



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

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Abstract

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.

Significance statement

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.

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

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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

colorful signals in relation to reproductive success and female preferences has been well studied across taxa (Andersson 1994; Andersson and Simmons 2006; Clutton-Brock 2007). However, there is no reason to expect that, even if one sex is choosy, the other sex should nonetheless not choose or discriminate between mates too, particularly when mating is associated with energetic costs and risks of disease transmission (Thrall et al. 2000; Edward and Chapman 2011; Lukas and Clutton-Brock 2014). Indeed, there is increasing evidence that females also display colorful traits which are attractive to males in birds (Amundsen 2000; Torres and Velando 2005; Griggio et al. 2005, 2009), lizards (LeBas and Marshall 2000; Weiss 2002; Baird 2004), fishes (Amundsen and Forsgren 2001, 2003), and insects (Hopkins et al. 2015). It is therefore important to investigate the information content and potential signaling function of these female colorful traits in relation to mating strategies and reproductive success.

Primates are the most colorful group of mammals, with males and females of many species expressing red skin coloration of the face, chest, ano-genital area, and hindquarters (Dixson 2012). Male skin coloration has been found to correlate with some aspects of male-male competition, such as dominance rank or one-male unit holding status (mandrills, *Mandrillus sphinx*: Setchell and Dixson 2001; geladas, *Theropithecus gelada*: Bergman et al. 2009; drills, *Mandrillus leucophaeus*: Marty et al. 2009; snub-nosed monkeys, *Rhinopithecus bieti*: Grueter et al. 2015), or to predict the likelihood of aggression (rhesus macaques, *Macaca mulatta*: Petersdorf et al. 2017). Male coloration, independently of social rank, can also influence attractiveness to females and mating success in rhesus macaques (Waitt et al. 2003; Dubuc et al. 2014a, 2015). Thus, male coloration can evolve under intra- or inter-sexual selection in primates. Perhaps partly as a result, studies of the role of primate female non-specific colorful traits (i.e., traits expressed by both sexes) may have been limited by the classic view of sexual selection that emphasizes male competition and female choice. Female coloration may indeed represent a by-product or a “correlated response” of selection for ornamentation in males (Lande 1980), with no clear adaptive value in females. Thereby, the expression of colorful traits in females could be maintained because they do not impose any costs on females, although it is complicated to accurately assess such signaling costs.

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

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

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

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

Our study aims to identify the potential information content of female Japanese macaque faces and hindquarters in a mating context, to determine whether skin coloration (redness and luminance) is informative about intra-cycle variation (timing of the fertile phase), inter-cycle variation (number of consecutive cycles, conception probability), and individual characteristics (social rank, body mass, and parity or age).

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

consecutive cycles increases. We also predict that conceptive cycles will be darker/redder compared with non-conceptive cycles.

3. Individual characteristics. If social rank influences female skin coloration, we predict that higher-ranking females will be darker/redder than lower-ranking females. Similarly, if there is a relationship between female body mass and skin coloration, we predict that females that were heavier prior to the beginning of the mating season will be darker/redder than lighter females. Finally, if parity (or age) influences skin coloration, we predict that females with higher parity (or older females) will have darker/redder faces or hindquarters.

Methods

Subjects and housing

We collected data during the 2011–2012 mating season, from early November to late January, from a captive population of Japanese macaques living in a 1210-m² outdoor enclosure at the Primate Research Institute of Kyoto University (KUPRI, Inuyama, Japan). The group was composed of 39 individuals: 13 adult females (mean \pm SD = 10.64 \pm 6.84 years old, range = 5–27), 6 sexually immature females (2.79 \pm 0.81 years old, range = 1–4), 3 adult males (10.67 \pm 3.06 years old, range = 8–14), 12 sexually immature males (2.99 \pm 1.05 years old, range = 1–4), and 5 infants less than 1 year old. Animals were fed twice daily between 11:00 a.m. and 12:00 p.m. and between 4:00 p.m. and 5:00 p.m. Water was supplied *ad libitum*. Animal care and maintenance comply with the current laws of Japan, which are in accordance with NIH standards. All adult (> 5 years old) and sexually active females in this group ($N = 13$ females) were included in this study. We did not include subadult females to avoid confounding factors due to maturational age, and because subadult females do not conceive and may have unusual menstrual cycles and patterns of circulating reproductive hormones. Females were naturally cycling, i.e., with no hormonal contraceptive treatment. Female social ranks were monitored using focal (total 524 \times 30-min focal observation, five focal observations per week per female) and *ad libitum* observations evenly distributed during the study period and were assessed by transcribing agonistic interactions for which a clear win/loss outcome was identified into an agonistic interaction matrix. We calculated the normalized David's score (NDS) to assess female social rank positions (de Vries et al. 2006). Female parity (total number of infants born divided by the number of years post-adulthood, defined as 5 years old)

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

Hormonal analyses and determination of ovulation dates

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

Assessment of skin coloration—redness and luminance

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

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

Data analysis

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

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



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

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

To analyze variation in female redness and luminance, we 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)

the residuals and plots of the residuals against fitted values. We also calculated the conditional and marginal coefficients of determination (R^2c and R^2m) of all full models using the package MuMIn (Nakagawa and Schielzeth 2013).

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

Results

Hindquarter redness and luminance co-varied; females with redder hindquarters also had darker hindquarters (LRT: $\chi^2 = 8.10$, $\Delta df = 1$, $P = 0.044$). Facial redness and luminance also co-varied; females with redder faces also had darker faces (LRT: $\chi^2 = 3.73$, $\Delta df = 1$, $P = 0.05$). Comparisons between full and null models showed that hindquarter luminance, hindquarter redness, and facial luminance were related to the tested female predictors (LRTs: hindquarter luminance: $\chi^2 = 15.65$, $\Delta df = 7$, $P = 0.029$, $R^2m = 0.15$, $R^2c = 0.18$; hindquarter redness: $\chi^2 = 24.97$, $\Delta df = 7$, $P < 0.001$, $R^2m = 0.18$, $R^2c = 0.18$; facial luminance: $\chi^2 = 15.16$, $\Delta df = 7$, $P = 0.034$, $R^2m = 0.16$, $R^2c = 0.29$). Facial redness was not related to the tested predictors ($\chi^2 = 5.71$, $\Delta df = 7$, $P = 0.57$, $R^2m = 0.05$, $R^2c = 0.13$).

1. Intra-cycle variation

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

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

2. Inter-cycle variation

Models including cycle number better explained the observed color variance in hindquarter redness and facial luminance (LRTs, respectively: $\chi^2 = 5.90$, $\Delta df = 1$, $P = 0.015$; $\chi^2 = 6.29$, $\Delta df = 1$, $P = 0.012$). Hindquarters became significantly less red and faces lighter as the number of consecutive menstrual cycles increased (Tables 2 and 3). Models including conception better explained the observed color variance in hindquarter redness (LRT: $\chi^2 = 5.20$, $\Delta df = 1$, $P = 0.023$). Hindquarters were significantly redder during non-conceptive cycles compared with conceptive ones (Table 2).

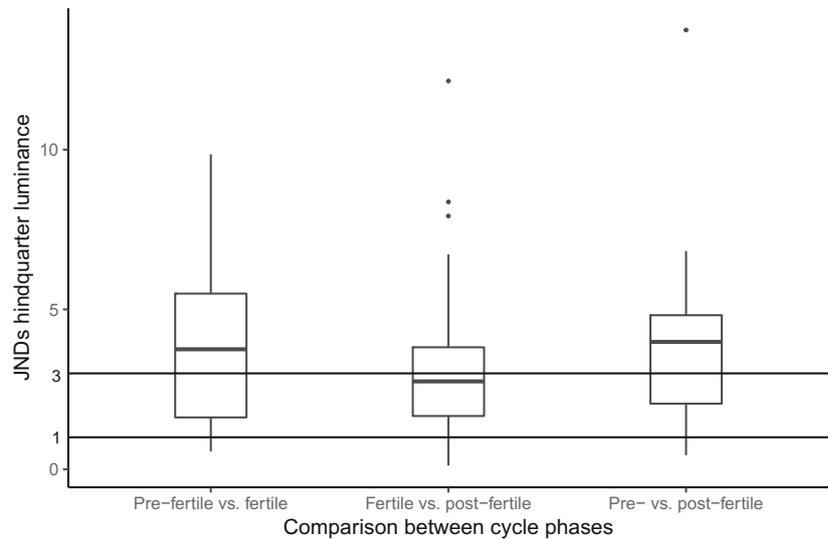
3. Female characteristics

Models including social rank better explained the observed color variance in hindquarter luminance and redness (LRTs, respectively: $\chi^2 = 6.45$, $\Delta df = 1$, $P = 0.011$; $\chi^2 = 4.71$, $\Delta df = 1$, $P = 0.030$). High-ranking females had significantly darker hindquarters and exhibited a trend for redder hindquarters (Tables 1 and 2, Fig. 4). Female hindquarters or facial coloration were not related to parity (LRT, all $P > 0.10$). Models including body mass better explained the observed color variance in hindquarter redness and facial luminance (LRT, respectively: $\chi^2 = 5.09$, $\Delta df = 1$, $P = 0.024$; $\chi^2 = 3.92$, $\Delta df = 1$, $P = 0.048$). Heavier females exhibited a trend for redder hindquarters and lighter faces (Tables 2 and 3). Differences in skin coloration between females are highly perceptible for luminance (mean \pm SD JNDs; face 26.74 ± 3.84 ; hindquarters 21.62 ± 4.99); chromatic variation was less perceptible (mean \pm SD JNDs; face 1.52 ± 0.85 ; hindquarters 1.93 ± 1.28), but mean color differences would still be discriminable in good lighting conditions (i.e., they differ by about 1 JND). Figure 2 presents examples of individual variation in facial luminance. All factor-level differences not reported here were non-significant (see Tables 1, 2 and 3).

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

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



Discussion

Using quantitative and biologically valid measures of coloration, our results show that information regarding inter-cycle differences and specific female characteristics relevant to mate choice is potentially indicated by variation in Japanese macaque skin coloration. Our study demonstrates that female skin (face and hindquarter) coloration (redness and luminance) does not convey reliable information about the timing of the fertile phase, as perceived by the Japanese macaque visual system. Our results instead show that female skin coloration is linked to the number of consecutive cycles, the probability of conception across cycles, female social rank, and potentially body mass prior to the mating season, but not to parity. Observed variation in female coloration is likely perceptible under good 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 signaling ovulation probability across the cycle while concealing its exact timing. Concealing the timing of

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

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

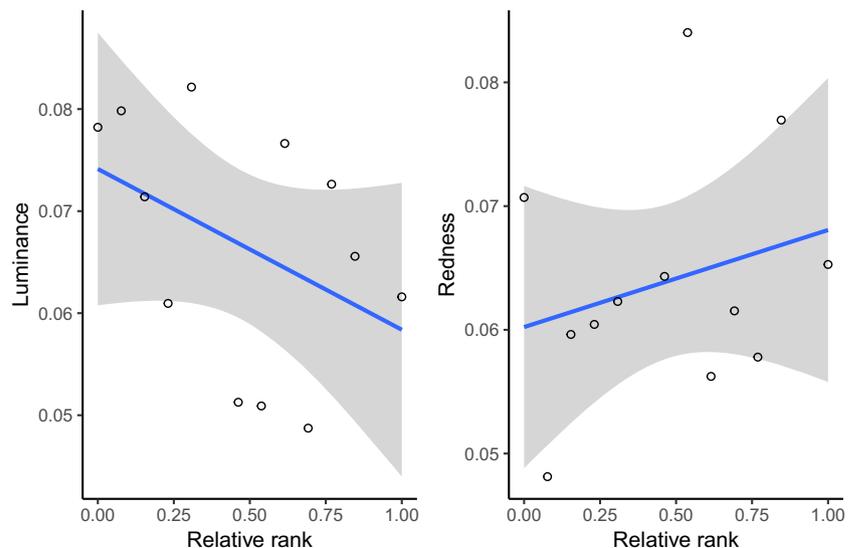
Table 3 Results of LMM examining the relationship between female facial luminance and the tested predictors. For each categorical comparison, the first level indicates the baseline

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

ovulation could reduce monopolization by higher-ranking males while increasing the pool of potential mates, therefore simultaneously confusing paternity across males and decreasing the risk of infanticide (van Schaik 2000; van Schaik et al. 2000, 2004). In species with polygynandrous mating and relatively high reproductive synchrony, males are less able to monopolize access to all fertile females and multiple fertile females may be competing for the same males. This can result in an increase in intra-sexual competition (in both females and males) and in selection for the trait to be informative about differences between females. Males that chose between females based on their hindquarter coloration would benefit if such signals indicate a female's reproductive value. This is consistent with the promiscuous nature of Japanese macaques mating activity, with females having multiple partners, actively discriminating between mates, and engaging in sneak copulations, and with the alpha male not being able to monopolize all conceptions (Huffman 1992; Inoue et al. 1993; Soltis et al. 1997; Hayakawa 2007; Inoue and Takenaka 2008; Fujita 2010).

Female hindquarters were redder during non-conceptive cycles and became less red as the number of consecutive cycles increased. This color change across cycles may be a signal indicating the probability of conception that could be used by males to optimally allocate mating efforts to the first menstrual cycle. However, in our sample, females conceived during the beginning of the mating season (November–December) from their first ($N=2$ females) or second cycle ($N=3$ females), such that being the first or second cycle, and being theceptive cycle, are confounded. As such, the relationship between hindquarter redness and the probability of conception across cycles may be due to the fact that females happened to conceive in early cycles in this species, rather than because of a direct relationship between skin coloration and conception. In our previous study, we found that female face luminance varied between pre- and post-conception months (Rigail et al. 2015). The fact that in the present study only hindquarter redness was related to conception is puzzling. Hindquarter coloration may be more sensitive to changes in the ratio of sex hormones either between cycle

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)



phases (luminance) or around egg fertilization (redness), while face coloration may indicate changes across longer periods (cycling vs. pregnancy periods). Further studies on tissue-specific expression in estrogen receptor sensitivity (in face and hindquarter areas) would help to clarify this question.

Female skin coloration also appears to be potentially informative about some specific individual characteristics. So far, a relationship between social rank and skin coloration had only been reported for males in primates (face: Setchell and Wickings 2005; Marty et al. 2009; chest: Bergman et al. 2009) as well as in birds (Pryke et al. 2002; Mennill et al. 2003), fishes (Barlow 1973; Barlow and Wallach 1976; Volpato et al. 2003), and lizards (Thompson and Moore 1991; Martín and López 2009). Our study is the first to report this relationship for females in a primate species, with higher ranking females having darker and redder hindquarters. However, these differences in skin coloration may potentially be more related to female lineage than social rank per se. In this species, females typically acquire ranks just below those of their mothers, meaning that all females of a given matriline have similar social ranks (Koyama 1967). There is evidence that skin coloration is heritable in another macaque species (rhesus macaques: Dubuc et al. 2014b). Therefore, the apparent effect of social rank on skin coloration could instead be due to genetic inheritance, in which females inherit both higher dominance and redder/darker hindquarters from their mother. Regarding the relationship between female condition and coloration, we hypothesized that females who were heavier prior to the mating season would be redder and darker; however, our results do not fully support this prediction. The relationship between skin coloration and body mass is still equivocal in female (Setchell and Wickings 2004a; Setchell et al. 2006b; Rigail et al. 2017) and male (Higham et al. 2013) primates, and further studies compiling larger datasets are needed to investigate this particular question. We found that variation in female skin coloration did not correlate with parity, in agreement with our previous results from another population of Japanese macaques (Rigail et al. 2017). Our results differ to previous findings from other primates (mandrills: Setchell et al. 2006b; olive baboons: Higham et al. 2008; rhesus macaques: Dubuc et al. 2014b), birds (Amundsen 2000; Pilastro et al. 2003; Jawor et al. 2004; Doutrelant et al. 2008; Griggio et al. 2009), lizards (Weiss 2002, 2016; Weiss et al. 2009), and insects (LeBas et al. 2003) in which female colorful traits correlate with indices of fecundity. While skin coloration may reflect different female characteristics across species, the larger data sets of the previous primate studies may have also provided better statistical power to highlight the link between female skin coloration and parity. In long-lived and social species, group-member males may not need a visual signal of female

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

Our study adds to the growing evidence that female coloration may serve different signaling functions across species by showing that sexual skin color can signal inter-cycle variation and some female characteristics in a primate species lacking obvious ovulatory signaling. Future studies should investigate more deeply the role of female skin coloration in driving mating strategies and sexual communication by examining the relationship between sexual behaviors, skin coloration, reproductive status, individual characteristics, and indices of quality (e.g., heritable traits). Such research would help answer outstanding questions in this system, such as the following: does female coloration correlate with heritable traits associated with higher reproductive success? Do males prefer redder/darker females? Does female coloration co-vary with behavioral, auditory, and olfactory traits to signal inter- and intra-cycle variation? Studies addressing these questions will help to clarify if and why males and females attend to this colorful trait in Japanese macaques. Ultimately, this research helps to clarify the underlying mechanisms leading to the development of female colorful traits.

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Compliance with ethical standards

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

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