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Lucie Rigaille, James Higham, Sandra Winters, Cécile Garcia. The redder the better? Information content of red skin coloration in female Japanese macaques. *Behavioral Ecology and Sociobiology*, 2019, 73 (8), pp.103. 10.1007/s00265-019-2712-x . hal-04251747

HAL Id: hal-04251747

<https://hal.science/hal-04251747>

Submitted on 7 Nov 2023

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ORIGINAL ARTICLE

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The redder the better? Information content of red skin coloration in female Japanese macaques

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Lucie Rigai¹ · James P. Higham² · Sandra Winters² · Cécile Garcia³

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Received: 21 August 2018 / Revised: 31 May 2019 / Accepted: 10 June 2019
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Abstract

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Primates appear unusual among mammals in the expression of female colorful ornaments in the absence of sex role reversal. Most studies of female ornamentation in primates have focused on the sexual signaling function of female exaggerated anogenital swellings in female-female competition and male attraction, but other female colorful ornaments, such as red skin coloration, may also contain information about reproductive status and individual characteristics. We analyzed variation in facial and hindquarter coloration (redness and luminance) according to the timing of the fertile phase (intra-cycle variation), the cycle number, whether the cycle was conceptive or non-conceptive (inter-cycle variation), and in relation to individual characteristics (social rank, parity, and body mass) in 12 captive female Japanese macaques (*Macaca fuscata*). While facial and hindquarter coloration did not accurately indicate the timing of the fertile phase, variation in hindquarter luminance signaled perceptible differences between pre- and post-ovulation stages. Hindquarters became less red, and faces were lighter as the number of consecutive cycles increased. Hindquarters were redder during non-conceptive cycles compared with conceptive ones. Individual variation in skin redness and luminance appeared perceptible under good light conditions. Higher-ranking females had darker hindquarters. We also found that variation in female skin coloration may contain information about differences in body mass but not in parity. Female skin coloration in Japanese macaques may thus be more indicative of inter-cycle variation and various specific female characteristics than the timing of the fertile phase. Our study provides insight into the potential information content of this signal and demonstrates the characteristics that males might be selecting for should males prefer redder females.

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Significance statement

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Primates are the most colorful group of mammals. Females of some primate species display red skin color that is suggested to play a role in mate attraction by reflecting reproductive status or individual characteristics. In Japanese macaques, a species lacking accurate behavioral and auditory indices of the probability of ovulation, female red skin coloration (face and hindquarters) may influence mating activity. Our study shows that this colorful trait does not contain information about the timing of the fertile phase and parity but may indicate inter-cycle differences and some female characteristics. Our findings add to a growing body of research on the possible roles and functions of female colorful ornaments in animal sexual communication.

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Keywords Skin coloration · Sexual communication · Signal content · Reproductive status · *Macaca fuscata*

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Communicated by D. P. Watts

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Introduction

In a wide range of animals, both sexes express secondary sexual traits such as colorful signals, with males often exhibiting exaggerated trait expression relative to females (Darwin 1871; Andersson 1994). Sex differences in reproductive costs are thought to result in selection pressure on males to express traits that attract females (reviewed in Clutton-Brock 2004; David and Heeb 2009). As a result, the function of male

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47 colorful signals in relation to reproductive success and female
48 preferences has been well studied across taxa (Andersson
49 1994; Andersson and Simmons 2006; Clutton-Brock 2007).
50 However, there is no reason to expect that, even if one sex is
51 choosy, the other sex should nonetheless not choose or dis-
52 criminate between mates too, particularly when mating is as-
53 sociated with energetic costs and risks of disease transmission
54 (Thrall et al. 2000; Edward and Chapman 2011; Lukas and
55 Clutton-Brock 2014). Indeed, there is increasing evidence that
56 females also display colorful traits which are attractive to
57 males in birds (Amundsen 2000; Torres and Velando 2005;
58 Griggio et al. 2005, 2009), lizards (LeBas and Marshall
59 2000; Weiss 2002; Baird 2004), fishes (Amundsen and
60 Forsgren 2001, 2003), and insects (Hopkins et al. 2015).
61 It is therefore important to investigate the information con-
62 tent and potential signaling function of these female col-
63 orful traits in relation to mating strategies and reproductive
64 success.

65 Primates are the most colorful group of mammals, with
66 males and females of many species expressing red skin color-
67 ation of the face, chest, ano-genital area, and hindquarters
68 (Dixson 2012). Male skin coloration has been found to corre-
69 late with some aspects of male-male competition, such as
70 dominance rank or one-male unit holding status (mandrills,
71 *Mandrillus sphinx*: Setchell and Dixson 2001; geladas,
72 *Theropithecus gelada*: Bergman et al. 2009; drills,
73 *Mandrillus leucophaeus*: Marty et al. 2009; snub-nosed mon-
74 keys, *Rhinopithecus bieti*: Grueter et al. 2015), or to predict
75 the likelihood of aggression (rhesus macaques, *Macaca*
76 *mulatta*: Petersdorf et al. 2017). Male coloration, independ-
77 tly of social rank, can also influence attractiveness to females
78 and mating success in rhesus macaques (Waitt et al. 2003;
79 Dubuc et al. 2014a, 2015). Thus, male coloration can evolve
80 under intra- or inter-sexual selection in primates. Perhaps part-
81 ly as a result, studies of the role of primate female non-specific
82 colorful traits (i.e., traits expressed by both sexes) may have
83 been limited by the classic view of sexual selection that em-
84 phasizes male competition and female choice. Female color-
85 ation may indeed represent a by-product or a “correlated re-
86 sponse” of selection for ornamentation in males (Lande 1980),
87 with no clear adaptive value in females. Thereby, the expres-
88 sion of colorful traits in females could be maintained because
89 they do not impose any costs on females, although it is com-
90 plicated to accurately assess such signaling costs.

91 Alternatively, the expression of female colorful traits could
92 be maintained by selection due to an adaptive signaling func-
93 tion that may influence male mate choice in primates. There is
94 already some evidence that males show mating preferences
95 based on female characteristics, such as age or parity
96 (Anderson 1986; Muller et al. 2006; Setchell and Wickings
97 2006) and social rank (Setchell and Wickings 2006; Garcia
98 et al. 2009; Rigaiil et al. 2013). Some colorful traits exhibited
99 by female primates also appear to be attractive to males,

100 suggesting a role for sexual selection (sexual swellings: 100
101 Deschner et al. 2004; but see Fitzpatrick et al. 2015; skin 101
102 coloration: Waitt et al. 2006; Higham et al. 2011; Pflüger 102
103 et al. 2014). Female primates exhibit a range of colorful sig- 103
104 nals that could be related to a variety of signaling functions 104
105 (Bradley and Mundy 2008), yet the majority of research in this 105
106 area has focused on sexual swellings as indicators of fertility 106
107 status or female fitness (e.g., Nunn 1999; Zinner et al. 2002; 107
108 Deschner et al. 2004; Setchell and Wickings 2004a; Setchell 108
109 et al. 2006a; Higham et al. 2008; Fitzpatrick et al. 2015; Street 109
110 et al. 2016). Nevertheless, other colorful female signals could 110
111 also play a role in reproductive signaling. Red skin coloration 111
112 is linked to changes in concentrations of circulating estrogens, 112
113 which bind to estrogen receptors in the skin, modulating blood 113
114 flow (luminance: how dark or light the skin appears) and the 114
115 amount of oxygenated blood (redness: at least partially 115
116 reflecting the color of the blood itself) in the skin (Rhodes 116
117 et al. 1997). Female red skin coloration may thus indicate 117
118 reproductive status. For instance, female facial coloration 118
119 varies between follicular and luteal phases in mandrills 119
120 (Setchell et al. 2006b), cycling and pregnancy periods in 120
121 Japanese macaques (*Macaca fuscata*: Rigaiil et al. 2015), 121
122 and indicates ovulation timing in rhesus macaques (Dubuc 122
123 et al. 2009; Higham et al. 2010). Female skin coloration 123
124 may also correlate with some individual characteristics. 124
125 There is evidence that female skin coloration correlates with 125
126 parity or age, which are usually correlated, with females hav- 126
127 ing more infants being darker or redder (Setchell et al. 2006b; 127
128 Higham et al. 2008; Dubuc et al. 2014b; but see Rigaiil et al. 128
129 2017). While social rank often correlates with skin coloration 129
130 in males, previous studies have found no such relationship in 130
131 female mandrills (Setchell and Wickings 2004a; Setchell et al. 131
132 2006b), olive baboons (*Papio anubis*: Higham et al. 2008; 132
133 Rigaiil et al. 2013), and Japanese macaques (Rigaiil et al. 133
134 2017). Female condition, often indexed using body mass, 134
135 may also affect a female’s ability to cope with the energetic 135
136 costs associated with reproduction, mating, and signaling, 136
137 thus potentially influencing the likelihood of conception 137
138 (Japanese macaques: Mori 1979; Garcia et al. 2011; olive 138
139 baboons: Bercovitch 1987; mandrills: Setchell and Wickings 139
140 2004b). However, the relationship between female body mass 140
141 and skin coloration is still unclear for these species (Setchell 141
142 and Wickings 2004a; Setchell et al. 2006b; Rigaiil et al. 2017).

143 In Japanese macaques, both males and females express red 143
144 coloration of the face and hindquarters that peaks during the 144
145 mating season along with concentrations of sexual hormones 145
146 (Fooden and Aimi 2005). Males show increased attention to- 146
147 ward intensely colored female faces, suggesting that skin col- 147
148 oration could play a role in mate attraction and could have a 148
149 signaling function (Pflüger et al. 2014). Adult females do not 149
150 exhibit sexual swellings or obvious behavioral or auditory 150
151 indicators of ovulation (proceptive behaviors, estrus and cop- 151
152 ulation calls, O’Neill et al. 2004; Garcia et al. 2009). While 152

153 skin coloration may influence mating activity, it is unclear
 154 what may be signaled by variation in this trait. One hypothesis
 155 is that female skin coloration might indicate intra-cycle varia-
 156 tion in the likelihood of ovulation. While a previous study
 157 found that variation in female facial coloration signals early
 158 gestation (Rigaill et al. 2015), it is still unclear whether skin
 159 coloration contains information about the timing of the fertile
 160 phase (Fujita et al. 2004). Female skin coloration might also
 161 signal inter-cycle differences. Female Japanese macaques tend
 162 to conceive during their first menstrual cycles in a given mat-
 163 ing season (Fujita et al. 2004; O'Neill et al. 2004; Fooden and
 164 Aimi 2005; Garcia et al. 2009). The underlying behavioral and
 165 hormonal mechanisms leading to a decrease in conception
 166 probability (and possibly in hormonal concentrations) after
 167 the first cycles are unknown, although energetic costs related
 168 to reproduction and thermoregulation may play a role (Fooden
 169 and Aimi 2003; Garcia et al. 2011; Takeshita et al. 2014). Skin
 170 coloration may correlate with inter-cycle differences of the
 171 likelihood of conception or in hormonal concentrations, with
 172 coloration during conceptive or first cycles being redder/
 173 darker than during non-conceptive or following cycles.
 174 Another non-mutually exclusive hypothesis is that female skin
 175 coloration is potentially informative about individual condi-
 176 tion and characteristics such as social rank, age or parity, and
 177 body mass. In a previous study, we found no relationship
 178 between female face coloration and individual characteristics
 179 in a wild population of Japanese macaques (Rigaill et al.
 180 2017). However, this study focused on facial coloration only
 181 with a small number of females from a population under high
 182 energetic constraints, which may have led to inconclusive re-
 183 sults. Additional data from a more controlled environment and
 184 a larger sample size would thus help to further investigate the
 185 possible signaling functions of female skin coloration in
 186 Japanese macaques.

187 Our study aims to identify the potential information content
 188 of female Japanese macaque faces and hindquarters in a mat-
 189 ing context, to determine whether skin coloration (redness and
 190 luminance) is informative about intra-cycle variation (timing
 191 of the fertile phase), inter-cycle variation (number of consec-
 192 utive cycles, conception probability), and individual charac-
 193 teristics (social rank, body mass, and parity or age).

- 194 1. Intra-cycle variation. If female skin coloration is related to
 195 changes in reproductive hormones across the menstrual
 196 cycle, and thus to the timing of the fertile phase within a
 197 cycle, we predict that faces or hindquarters will be darker/
 198 redder (i.e., stronger signal) during the fertile phase com-
 199 pared with the pre- and post-fertile phases.
 200 2. Inter-cycle variation. If skin coloration is modulated by
 201 changes in sex hormone concentrations (i.e., a decrease in
 202 hormonal concentrations across cycles) and indicates the
 203 probability of conception, we predict that female faces or
 204 hindquarters will become less red/lighter as the number of

- consecutive cycles increases. We also predict that concep- 205
 tive cycles will be darker/redder compared with non- 206
 conceptive cycles. 207
 3. Individual characteristics. If social rank influences female 208
 skin coloration, we predict that higher-ranking females 209
 will be darker/redder than lower-ranking females. 210
 Similarly, if there is a relationship between female body 211
 mass and skin coloration, we predict that females that 212
 were heavier prior to the beginning of the mating season 213
 will be darker/redder than lighter females. Finally, if parity 214
 (or age) influences skin coloration, we predict that fe- 215
 males with higher parity (or older females) will have 216
 darker/redder faces or hindquarters. 217

Methods 218

Subjects and housing 219

220 We collected data during the 2011–2012 mating season,
 221 from early November to late January, from a captive pop-
 222 ulation of Japanese macaques living in a 1210-m² outdoor
 223 enclosure at the Primate Research Institute of Kyoto
 224 University (KUPRI, Inuyama, Japan). The group was
 225 composed of 39 individuals: 13 adult females (mean ±
 226 SD = 10.64 ± 6.84 years old, range = 5–27), 6 sexually im-
 227 mature females (2.79 ± 0.81 years old, range = 1–4), 3
 228 adult males (10.67 ± 3.06 years old, range = 8–14), 12
 229 sexually immature males (2.99 ± 1.05 years old, range =
 230 1–4), and 5 infants less than 1 year old. Animals were fed
 231 twice daily between 11:00 a.m. and 12:00 p.m. and be-
 232 tween 4:00 p.m. and 5:00 p.m. Water was supplied ad
 233 libitum. Animal care and maintenance comply with the
 234 current laws of Japan, which are in accordance with
 235 NIH standards. All adult (> 5 years old) and sexually ac-
 236 tive females in this group (N = 13 females) were included
 237 in this study. We did not include subadult females to
 238 avoid confounding factors due to maturational age, and
 239 because subadult females do not conceive and may have
 240 unusual menstrual cycles and patterns of circulating re-
 241 productive hormones. Females were naturally cycling,
 242 i.e., with no hormonal contraceptive treatment. Female
 243 social ranks were monitored using focal (total 524 × 30-
 244 min focal observation, five focal observations per week
 245 per female) and ad libitum observations evenly distributed
 246 during the study period and were assessed by transcribing
 247 agonistic interactions for which a clear win/loss outcome
 248 was identified into an agonistic interaction matrix. We
 249 calculated the normalized David's score (NDS) to assess
 250 female social rank positions (de Vries et al. 2006). Female
 251 parity (total number of infants born divided by the
 252 number of years post-adulthood, defined as 5 years old)

253 and body mass prior to the beginning of the mating season
 254 (as measured on 18 October 2011) were provided by
 255 the Center for Human Modeling Research of KUPRI.

256 **Hormonal analyses and determination of ovulation**
 257 **dates**

258 To determine each female's reproductive status, we collected
 259 an average of $29.31 \pm SD 3.17$ fecal samples per female (total = 381,
 260 range per female = 24–34). Because female Japanese macaques do not display obvious signs of ovulation
 261 such as sexual swellings, the fecal samples could not be associated
 262 a priori to a cycle phase thus limiting any bias in our determination
 263 of the reproductive status. We collected fecal samples in their entirety
 264 immediately after voiding, with most samples collected between 8:00 a.m.
 265 and 12:00 p.m. We bagged and labeled fecal samples and stored them on ice
 266 until transfer to a freezer 0–2 h later. All samples were then stored at
 267 $-20\text{ }^{\circ}\text{C}$ until processing. We collected samples on average every 1.59 days
 268 (range = 0–4 days) to accurately assess the ovarian cycle (Hodges and Heistermann 2011).
 269 Fecal samples were analyzed for pregnanediol-3-glucuronide (PdG) using
 270 enzyme immunoassays as described by Garcia et al. (2009). The presumed
 271 day of ovulation and the periovulatory period of each ovarian cycle were
 272 determined using fecal PdG profiles. The fertile phase was defined as a
 273 period of 5 days (covering a 2-day window for ovulation plus three preceding
 274 days to account for sperm longevity in the reproductive tract (humans: Wilcox
 275 et al. 1995)); the 5-day period preceding this phase represented the pre-fertile
 276 phase, while the 5 days following the fertile phase were defined as the post-fertile
 277 phase. We observed a total of 24 ovarian cycles (mean \pm SD per female =
 278 2.0 ± 0.83 , range = 1–3), and the majority of these cycles were non-conceptive
 279 (19/24). Hormonal profiles showed that one of the 13 females had abnormal
 280 hormonal variations and failed to cycle for the entire duration of the study.
 281 This non-cycling female was subsequently excluded from the analysis.

289 **Assessment of skin coloration—redness and luminance**
 290

291 We took images of female faces and hindquarters in the morning
 292 between 11:00 a.m. and 12:00 p.m. every 2 days. We used a Canon EOS 350D
 293 camera with an 8-megapixel CMOS sensor and an EF 28–135 mm f/3.5–5.6 IS
 294 USM lens. We standardized images by daily manual setting of the white balance
 295 using an X-Rite White Balance Card (GretagMacbeth ColorChecker) and then
 296 by taking a picture of a Gretag X-Rite Color Checker (24 colored squares of
 297 known and varying reflectance) in the exact same conditions as those for
 298 the subject (i.e., camera settings and distance, orientation from the camera).
 299 We assessed color from the whole face and

hindquarter areas excluding the eyes, nose, forehead, and tail. 302
 We extracted reflectance spectra from these areas using 303
 ColourWorker software (Chrometics Ltd. available at <http://www.chrometrics.com>). 304
 The extraction of reflectance spectra was done by a technician who was not 305
 involved in data collection and blind to subject characteristics. We converted 306
 these spectra into quantal catches, i.e., the stimulation of Japanese macaque 307
 photoreceptors. We measured quantal catches for the red (longwave (LW)) and 308
 green (mediumwave (MW)) photoreceptors using equations and macaque cone 309
 ratio and spectral sensitivity values given elsewhere (Stevens et al. 2009; 310
 Higham et al. 2010). In trichromatic primates, such as Japanese macaques, 311
 chromatic (wavelength of light) and achromatic (light vs. dark) variations 312
 in color are perceived based on relative photoreceptor simulation (Stevens et al. 313
 2009). Based on the quantal catch data for both facial and hindquarter 314
 coloration, we calculated chromatic variation in redness based on the red-green 315
 opponency channel $((LW - MW) / (LW + MW))$; higher values indicate a 316
 redder color) and achromatic variation based on the luminance channel 317
 $((LW + MW) / 2)$; higher values indicate a lighter color) (Osorio and Vorobyev 318
 2005). We used the receptor noise model (Vorobyev and Osorio 1998) and the 319
 quantal catch data to determine how discriminable two different colors are 320
 likely to appear to the macaque visual system by calculating just noticeable 321
 differences (JNDs), which scale color distances by the minimal amount by 322
 which stimulus intensity must be changed in order to produce a perceptible 323
 difference in color. JND values below 1 indicate that differences between two 324
 colors are not perceptible, values between 1 and 3 indicate perceptible 325
 differences under good light conditions, and values > 3 indicate perceptible 326
 differences even when light conditions deteriorate (Siddiqi et al. 2004). We 327
 measured intra-cycle (i.e., for each cycle, each data point is compared with 328
 that cycle's least red/dark image) and inter-female (i.e., each female data 329
 point is compared with the least red/dark value in the data set) perceptible 330
 differences in face and hindquarter coloration. We refer to opponency channel 331
 calculations as "redness" and "luminance" and JND calculations as "intra-cycle 332
 JND redness/luminance" and "inter-female JND redness/luminance." 333
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Data analysis

343 We used face and hindquarter images from the pre-, post-, and 344
 fertile phases of 12 females for color analyses (24 menstrual 345
 cycles in total, 6.2 images per cycle per female in average, 292 346
 images in total). Examples of images are given in Figs. 1 and 347
 2. Our statistical approach was designed to test whether female 348
 skin coloration was related to cycle phase, the conceptive 349
 nature of the cycle (hereafter "conception"), the number of 350
 consecutive menstrual cycles, age, social rank, parity, and 351
 body mass prior to the mating season. We ran general linear 352

Fig. 1 Images of one female hindquarters across different cycle phases of one menstrual cycle: pre-fertile phase (left), fertile phase (middle), and post-fertile phase (right)



353 mixed-effects models (LMMs) fitted by maximum likelihood
 354 to examine variation in female facial and hindquarter coloration
 355 separately using nlme (Pinheiro et al. 2014) and lmerTest
 356 (Kuznetsova et al. 2017) packages in R version 3.3.3. We
 357 checked for correlations between our predictor variables to
 358 avoid potential confounding effects of multi-collinearity.
 359 Female parity did not correlate with body mass ($r_s = -0.49$,
 360 $P = 0.10$, $N = 12$) or rank ($r_s = -0.24$, $P = 0.45$, $N = 12$).
 361 Female body mass was not correlated with rank ($r_s = -0.03$,
 362 $P = 0.94$, $N = 12$).

363 We first investigated whether facial and hindquarter redness
 364 and luminance co-varied by constructing two LMMs
 365 for both facial and hindquarter coloration as follows: response
 366 variable: redness; predictor variable: luminance; random factors:
 367 cycle number nested into female identity. We compared
 368 the fitted models with their respective null models in which
 369 the predictor variable was removed but the random effect
 370 structure was maintained via a likelihood ratio test (LRT).

371 To analyze variation in female redness and luminance, we
 372 constructed four LMMs in which the response variable was

either facial redness, facial luminance, hindquarter redness, or
 hindquarter luminance. Inspection of the cumulative distribution
 functions of each response variable revealed good fits to the
 lognormal distribution, so each variable was log-transformed
 prior to model fitting. For all four models, we constructed a
 full model which included cycle phase (three categories: pre-fertile,
 fertile, and post-fertile phases), conception (two categories:
 conceptive and non-conceptive cycles), cycle number (continuous),
 social rank (continuous), parity (continuous), and body mass
 (continuous) as fixed effects and female identity as a random
 effect. All continuous predictors were scaled and centered prior
 to model fitting to facilitate interpretation of the parameter
 estimates (effect size of the predictors).

We then performed LRTs comparing each of the four full
 fitted models to their respective null models in which the
 predictor variables were removed but the random effect
 structure was maintained. If a full model outperformed its
 respective null model, we then tested the statistical significance
 of each predictor variable using LRTs, comparing the full
 model to reduced models in which single predictors were
 removed in order to get the overall effect of this predictor.
 We also report estimates and pairwise comparisons across all
 factor levels of each full model for a better interpretation of
 our results. We report parameter estimates with their respective
 95% confidence intervals. Our statistical approach forces
 comparisons of all categorical predictor levels against a
 baseline intercept term (here: the fertile phase by default
 for cycle phase). To obtain pairwise comparisons across all
 factor levels, we relevelled this factor (setting the pre-fertile
 phase as the baseline) and re-ran models as necessary. We
 did not further report on parameter estimates of full models
 that did not outperform their respective null models. We
 ensured that all relevant model assumptions were met by
 visually inspecting histograms of



Fig. 2 Images showing one of the darkest female faces (left) and one of the lightest female faces (right) across all images used for color analyses ($N = 12$ females and 292 pictures)

407 the residuals and plots of the residuals against fitted values.
 408 We also calculated the conditional and marginal coefficients
 409 of determination (R^2_c and R^2_m) of all full models using the
 410 package MuMIn (Nakagawa and Schielzeth 2013).

411 **Data availability** The datasets generated and analyzed during
 412 the current study are available from the corresponding author
 413 on reasonable request.

414 **Results**

415 Hindquarter redness and luminance co-varied; females with
 416 redder hindquarters also had darker hindquarters (LRT: $\chi^2 =$
 417 8.10 , $\Delta df = 1$, $P = 0.044$). Facial redness and luminance also
 418 co-varied; females with redder faces also had darker faces
 419 (LRT: $\chi^2 = 3.73$, $\Delta df = 1$, $P = 0.05$). Comparisons between
 420 full and null models showed that hindquarter luminance, hind-
 421 quarter redness, and facial luminance were related to the tested
 422 female predictors (LRTs: hindquarter luminance: $\chi^2 = 15.65$,
 423 $\Delta df = 7$, $P = 0.029$, $R^2_m = 0.15$, $R^2_c = 0.18$; hindquarter red-
 424 ness: $\chi^2 = 24.97$, $\Delta df = 7$, $P < 0.001$, $R^2_m = 0.18$, $R^2_c = 0.18$;
 425 facial luminance: $\chi^2 = 15.16$, $\Delta df = 7$, $P = 0.034$, $R^2_m = 0.16$,
 426 $R^2_c = 0.29$). Facial redness was not related to the tested pre-
 427 dictors ($\chi^2 = 5.71$, $\Delta df = 7$, $P = 0.57$, $R^2_m = 0.05$, $R^2_c = 0.13$).

428 1. Intra-cycle variation

429 Models including cycle phase better explained the ob-
 430 served color variance in hindquarter luminance only (LRT:
 431 $\chi^2 = 6.53$, $\Delta df = 2$, $P = 0.038$). Hindquarters became signifi-
 432 cantly lighter (i.e., higher luminance) during the post-fertile
 433 phase compared with the pre-fertile phase, but there were no
 434 differences between the fertile phase and the other two cycle
 435 phases (Table 1). Figure 1 presents examples of intra-cycle
 436 variation in hindquarter luminance. Intra-cycle variation in
 437 hindquarter luminance may be perceptible to males under
 438 good light conditions: averaging across JND comparisons to

the lightest value for each female across cycle phases shows 439
 that cycle phases differ in coloration by about 1 JND (Fig. 3). 440

2. Inter-cycle variation 441

442 Models including cycle number better explained the ob- 443
 served color variance in hindquarter redness and facial lumi- 444
 nance (LRTs, respectively: $\chi^2 = 5.90$, $\Delta df = 1$, $P = 0.015$; 445
 $\chi^2 = 6.29$, $\Delta df = 1$, $P = 0.012$). Hindquarters became signifi- 446
 cantly less red and faces lighter as the number of consecutive 447
 menstrual cycles increased (Tables 2 and 3). Models including 448
 conception better explained the observed color variance in 449
 hindquarter redness (LRT: $\chi^2 = 5.20$, $\Delta df = 1$, $P = 0.023$). 450
 Hindquarters were significantly redder during non- 451
 conceptive cycles compared with conceptive ones (Table 2). 452

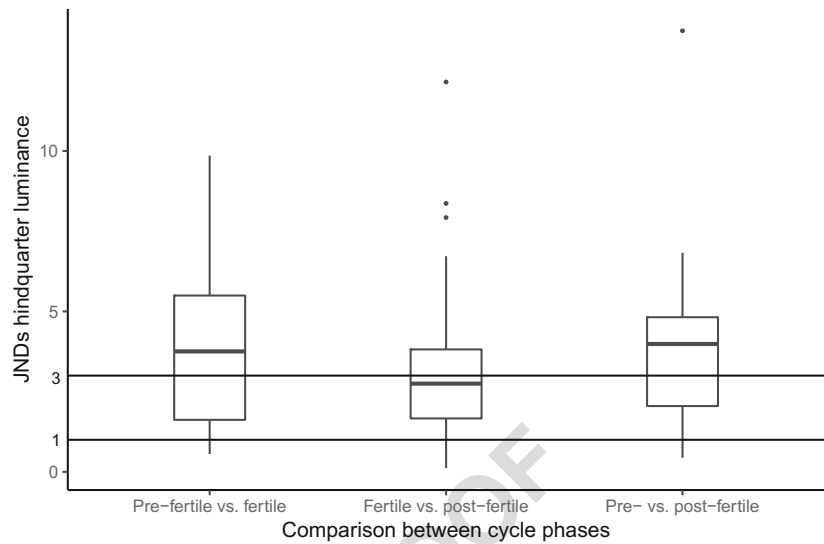
3. Female characteristics 453

454 Models including social rank better explained the observed 455
 color variance in hindquarter luminance and redness (LRTs, 456
 respectively: $\chi^2 = 6.45$, $\Delta df = 1$, $P = 0.011$; $\chi^2 = 4.71$, $\Delta df =$ 457
 1 , $P = 0.030$). High-ranking females had significantly darker 458
 hindquarters and exhibited a trend for redder hindquarters 459
 (Tables 1 and 2, Fig. 4). Female hindquarters or facial color- 460
 ation were not related to parity (LRT, all $P > 0.10$). Models 461
 including body mass better explained the observed color var- 462
 iance in hindquarter redness and facial luminance (LRT, re- 463
 spectively: $\chi^2 = 5.09$, $\Delta df = 1$, $P = 0.024$; $\chi^2 = 3.92$, $\Delta df = 1$, 464
 $P = 0.048$). Heavier females exhibited a trend for redder hind- 465
 quarters and lighter faces (Tables 2 and 3). Differences in skin 466
 coloration between females are highly perceptible for lumi- 467
 nance (mean \pm SD JNDs; face 26.74 ± 3.84 ; hindquarters 468
 21.62 ± 4.99); chromatic variation was less perceptible (mean 469
 \pm SD JNDs; face 1.52 ± 0.85 ; hindquarters 1.93 ± 1.28), but 470
 mean color differences would still be discriminable in good 471
 lighting conditions (i.e., they differ by about 1 JND). Figure 2 472
 presents examples of individual variation in facial luminance. 473

t1.1 **Table 1** Results of LMM examining the relationship between female hindquarter luminance and the tested predictors. For each categorical comparison, the first level indicates the baseline

t1.2	Predictors	Lower CI	Upper CI	Value	Std. error	<i>t</i>	<i>P</i>
t1.3	Cycle number	-0.013	0.158	0.072	0.045	1.626	0.106
t1.4	Rank	-0.208	-0.029	-0.118	0.040	-2.955	0.018
t1.5	Parity	-0.192	0.021	-0.086	0.047	-1.805	0.109
t1.6	Body mass	-0.135	0.063	0.036	0.044	-0.810	0.441
t1.7	Non-conceptive vs. conceptive	-0.141	0.182	0.020	0.084	0.243	0.809
t1.8	Fertile vs. post-fertile phases	-0.020	0.252	0.116	0.071	1.657	0.102
t1.9	Fertile vs. pre-fertile phases	-0.197	0.079	-0.059	0.072	-0.818	0.415
t1.10	Pre- vs. post-fertile phases	0.038	0.312	0.175	0.071	2.462	0.015

Fig. 3 Intra-cycle variation in hindquarter luminance, measured as just noticeable differences (JNDs). JNDs below 1 are not perceptible; differences between 1 and 3 are perceptible under good light conditions, and differences greater than 3 JNDs are perceptible across all lighting conditions. Plot shows the median (black horizontal line), the first and third quartiles (top and bottom of the box), the maximum and minimum JND values (top and lower whiskers), and outliers (points)



474 All factor-level differences not reported here were non-
475 significant (see Tables 1, 2 and 3).

476 **Discussion**

477 Using quantitative and biologically valid measures of coloration,
478 our results show that information regarding inter-cycle
479 differences and specific female characteristics relevant to mate
480 choice is potentially indicated by variation in Japanese macaque
481 skin coloration. Our study demonstrates that female skin
482 (face and hindquarter) coloration (redness and luminance)
483 does not convey reliable information about the timing
484 of the fertile phase, as perceived by the Japanese macaque
485 visual system. Our results instead show that female skin coloration
486 is linked to the number of consecutive cycles, the probability of
487 conception across cycles, female social rank, and potentially body
488 mass prior to the mating season, but not to parity. Observed
489 variation in female coloration is likely perceptible under good
490 light conditions, lending biological

credibility to these results. Future research should assess male
behavior to determine whether this information influences
male mate choice decisions.

Previous studies have showed that female skin coloration
or the size of the colorful trait can indicate reproductive status
or ovulation timing in some primate (Setchell et al. 2006b;
Dubuc et al. 2009; Higham et al. 2010; Burriss et al. 2015)
and lizard species (Galán 2000; Weiss 2002; Jessop et al.
2009). However, we found that female skin coloration does
not accurately indicate the timing of the fertile phase in
Japanese macaques. This suggests that females in this species
either conceal or do not advertise ovulation, at least through
the multiple traits that have been measured, including skin
coloration, proceptive behaviors, estrus, and copulation calls
(O'Neill et al. 2004; Garcia et al. 2009). However, we found
that hindquarter luminance may signal pre- vs. post-ovulation
periods. Changes in skin coloration could be a by-product of
changes in the concentration of circulating hormones over the
course of the cycle, but they may also serve a signaling function
if males attend to this signal. Females may benefit from

t2.1 **Table 2** Results of LMM examining the relationship between hindquarter redness and the tested predictors. For each categorical comparison, the first level indicates the baseline

t2.2 Predictors	Lower CI	Upper CI	Value	Std. error	t	P
t2.3 Cycle number	-0.165	-0.018	-0.091	0.038	-2.385	0.019
t2.4 Rank	-0.003	0.122	0.060	0.028	2.128	0.066
t2.5 Parity	-0.105	0.052	-0.027	0.035	-0.760	0.469
t2.6 Body mass	-0.001	0.146	0.072	0.033	2.211	0.058
t2.7 Non-conceptive vs. conceptive	-0.279	-0.021	-0.150	0.067	-2.237	0.027
t2.8 Fertile vs. post-fertile phases	-0.126	0.123	-0.002	0.065	-0.024	0.981
t2.9 Fertile vs. pre-fertile phases	-0.184	0.069	-0.057	0.066	-0.869	0.387
t2.10 Pre- vs. post-fertile phases	-0.069	0.181	0.056	0.065	0.856	0.394

t3.1 **Table 3** Results of LMM examining the relationship between female facial luminance and the tested predictors. For each categorical comparison, the first level indicates the baseline

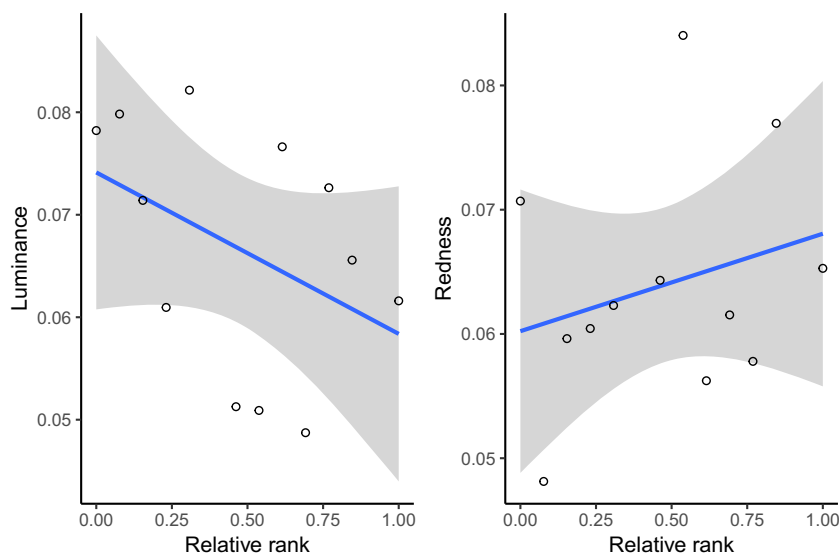
t3.2	Predictors	Lower CI	Upper CI	Value	Std. error	<i>t</i>	<i>P</i>
t3.3	Cycle number	0.020	0.157	0.088	0.035	2.492	0.014
t3.4	Rank	-0.142	0.049	-0.047	0.043	-1.102	0.303
t3.5	Parity	-0.064	0.150	0.043	0.048	0.897	0.396
t3.6	Body mass	-0.005	0.192	0.093	0.044	2.119	0.067
t3.7	Non-conceptive vs.ceptive	-0.041	0.243	0.101	0.074	1.365	0.175
t3.8	Fertile vs. post-fertile phases	-0.092	0.107	0.007	0.052	0.144	0.886
t3.9	Fertile vs. pre-fertile phases	-0.092	0.111	0.010	0.053	0.185	0.853
t3.10	Pre- vs. post-fertile phases	-0.102	0.098	-0.002	0.052	-0.045	0.964

511 signaling ovulation probability across the cycle while
 512 concealing its exact timing. Concealing the timing of ovula-
 513 tion could reduce monopolization by higher-ranking males
 514 while increasing the pool of potential mates, therefore simul-
 515 taneously confusing paternity across males and decreasing the
 516 risk of infanticide (van Schaik 2000; van Schaik et al. 2000,
 517 2004). In species with polygynandrous mating and relatively
 518 high reproductive synchrony, males are less able to monopo-
 519 lize access to all fertile females and multiple fertile females
 520 may be competing for the same males. This can result in an
 521 increase in intra-sexual competition (in both females and
 522 males) and in selection for the trait to be informative about
 523 differences between females. Males that chose between fe-
 524 males based on their hindquarter coloration would benefit if
 525 such signals indicate a female's reproductive value. This is
 526 consistent with the promiscuous nature of Japanese macaques
 527 mating activity, with females having multiple partners, active-
 528 ly discriminating between mates, and engaging in sneak cop-
 529 ulations, and with the alpha male not being able to monopolize
 530 all conceptions (Huffman 1992; Inoue et al. 1993; Soltis et al.

1997; Hayakawa 2007; Inoue and Takenaka 2008; Fujita 531
 2010). 532

Female hindquarters were redder during non-conceptive 533
 cycles and became less red as the number of consecutive cy- 534
 cles increased. This color change across cycles may be a sig- 535
 nal indicating the probability of conception that could be used 536
 by males to optimally allocate mating efforts to the first men- 537
 strual cycle. However, in our sample, females conceived dur- 538
 ing the beginning of the mating season (November– 539
 December) from their first ($N=2$ females) or second cycle 540
 ($N=3$ females), such that being the first or second cycle, 541
 and being theceptive cycle, are confounded. As such, 542
 the relationship between hindquarter redness and the proba- 543
 bility of conception across cycles may be due to the fact that 544
 females happened to conceive in early cycles in this species, 545
 rather than because of a direct relationship between skin study, 546
 we found coloration and conception. In our previous that fe- 547
 male face luminance varied between pre- and post-conception 548
 months (Rigaill et al. 2015). The fact that in the present study 549
 only hindquarter redness was related to conception is 550

Fig. 4 Variation in hindquarter luminance and redness across female relative social rank. Each dot represents the mean intra-cycle value in hindquarters coloration per female (controlled for cycle number). Blue lines indicate the linear fits with their 95% confidence intervals (shaded grey)



551 puzzling. Hindquarter coloration may be more sensitive to
 552 changes in the ratio of sex hormones either between cycle
 553 phases (luminance) or around egg fertilization (redness), while
 554 face coloration may indicate changes across longer periods
 555 (cycling vs. pregnancy periods). Further studies on tissue-
 556 specific expression in estrogen receptor sensitivity (in face
 557 and hindquarter areas) would help to clarify this question.

558 Female skin coloration also appears to be potentially infor-
 559 mative about some specific individual characteristics. So far, a
 560 relationship between social rank and skin coloration had only
 561 been reported for males in primates (face: Setchell and
 562 Wickings 2005; Marty et al. 2009; chest: Bergman et al.
 563 2009) as well as in birds (Pryke et al. 2002; Mennill et al.
 564 2003), fishes (Barlow 1973; Barlow and Wallach 1976;
 565 Volpato et al. 2003), and lizards (Thompson and Moore
 566 1991; Martín and López 2009). Our study is the first to report
 567 this relationship for females in a primate species, with higher
 568 ranking females having darker and redder hindquarters.
 569 However, these differences in skin coloration may potentially
 570 be more related to female lineage than social rank per se. In
 571 this species, females typically acquire ranks just below those
 572 of their mothers, meaning that all females of a given matriline
 573 have similar social ranks (Koyama 1967). There is evidence
 574 that skin coloration is heritable in another macaque species
 575 (rhesus macaques: Dubuc et al. 2014b). Therefore, the appar-
 576 ent effect of social rank on skin coloration could instead be
 577 due to genetic inheritance, in which females inherit both
 578 higher dominance and redder/darker hindquarters from their
 579 mother. Regarding the relationship between female condition
 580 and coloration, we hypothesized that females who were heav-
 581 er prior to the mating season would be redder and darker;
 582 however, our results do not fully support this prediction. The
 583 relationship between skin coloration and body mass is still
 584 equivocal in female (Setchell and Wickings 2004a; Setchell
 585 et al. 2006b; Rigail et al. 2017) and male (Higham et al. 2013)
 586 primates, and further studies compiling larger datasets are
 587 needed to investigate this particular question. We found that
 588 variation in female skin coloration did not correlate with par-
 589 ity, in agreement with our previous results from another pop-
 590 ulation of Japanese macaques (Rigail et al. 2017). Our results
 591 differ to previous findings from other primates (mandrills:
 592 Setchell et al. 2006b; olive baboons: Higham et al. 2008;
 593 rhesus macaques: Dubuc et al. 2014b), birds (Amundsen
 594 2000; Pilastro et al. 2003; Jawor et al. 2004; Doutrelant
 595 et al. 2008; Griggio et al. 2009), lizards (Weiss 2002, 2016;
 596 Weiss et al. 2009), and insects (LeBas et al. 2003) in which
 597 female colorful traits correlate with indices of fecundity.
 598 While skin coloration may reflect different female character-
 599 istics across species, the larger data sets of the previous pri-
 600 mate studies may have also provided better statistical power to
 601 highlight the link between female skin coloration and parity.
 602 In long-lived and social species, group-member males may
 603 not need a visual signal of female characteristics, as these

604 males may have accumulated knowledge about female social 604
 605 rank or reproductive history across breeding years (Sheehan 605
 606 and Bergman 2015), yet such a signal may be of interest for 606
 607 newly immigrant and peripheral males. Extra-group copula- 607
 608 tions are not rare in mammals, including in primates (Isvaran 608
 609 and Clutton-Brock 2007; Mitani et al. 2012). In the absence of 609
 610 clear ovulatory signaling, “naïve” males may thus use female 610
 611 skin coloration to make their mating decisions and copulate 611
 612 with females which are more likely to conceive (i.e., discrim- 612
 613 inating across cycles and among females). Face coloration 613
 614 could therefore play a role in modulating female and male 614
 615 reproductive success through intra-sexual competition. 615

616 Our study adds to the growing evidence that female 616
 617 coloration may serve different signaling functions across 617
 618 species by showing that sexual skin color can signal 618
 619 inter-cycle variation and some female characteristics in 619
 620 a primate species lacking obvious ovulatory signaling. 620
 621 Future studies should investigate more deeply the role 621
 622 of female skin coloration in driving mating strategies 622
 623 and sexual communication by examining the relation- 623
 624 ship between sexual behaviors, skin coloration, repro- 624
 625 ductive status, individual characteristics, and indices of 625
 626 quality (e.g., heritable traits). Such research would help 626
 627 answer outstanding questions in this system, such as the 627
 628 following: does female coloration correlate with herita- 628
 629 ble traits associated with higher reproductive success? 629
 630 Do males prefer redder/darker females? Does female 630
 631 coloration co-vary with behavioral, auditory, and olfacto- 631
 632 ry traits to signal inter- and intra-cycle variation? 632
 633 Studies addressing these questions will help to clarify 633
 634 if and why males and females attend to this colorful 634
 635 trait in Japanese macaques. Ultimately, this research 635
 636 helps to clarify the underlying mechanisms leading to 636
 637 the development of female colorful traits. 637

638 **Acknowledgments** We thank Amélie Chimènes for her help with the 638
 639 preparation of the digital photography. We also thank The Center for 639
 640 Human Evolution Modeling Research of the Primate Research Institute 640
 641 and M.A. Huffman for use of the primate facilities. We thank Prof. David 641
 642 P. Watts and two anonymous reviewers for their constructive comments 642
 643 on earlier versions of this manuscript. 643

644 **Funding information** This work was financially supported by the Centre 644
 645 National de la Recherche Scientifique (France) to CG. LR is currently 645
 646 funded by the Human and Nature Interlaced Life Science Unit (Kyoto 646
 647 University, Japan) Research Coordination Alliance. 647
 648

649 **Compliance with ethical standards**

650 **Conflict of interest** The authors declare that they have no conflict of 650
 651 interest. 651

652 **Ethical approval** The Center for Human Evolution Modeling Research 652
 653 of the Primate Research Institute reviewed and approved our research 653
 654 protocol in agreement with the Guidelines for the Care and Use of 654
 655 Nonhuman Primates of the Kyoto University Primate Research Institute. 655

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