115 cycle probability of ovulation while concealing its exact timing and face colouration may
116 indicate early pregnancy (Rigaill et al., 2015, 2019). Hindquarter colouration may also contain
117 information about the inter-cycle probability of conception (Rigaill et al., 2019). Lastly, there
118 is some evidence that skin colouration may reflect inter-individual variation (e.g., social rank,
119 weight, but not parity, Rigaill et al., 2017, 2019). Pflüger and colleagues (2014) showed that
120 males increased attention toward an experimentally intense red-coloured version of an unknown
121 female face. Thus, female colouration may be a sexually selected trait involved in mate choice
122 in Japanese macaques if males appropriately use this colourful trait to inform their mating
123 decisions. Yet, to our knowledge, no study has tested this hypothesis in a non-forced-choice
124 discrimination situation.

125 Our study thus aims at identifying the potential role of female Japanese macaque face
126 and hindquarter colouration (luminance and redness) on the likelihood that a male will engage
127 or maintain sexual interactions with a female. If female colouration acts as a fertility signal
128 modulating mate choice, we hypothesised that males should display more sexual behaviours
129 toward darker/redder (i.e., stronger signal) females. We further hypothesised that the
130 relationship between male response and female colouration should vary according to a) intra-
131 cycle (timing of the fertile phase), b) inter-cycle (number of consecutive cycles and probability
132 of conception across cycles), and/or c) inter-individual (age, social rank, weight, and parity)
133 variation. If so, we predicted a positive relationship between male sexual behaviours and
134 darker/redder female colouration a) when the likelihood of ovulation is the highest (i.e., during
135 pre- and fertile phases vs. the post-fertile phase), b) during cycles that lead to conception (i.e.,
136 during conceptive cycles and the first cycles of a given mating season), and/or c) with older,
137 higher ranking, heavier, and possibly multiparous females.

138

139 **Methods**

140 **Subjects and housing**

141 We collected data during the 2011-2012 mating season, from early November to late January,
142 from a captive population of Japanese macaques living in a 1,210 m² outdoor enclosure at Kyoto
143 University Primate Research Institute (KUPRI, Inuyama, Japan). The group was composed of
144 39 individuals consisting of 13 adult females (> five years, mean \pm SD = 10.64 \pm 6.84 years,
145 range = 5-27), 6 sexually immature females (2.79 \pm 0.81 years, range = 1-4), 3 adult males (>
146 six years, 10.67 \pm 3.06 years, range = 8-14), 12 sexually immature males (2.99 \pm 1.05 years,
147 range = 1-4), and 5 infants less than one year old. All adult and sexually active females and
148 males in this group were included in this study. The ratio of adult males to adult females is
149 similar to other captive and wild populations from studies of sexual behaviours and mating

150 strategies (Fooden & Aimi, 2005; Fujita, 2010). We did not include subadult males/females to
151 avoid confounding factors due to maturational age. Females were naturally cycling, i.e., with
152 no hormonal contraceptive treatment. Female age, weight at the beginning of the mating season
153 (to the nearest 100g), and parity (total number of infants born divided by the number of years
154 post-adulthood) were provided by the Center for Human Modeling Research of KUPRI.
155 Animals were fed twice daily between 11:00 AM and 12:00 PM and between 4:00 PM and 5:00
156 PM. Water was supplied *ad libitum*. The Center for Human Evolution Modeling Research of
157 the Primate Research Institute reviewed and approved our research protocol in agreement with
158 the Guidelines for the Care and Use of Nonhuman Primates of the Kyoto University Primate
159 Research Institute.

160

161 **Behavioral observations**

162 One observer collected behavioural data using focal animal sampling distributed from 7:00 AM
163 to 5:00 PM, 7 days a week for 3 months. We used a female-centered approach because of the
164 need to assess female trait variation in order to address the question of male responses. We
165 followed each focal female 2 hours per week in 4 blocks of 30-min continuous focal samples
166 equally distributed across days and females. During focal observations, we recorded all social
167 and sexual behaviours between males and females, along with the direction of the behaviour
168 between the focal female and any identified adult male. We recorded all occurrences of female
169 presentations, female approaches, female mounts, female vocalisations (oestrus and copulation
170 calls), male approaches, male holding behaviours, male inspections of female genitals (i.e.,
171 visual and/or tactile and/or olfactory inspections of the female genital area), and male mounts
172 (i.e., ejaculatory and non-ejaculatory). The number of observed records for each behaviour is
173 given in Table 1. Female and male social ranks were assessed by transcribing agonistic
174 interactions for which a clear win/loss outcome was identified into an agonistic interaction

175 matrix. We then calculated the Normalized David's Score (NDS) to assess female social rank
176 positions (de Vries et al., 2006). Given that there were only three adult males in the group, male
177 ranks were assessed as alpha (winning all agonistic interactions), beta (defeating all males
178 except the alpha male), and gamma (losing all agonistic interactions) directly from the agonistic
179 interaction matrix.
180

| | Sum |
|-----------------------------|-----|
| <i>Female behaviours</i> | |
| Presentations | 10 |
| Approaches | 86 |
| Mounts | 86 |
| <i>Male behaviours</i> | |
| Approaches | 153 |
| Holding behaviors | 54 |
| Genital inspections | 39 |
| Mounts | 75 |
| <i>Female vocalisations</i> | 30 |

181
182 **Table 1.** Total number of female behaviours, male behaviours, and female vocalisations
183 recorded.

184

185 **Female colouration**

186 One experimenter took digital images of female face and hindquarters every two days in the
187 morning between 11:00 AM and 12:00 PM. We used a Canon EOS 350D camera with an 8
188 megapixel CMOS sensor and an EF28–135 mm f/3.5–5.6 IS USM lens. Images were
189 standardized by daily manual setting of the white balance using an X-Rite White Balance Card
190 and a Gretag X-Rite Color Checker (GretagMacbeth ColorChecker). For each female's photo,
191 we assessed colour from the whole face and hindquarter areas excluding the eyes, nose,
192 forehead, and tail. A technician who was blind to females' identity and characteristics extracted
193 reflectance spectra using Colourworker software (Chrometics Ltd. Website, available:

194 <http://www.chrometrics.com>). These spectra were converted into quantal catches, i.e., the
195 stimulation of Japanese macaque photoreceptors (Rigail et al., 2019) using equations and
196 macaque cone ratio and spectral sensitivity values given elsewhere (Higham et al., 2010;
197 Stevens et al., 2009). Based on the quantal catch data for both face and hindquarter colouration,
198 we calculated luminance (how light/dark the skin appears) and redness (variation in chromatic
199 parameters) data.

200

201 **Female reproductive status**

202 To determine each female's reproductive status, we collected a total of 381 faecal samples
203 (mean \pm SD per female = 29.31 ± 3.17 , range = 24-34) on average every 1.59 days (range = 0-
204 4 days) to accurately assess the ovarian cycle (Hodges & Heistermann, 2011). We collected
205 faecal samples in their entirety immediately after voiding, with most samples collected between
206 8:00 AM and 12:00 PM. All samples were then stored at -20°C until processing. Faecal samples
207 were analysed for pregnanediol-3-glucuronide (PdG) using enzyme immunoassays as
208 previously described by Garcia et al. (2009) to assess the presumed day of ovulation and the
209 periovulatory period (15-day period around the estimated ovulation) of each ovarian cycle. The
210 onset of the luteal phase was determined as the sample with a faecal PdG concentration which
211 was at least two standard deviations greater than the mean PdG concentration of the 3–4
212 preceding baseline values (Hodges & Heistermann, 2011). We determined the 2-day window
213 for ovulation as days -2 and -3 relative to the faecal PdG rise. The fertile phase was defined as
214 a period of five days (covering a two-day window for ovulation plus three preceding days to
215 account for sperm longevity in the reproductive tract (Behboodi et al., 1991). The five-day
216 period preceding the fertile phase represented the pre-fertile phase, while the five-day period
217 following the fertile phase was defined as the post-fertile phase. We recorded a total of 24
218 ovarian cycles (mean \pm SD per female = 2.0 ± 0.83 , range = 1-3) and the majority of these

219 cycles were non-conceptive (19/24). One female failed to cycle during the study and was thus
220 excluded from the analysis.

221

222 **Data analysis**

223 We restricted our analyses to the pre-fertile, fertile, and post-fertile phases. We used 173 focal
224 observations with matching female photo (i.e., focal and photo on the same observation day)
225 for the analyses (mean \pm SD = 7.53 ± 1.21 per female and per cycle). We built our dataset based
226 on the 30-min focal observations and attributed one line to each focal female – male dyad per
227 focal observation (i.e., three lines per focal female), which was the unit of analysis.

228 We carried out our analyses in R version 3.3.3. Before running the statistical analyses,
229 we checked for correlations between our variables of interest. Female weight correlated with
230 parity ($r_s = -0.50$, $P < 0.001$) and age ($r_s = 0.73$, $P < 0.001$). Parity correlated with age ($r_s = -$
231 0.42 , $P < 0.001$). Parity also weakly correlated with female social rank ($r_s = -0.25$, $P < 0.001$).
232 We thus excluded female age and weight from our analyses. None of the female behaviours
233 (i.e., presentations, approaches, and mounts) were correlated with each other (all $P > 0.05$).
234 None of the male behaviours (i.e., approaches, holding behaviours, genital inspections, and
235 mounts) were correlated with each other (all $P > 0.05$).

236 We aimed at testing whether the likelihood of a male behavioural response (binary
237 variable: 1 = occurrence, 0 = non-occurrence) toward a female was predicted by female
238 colouration, i.e., whether males were more likely to engage in or maintain sexual interactions
239 with darker/redder females. The little occurrences of copulatory event alone prevented us from
240 analysing the effect of female colouration on this behaviour only. We thus computed a binary
241 response variable that corresponded to a male behavioural response as the occurrence of at least
242 one of the behaviours involved in establishing and maintaining consortship that were displayed
243 by the interacting male of the dyad (i.e., approaches, holding behaviours, genital inspections,

244 and copulations). Similarly, we also computed a binary variable that corresponded to a female
245 behavioural display (hereafter, *female behaviours*), as the occurrence of at least one of the
246 behaviours involved in establishing and maintaining consortship that were displayed by the
247 interacting female of the dyad (i.e., presentations, approaches, and mounts).

248 We built a series of generalized linear mixed models with a binomial error structure and
249 logit link function with the function `glmer` from the `lme4` package (Bates et al., 2015) to
250 investigate the relationship between male behavioural response (binary response variable) and
251 female hindquarter and face luminance and redness (continuous predictor variables). Inspection
252 of the cumulative distribution functions revealed good fits to the normal distribution for
253 hindquarter luminance and to the lognormal distribution for face luminance, face redness, and
254 hindquarter redness. We first constructed three different models to test the relationship between
255 male behaviours and female face colouration (luminance and redness), male behaviours and
256 female hindquarter colouration (luminance and redness), and male behaviours and female face
257 and hindquarter colouration (luminance and redness). To account for a) intra-cycle, b) inter-
258 cycle, and c) inter-individual effects on the potential relationship between female colouration
259 and male response, our three models included interactions between female colouration and a)
260 the cycle phase (categorical variable, three levels: pre-fertile, fertile, and post-fertile phases),
261 b) the number of consecutive cycles (continuous variable) and the conceptive nature of the cycle
262 (binary variable: 1 = conceptive, 0 = non-conceptive cycles, hereafter *conception*), and c)
263 female social rank (continuous variable) and parity (continuous variable). We also included
264 female behaviours (binary variable) and male social rank (categorical variable, three levels:
265 alpha, beta, gamma) as covariates to account for the potential effects of female direct
266 solicitation and male social attributes on mating decisions. Finally, the date of the focal, female
267 identity, and male identity were included as random factors. We also constructed a null model
268 in which the predictor variables and all covariates were removed but the random effects

269 structure was maintained. All continuous variables were standardized to mean = 0 and SD = 1
270 prior to modelling to improve model performance and interpretability (Harrison et al., 2018).
271 We checked for variance inflation ($\text{GVIF}^{(1/(2 \times \text{DF}))} < 3$) using the car package (Fox & Weisberg,
272 2019); we excluded the number of consecutive cycles from the models due to variance inflation.
273 We ensured that all relevant model assumptions (homogeneity of the residuals and stability of
274 estimates) were met by visually inspecting histograms of the residuals and plots of residuals
275 against fitted values.

276 We used an information-theory approach to objectively compare and rank the four
277 candidate models (i.e., null model, face colouration model, hindquarter colouration model, and
278 face and hindquarter colouration model) in terms of how well they fitted the existing data. This
279 method allowed us to assess the likelihood that one or more models among the candidates is/are
280 best supported by the data (Burnham et al., 2011; Symonds & Moussalli, 2011). We used the
281 function model.sel of the MuMIn package (Bartoń, 2020) to rank models based on their
282 respective Akaike's information criterion corrected for small sample size (AICc values). We
283 considered models with ΔAICc (the difference in AICc values between the smallest AICc and
284 the other AICc values) below four as competitive models with the plausibly best model in the
285 set of candidate models (Burnham & Anderson, 2002). We reported the weight of the models
286 which indicates to what extent one candidate model is more likely than another to provide a
287 reasonable explanation of the variance in the data, along with the evidence ratio (ER) which
288 indicates the extent to which the higher-ranked model is more parsimonious than another
289 candidate model. We also reported the marginal (fixed effects alone) and conditional (fixed
290 effects and random structures) coefficients of determination (R^2_m and R^2_c) of all models using
291 the function r.squaredGLMM (Nakagawa & Schielzeth, 2013). We extracted weighted
292 parameter estimates (β), standard errors (SE), and 95% confidence intervals (95% CIs) of model

293 intercepts and predictors from conditional averaging of the 4 candidate models (function
294 model.avg).

295

296 **Results**

297 Among the candidate models, the model including female hindquarter colouration (luminance
298 and redness) and covariates had the highest weight (0.998) and more than 499 times more
299 empirical support than the competing models (face colouration: $\Delta\text{AICc} = 12.3$; face and
300 hindquarter colouration: $\Delta\text{AICc} = 17.6$; null model: $\Delta\text{AICc} = 49.8$, Table 2). The fixed and
301 random effects explained around 28% of the observed variance in the occurrence of male
302 behavioural responses.

303 There was no effect of cycle phase (fertile vs. pre-fertile and post-fertile phases) on the
304 interaction between male behavioural responses and female colouration (luminance and redness
305 of the face and hindquarters, all $P > 0.50$, Table 3, Figure 1A). There was a slight tendency for
306 a higher probability of male behavioural responses when hindquarter luminance was high in
307 non-conceptive vs. conceptive cycles ($\beta = -0.96 \pm 0.52$ SE, $P = 0.068$, 95% CI = -1.98; 0.07,
308 Table 3, Figure 1B). In other words, our results suggest that during conceptive cycles, there
309 was a higher probability of male behavioural responses when the signal was strong (lower
310 luminance = darker hindquarters). However, female face and hindquarter colouration *per se* did
311 not explain variation in the occurrence of male behavioural responses (luminance and redness,
312 all $P > 0.05$, Table 3). Similarly, the likelihood of observing male sexual behaviours was not
313 influenced by cycle phase or the conceptive nature of the cycle (all $P > 0.50$, Table 3).

314 Males were more likely to display sexual behaviours toward females that have solicited
315 or interacted with them ($\beta = 2.99 \pm 0.42$ SE, $P < 0.001$, 95% CI = 2.15; 3.82, Table 3). Males
316 were also more likely to display sexual behaviours toward females of lower parity ($\beta = -1.17 \pm$
317 0.53 SE, $P = 0.026$, 95% CI = -2.20; -0.14, Table 3) and of higher social rank ($\beta = 0.60 \pm 0.28$

318 SE, $P = 0.031$, 95% CI = 0.05, 0.15, Table 3). Male social rank was positively related to the
 319 occurrence of male sexual behaviours (alpha vs. beta: $\beta = -0.97 \pm 0.37$ SE, $P = 0.010$, 95% CI
 320 = -1.71; -0.24, alpha vs. gamma: $\beta = -1.45 \pm 0.41$ SE, $P < 0.001$, 95% CI = -2.26; -0.65, Table
 321 3).
 322

| Models | k | logLik | AICc | ΔAICc | weight | ER | $R^2m - R^2c$ |
|----------------------------------|----------|---------------|-------------|--------------------------------|---------------|-----------|---------------------------------|
| Hindquarter colouration | 24 | -140.1 | 330.6 | 0.0 | 0.998 | - | 0.26 - 0.28 |
| Face colouration | 24 | -146.2 | 342.9 | 12.31 | 0.002 | 499 | 0.19 - 0.23 |
| Face and hindquarter colouration | 36 | -135.3 | 348.2 | 17.59 | 0.00 | - | 0.29 - 0.31 |
| Null | 4 | -186.2 | 380.4 | 49.84 | 0.00 | - | 0.00 - 0.14 |

323
 324 **Table 2.** Characteristics of candidate models. *k*: number of predictors, *AICc*: corrected Akaike's
 325 information criterion, Δ *AICc*: AICc difference between higher-ranked models and other
 326 candidate models., *weight*: model probabilities, *ER*: evidence ratios, $R^2m - R^2c$: marginal and
 327 conditional coefficients of determination. Candidate models are presented from higher-ranked
 328 to lower-ranked ones.
 329

| | β | SE | z-value | P | 95% CI |
|--|--------------|-------------|-------------|-------------------|---------------------|
| Intercept | -1.20 | 0.53 | 2.25 | 0.024 | -2.45; -0.16 |
| Face luminance | 0.21 | 0.44 | 0.47 | 0.64 | -0.66; 1.08 |
| Face redness | 0.39 | 0.60 | 0.64 | 0.52 | -0.79; 1.57 |
| Hindquarter luminance | 0.50 | 0.37 | 1.36 | 0.17 | -0.22; 1.23 |
| Hindquarter redness | -0.45 | 0.38 | 1.16 | 0.25 | -1.20; 0.31 |
| Female behaviour | 2.99 | 0.42 | 7.02 | < 0.001 | 2.15; 3.82 |
| Cycle phase (fertile vs. prefertile) | -0.09 | 0.42 | 0.21 | 0.84 | -0.90; 0.73 |
| Cycle phase (fertile vs. post-fertile) | -0.25 | 0.40 | 0.63 | 0.53 | -1.03; 0.53 |
| Conception | -0.25 | 0.56 | 0.44 | 0.66 | -1.35; 0.86 |
| Parity | -1.17 | 0.53 | 2.22 | 0.026 | -2.20; -0.14 |
| Female rank | 0.60 | 0.28 | 2.15 | 0.031 | 0.05; 1.15 |
| Male rank (alpha vs. beta) | -0.97 | 0.37 | 2.60 | 0.009 | -1.71; -0.24 |
| Male rank (alpha vs. gamma) | -1.45 | 0.41 | 3.54 | < 0.001 | -2.26; -0.65 |

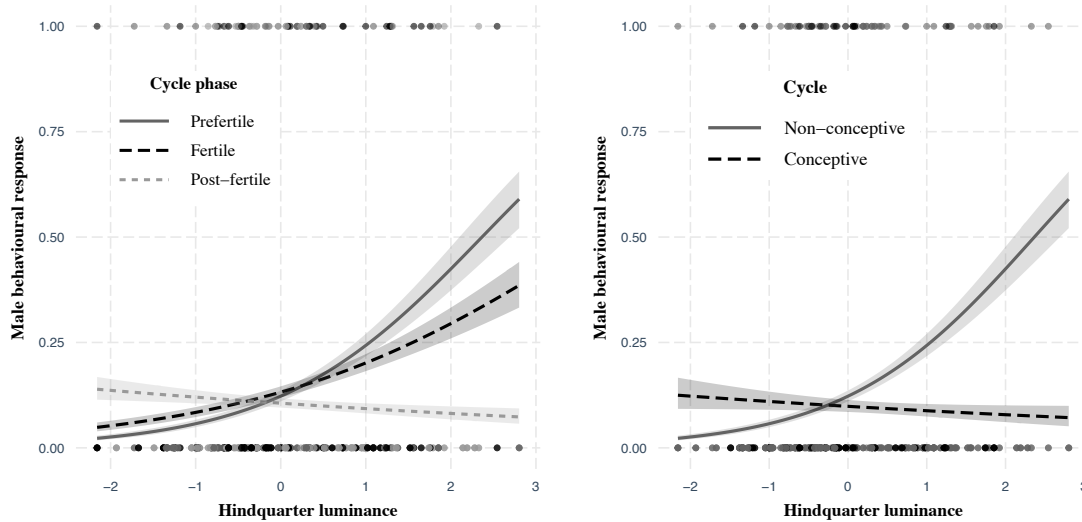
Interaction: face luminance x

| | | | | | |
|--|--------------|-------------|-------------|--------------|--------------------|
| Cycle phase (fertile vs. prefertile) | -0.43 | 0.47 | 0.91 | 0.36 | -1.34; 0.49 |
| Cycle phase (fertile vs. post-fertile) | -0.25 | 0.47 | 0.52 | 0.60 | -1.18; 0.68 |
| Conception | -0.50 | 0.47 | 1.07 | 0.28 | -1.42; 0.42 |
| Parity | 0.25 | 0.41 | 0.62 | 0.53 | -0.55; 1.06 |
| Female rank | 0.14 | 0.22 | 0.66 | 0.51 | -0.28; 0.57 |
| <hr/> | | | | | |
| Interaction: face redness x | | | | | |
| Cycle phase (fertile vs. prefertile) | 0.22 | 0.54 | 0.41 | 0.68 | -0.84; 1.29 |
| Cycle phase (fertile vs. post-fertile) | -0.01 | 0.52 | 0.03 | 0.97 | -1.04; 1.00 |
| Conception | -0.40 | -0.49 | 0.82 | 0.41 | -1.36; 0.55 |
| Parity | -0.05 | 0.43 | 0.13 | 0.90 | -0.89; 0.78 |
| Female rank | 0.28 | 0.21 | 1.33 | 0.18 | -0.13; 0.70 |
| <hr/> | | | | | |
| Interaction: hindquarter luminance x | | | | | |
| Cycle phase (fertile vs. prefertile) | 0.33 | 0.46 | 0.72 | 0.47 | -0.57; 1.22 |
| Cycle phase (fertile vs. post-fertile) | -0.65 | 0.40 | 1.61 | 0.11 | -1.44; 0.14 |
| Conception | <i>-0.96</i> | <i>0.52</i> | <i>1.82</i> | <i>0.068</i> | <i>-1.98; 0.07</i> |
| Parity | 0.00 | 0.37 | 0.00 | 1.00 | -0.73; 0.73 |
| Female rank | 0.07 | 0.20 | 0.33 | 0.74 | -0.32; 0.45 |
| <hr/> | | | | | |
| Interaction: hindquarter redness x | | | | | |
| Cycle phase (fertile vs. prefertile) | -0.53 | 0.51 | 1.04 | 0.30 | -1.53; 0.47 |
| Cycle phase (fertile vs. post-fertile) | -0.45 | 0.44 | 1.02 | 0.31 | -1.31; 0.41 |
| Conception | 0.56 | 0.64 | 0.88 | 0.38 | -0.70; 1.83 |
| Parity | 0.05 | 0.40 | 0.12 | 0.91 | -0.73; 0.83 |
| Female rank | 0.36 | 0.22 | 1.66 | 0.10 | -0.07; 0.78 |

330

331 **Table 3.** Model averaged parameters estimates (β) \pm adjusted standard errors (SE), z-value,
332 probability (P), and confidence intervals (95% CIs) from conditional averaging of all candidate
333 models. For each categorical comparison, the first level indicate baseline. Results for which CI
334 does not include zero are presented in bold, trends are presented in italic.

335



336

337 **Figure 1.** Interaction plot of the generalized linear mixed model exploring the relationship
338 between male behavioural response, female hindquarter luminance (log) across cycle phases
339 (A) and between conceptive vs. non-conceptive cycles (B).

340

341 Discussion

342 We examined male choice toward a non-sex-specific colourful ornament in a promiscuous
343 primate species with traditional sex roles and demonstrated that males did not bias their sexual
344 behaviours toward darker/redder females. Our results also showed that male Japanese macaques
345 did not seem to use female colouration (luminance and redness of the face and hindquarters) to
346 focus their mating effort on the most fertile period of the menstrual cycle, or during cycles that
347 lead to conception, or on “good quality” mates.

348 The lack of effect of female colouration on male sexual behaviours -or in other words,
349 the lack of male choice for darker/redder females- is surprising given that previous studies
350 suggested a potential role of female colouration on male mate choice in Japanese macaques
351 (face redness: Pflüger et al., 2014; face and hindquarter luminance and redness: Rigaiill et al.,
352 2019). While we investigated changes in male sexual behaviours toward group-member
353 females varying in skin colouration and characteristics, Pflüger et al. (2014) investigated male
354 responses toward two visual stimuli of an unknown female face. A red effect may have been

355 over-estimated due to the binary choice, the lack of familiarity with the stimuli which
356 significantly matters in communication (e.g., visual trait: Higham et al., 2011; odorant trait:
357 Setchell et al., 2010; auditory trait: Townsend et al., 2011), or the lack of precise measure of
358 attention such as tracking fine-scale eye movements (Hopper et al., 2020; Yorzinski et al., 2013).
359 Our present study demonstrated that female colouration is unlikely to be a sexual signal since
360 males did not appear to use this trait to discriminate when and with whom to mate to reproduce
361 efficiently. Skin colouration may thus correlate with female characteristics without having a
362 signalling function (correlation without causation). This highlights the importance of studying
363 traits suspected to play a role in sexual communication and mating strategies from both signaller
364 (what information may be contained) and perceiver (how the trait may affect behaviours)
365 perspectives. Alternatively, we cannot completely rule out that mate choice for female
366 colouration occurs in this species but that our data did not capture such effect. One may argue
367 that males of this group may not rely – or need to rely – on this colouration to make their mating
368 decisions as a result of the lower male-male competition due to the lack of peripheral males and
369 the monopolization of mating from the alpha male. However, if female colouration indeed plays
370 a role in male sexual strategies in this species where females vary in quality and female-female
371 competition is high, one may have expected the alpha male to express mate choice as he has
372 priority of access to mating. However, the alpha male did not appear to do so (see
373 supplementary material).

374 In the absence of male mate choice for a female trait and of a clear ovulatory signalling
375 in this species (Garcia et al., 2009; O’Neill et al., 2004; Rigail et al., 2019), does this mean that
376 males mate randomly? This is highly unlikely considering the energetic costs of extended sperm
377 production, prolonged consortship, and male-male competition (Matsubara, 2003; Thomsen et
378 al., 2006). While female colouration may not inform males about the probability of ovulation
379 or female characteristics, this traits appears to be involved in the communication of pregnancy

380 status (information content: Rigaiil et al., 2015). Moreover, males have been found to reduce
381 or avoid mating with pregnant females in populations facing higher energetic constrains (Fujita,
382 2010; Rigaiil et al., 2015). However, whether males indeed use female colouration to avoid
383 wasting energy in post-conceptive mating calls for further investigation. We also found in the
384 present study that males were more likely to respond to female solicitations that could be used
385 to apportion their mating effort toward receptive females vs. non-cycling females. Males may
386 thus adapt their mating strategies according to female behaviour and to their access to mate by
387 either intensifying mate guarding (higher-ranking males) or seizing a mating opportunity
388 (lower-ranking males). Monitoring female behaviours would ultimately benefit to both higher-
389 and lower-ranking males by balancing the costs and benefits of mate searching, direct
390 competition, and mating. Alternatively, male sexual behaviours may be a by-product response
391 of female mate choice which has been reported as an active reproductive strategy in Japanese
392 macaques (Huffman, 1991, 1992; Soltis et al., 1997). We also found that males may bias their
393 mate choice toward females at the beginning of their reproductive history and toward higher-
394 ranking females. This may be related to parental investment as lower-ranking females and/or
395 those toward the end of their reproductive history may have less energy to invest in future
396 offspring or be less capable to balance the costs of reproduction with other costs (e.g.,
397 competition, health) than higher-ranking females and/or those at the beginning of their
398 reproductive history (e.g., mandrills, Setchell & Wickings, 2006). More precise data on the
399 interaction between female behaviours and characteristics and male mate choice is needed to
400 better understand the process of male mate choice in Japanese macaques.

401 Studies of the role of non-sex-specific colourful ornaments displayed on feather or skin
402 have been relatively limited in comparison with sex-specific colourful ornaments in both males
403 and females. From this rather incomplete picture, it appears that male choice and preferences
404 for female traits may evolve because of the costs associated with reproduction. One factor may

405 be the cost of sexual signalling itself, when female ornamentations are costly to produce or
406 maintain and thus impact the energy allocated to reproduction and ultimately, offspring quality
407 and survival (Doutrelant et al., 2008, 2012; Griggio et al., 2009; Peters et al., 2011; Pilastro et
408 al., 2003), although it is complicated to accurately assess such signalling costs. Another factor
409 may be the shared costs of rearing offspring in socially monogamous species displaying extra-
410 pair copulations (Griggio et al., 2005; Mahr et al., 2012; Torres & Velando, 2005). Under such
411 conditions, both males and females would benefit from traits indicative of one's fecundity to
412 adjust their mating and parental effort according to the costs and prospective benefits of
413 signalling to and of reproducing with a particular mate. Alternatively, male choice for a
414 colourful trait has been also described in at least one promiscuous species with traditional sex
415 roles. In the territorial agamid lizards, female colourful traits appear to convey information
416 about receptivity: male choice may thus also evolve to maximize reproductive success when
417 mating decisions are limited or constrained (LeBas & Marshall, 2000).

418 To our knowledge, our study is among the few to report a lack of male choice for female
419 colouration (sockeye salmon: Foote et al., 2004; threespine sticklebacks: Wright et al., 2015).
420 A possible explanation could involve the operational sex ratio. A female-biased operational sex
421 ratio, i.e., when males are a limited resource, could favour female-female competition and
422 ornamentation. However, in seasonal breeders, it is likely that the number of cycling, receptive,
423 and defendable females within a group or location decreases rapidly during the mating season
424 as a consequence of reproductive synchrony (Ims, 1990; Thompson, 2018). Male-male
425 competition for the access to mates may thus strengthen which would select for male ornaments,
426 especially in species where the cost of reproduction is heavier on females than males. Such
427 scenario may explain the lack of male choice for female colouration in Japanese macaques.
428 Females are indeed more likely to conceive at the beginning of the mating season and to invest
429 high energy on gestation and maternal care while facing energetic stress from decreased food

430 availability and thermoregulation (Fujita, 2010; Garcia et al., 2010, 2011). Thus, female
431 colouration may only represent a correlated response of selection for ornamentation in males
432 (Lande, 1980). The signalling function of male colouration and its role on mate choice in
433 Japanese macaques is still unknown. However, evidence from other primate species suggests
434 that male colouration can correlate with some aspects of male-male competition (geladas,
435 *Theropithecus gelada*: Bergman et al., 2009; snub-nosed monkeys, *Rhinopithecus bieti*: Grueter
436 et al., 2015; drills, *Mandrillus leucophaeus*: Marty et al., 2009; rhesus macaques: Petersdorf et
437 al., 2017; mandrills: Setchell & Dixson, 2001) and may be used in female mate choice (rhesus
438 macaques: Dubuc, Allen, et al., 2014; Dubuc et al., 2016; Waitt et al., 2003).

439 In conclusion, we found no clear evidence that female colouration (luminance and
440 redness of the face and hindquarters) influence male mate choice in Japanese macaques. Female
441 colouration does not appear to be a sexually selected trait conveying relevant information about
442 intra-cycle, inter-cycle, and inter-individual differences in fecundity. However, future studies
443 should investigate the potential role of both female and male colouration in the communication
444 of reproductive status (e.g., cycling vs. non cycling, pregnancy), male-male competition, and
445 female mate choice to draft any definite conclusions. Whether reproductive seasonality and
446 reproductive costs influence the evolution of male mate choice and female traits remains an
447 open question, especially in primates for which little data is available. Further studies focusing
448 on the relationship between female/male colouration and male/female sexual behaviours and
449 mate choice in species facing different reproductive constraint should help to improve our
450 understanding of the role and evolution of non-sex-specific colourful ornaments in primates.

451

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459

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