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Does male mate choice select for female coloration in a promiscuous primate species?

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Abstract

The traditional view of sex roles and sexual selection emphasises the evolution of male ornaments as a result of female mate choice and male-male competition. Female ornaments are now receiving more attention, although their roles in mating decisions are still less well understood, especially considering cases in which colourful ornaments are expressed by both sexes. In this study, we analysed whether female skin coloration (luminance and redness of the face and hindquarters) influenced male mate choice and sexual behaviours in relation to intra-cycle (cycle phase), inter-cycle (number of consecutive cycles, conceptive nature of the cycle), and inter-individual (age, social rank, weight, and parity) variation in a captive social group of Japanese macaques (*Macaca fuscata*). Males did not preferentially choose darker/redder females. Moreover, males did not appear to use female skin coloration to apportion their mating efforts on the fertile phase of the menstrual cycle or during cycles that lead to conception, or to discriminate between females. Collectively, our results suggest that female skin coloration may not have been sexually selected in this species and that males mated regardless of such variation across females. To our knowledge, our study is among the few to report a lack of male choice for female coloration in a species where both sexes display ornamentation. Our findings provide novel insights on the role and evolution of female coloration in sexual signalling and mating decisions.

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

Introduction

Mate choice is a crucial process in reproduction. Individuals have to simultaneously choose and avoid potential mates based on the expected benefits (e.g., good genes, social support, reproductive success) and costs (e.g., disease transmission, energy costs, intra-sexual competition) associated with mating (Beltran-Bech & Richard, 2014; Møller et al., 1999; Thrall et al., 2000; Trivers, 1972). The traditional view of sex roles and sexual selection has emphasised the relationship between female mate choice and male competition, and, as a consequence, the function of male ornaments has been well studied (Andersson & Simmons, 2006, 2006; Cunningham & Birkhead, 1998; Fitzpatrick & Servedio, 2017). Perhaps partly as a result, the role of male mate choice on the evolution of female traits has been relatively less investigated. However, males too undergo energetic costs from mating due to courtship displays, mate guarding, and production of ejaculates (Balshine et al., 2002; Dewsbury, 1982; Harshman & Zera, 2007; Lukas & Clutton-Brock, 2014). Similarly, female competition can also arise when females vary in reproductive quality or when the number of females exceeds male mating or mate-guarding capacities such as in cases with a high ovarian cycle synchrony or with a female-biased operational sex ratio, i.e., ‘the ratio of fertile males to potentially fertile females ready to mate in a group at a given time’ (Amundsen, 2000; Bonduriansky, 2001; Edward & Chapman, 2011; Kvarnemo & Ahnesjö, 1996). Thus, male mate choice or mutual mate choice can evolve in some species to balance the ratio of costs/benefits inherent in mating (T. Clutton-Brock, 2007; Fitzpatrick & Servedio, 2018; Johnstone et al., 1996; Kokko et al., 2003).

There is increasing evidence that males discriminate among possible mates in species with traditional and reversed-sex roles and with different mating systems (from monogamy to polygynandry). Males may choose older females that have already successfully reproduced and raised offspring (spiny-footed lizards, *Acanthodactylus erythrurus*: Belliure et al., 2018; chimpanzees, *Pan troglodytes*: Muller et al., 2006; brown widow spiders, *Latrodectus geometricus*: Waner et al., 2018). Males may also choose females of higher social ranks

compared with lower-ranking ones. This may be particularly adaptative in species where social rank is maternally inherited: higher-ranking offspring may achieve better condition and higher survival than lower-ranking offspring (e.g., mandrills, *Mandrillus sphinx*: Setchell & Wickings, 2006). Males may also choose to mate with females which haven't yet copulated to reduce sperm competition and increase their reproductive success (house crickets, *Acheta domesticus*: Assis et al., 2017; wolf spiders, *Schizocosa ocreata*: Roberts & Uetz, 2005). To mate selectively, males may thus rely on female signals and/or express preferences for female traits that correlate with reproductive quality, such as pheromones (widow spiders, *Lactrodectus hesperus*: Baruffaldi & Andrade, 2015; humans, *Homo sapiens*: Gildersleeve et al., 2012; wolf spiders: Roberts & Uetz, 2005), body size (long-tailed dance flies, *Rhamphomyia longicauda*: Funk & Tallamy, 2000; LeBas et al., 2003; stalk-eyed flies, *Diasemopsis meigenii*: Harley et al., 2013; rainbow darters, *Etheostoma caeruleum*: Soudry et al., 2020; hermit crabs, *Pagurus middendorffii*: Wada et al., 2011), or vocal pitch (humans: Pisanski et al., 2018).

Among female traits, colourful ornaments have received more attention than others. In some species, females express sex-specific colourful ornaments whose colour and/or size are attractive to males. Such colourful ornaments are likely to be sexually selected traits as they correlate with indices of fecundity, such as sexual or egg maturity, readiness to spawn, brood size, or offspring condition (two-spotted gobies, *Gobiusculus flavescens*: Amundsen & Forsgren, 2001; collared lizards, *Crotaphytus collaris*: Baird, 2004; cichlid fishes, *Pelvicachromis taeniatus*: Baldauf et al., 2011; blue crabs, *Calinectes sapidus*: Baldwin & Johnsen, 2012; spiny-footed lizards: Belliure et al., 2018; cichlid fishes, *Mikrogeophagus ramizeri*: LaPlante & Delaney, 2020; pygmy halbeaks, *Dermogenys collettei*: Ogden et al., 2020; striped plateau lizards, *Sceloporus virgatus*: Weiss, 2002, 2016). Comparatively, the role of non-sex-specific colourful ornaments (i.e., ornaments expressed by both sexes) on male mate choice is still poorly understood. Female coloration may indeed represent a genetically

correlated response of selection for male traits with no clear adaptive value in females (Lande, 1980). Males may thus express no preference for such traits (three spined sticklebacks, *Gasterosteus aculeatus*: Wright et al., 2015) or preference may be merely explained by sensory exploitation rather than sexual selection (sockeye salmon, *Oncorhynchus nerka*: Foote et al., 2004). Alternatively, males can express preferences toward non-sex-specific colourful ornaments that reflect female reproductive state (rhesus macaque, *Macaca mulatta*: Dubuc et al., 2009; Higham et al., 2010, 2011, 2021; agamid lizards, *Ctenophorus ornatus*: LeBas & Marshall, 2000) or reproductive success (blue tits, *Cyanistes caeruleus*: Doutrelant et al., 2008, 2012; Mahr et al., 2012; rhesus macaques: Dubuc, Winters, et al., 2014; Higham et al., 2021; rock sparrows, *Petronia petronia*: Pilastro et al., 2003; Griggio et al., 2009, 2005; brown boobies, *Sula leucogaster*: Montoya et al., 2018; blue-footed boobies, *Sula nebouxii*: Torres & Velando, 2005). Therefore, in these species, female colourful ornaments may be key components of mating strategies and reproductive success of both males and females.

Here, we examine the potential role of female coloration on male mate choice in a promiscuous primate species, the Japanese macaque (*Macaca fuscata*). Female mate choice has been suggested as an important process modulating mating strategies in this species (Fujita, 2010). However, this does not mean that males should not choose or discriminate among potential mates. While their parental investment is mostly restricted to gamete contribution, male Japanese macaques deal with high costs associated with mating. Japanese macaques are seasonal breeders and multi-mount ejaculators and thus invest a non-negligible portion of their daily energy expenditure for somatic maintenance and mating itself (Fooden & Aimi, 2005; Matsubara, 2003; Thomsen et al., 2006). Like males of other species, male Japanese macaques also face physical and physiological costs associated with extended consortships and mate-guarding, reduced feeding activity, and male-male aggression leading to increased vigilance, injuries, or chronic stress (e.g., in several mammal species including primates: Alberts et al.,

1996; Girard-Buttoz et al., 2014; Higham & Maestriperi, 2014; Lukas & Clutton-Brock, 2014; Thompson & Georgiev, 2014). Males would thus benefit from discriminating among females and to focus their mating effort on mates that are fertile and of “good quality”. In Japanese macaques, both sexes express face and hindquarter red skin coloration (luminance: how light/dark the skin appears, redness: related to the colour of the blood itself) which is regulated through sex hormone secretion (Fooden & Aimi, 2005). Recent studies provided more insight into the potential signal content of female coloration in this species. Hindquarter coloration may signal the intra-cycle probability of ovulation while concealing its exact timing and face coloration may indicate early pregnancy (Rigaill et al., 2015, 2019). Hindquarter coloration may also contain information about the inter-cycle probability of conception (Rigaill et al., 2019). Lastly, there is some evidence that skin coloration may reflect inter-individual variation (e.g., social rank, weight, but not parity, Rigaill et al., 2017, 2019). Pflüger and colleagues (2014) showed that males increased attention toward an experimentally intense red-coloured version of an unknown female face. Thus, female coloration may be a sexually selected trait involved in mate choice in Japanese macaques if males appropriately use this colourful trait to inform their mating decisions. Yet, to our knowledge, no study has tested this hypothesis in a non-forced-choice discrimination situation.

Our study thus aims at identifying the potential role of female Japanese macaque face and hindquarter coloration (luminance and redness) on the likelihood that a male will engage or maintain sexual interactions with a female. If males use female coloration to make their mating decisions as suggested by previous studies (Pflüger et al., 2014; Rigaill et al., 2015, 2019), we hypothesised that males should display more sexual behaviours toward darker/redder (i.e., stronger signal) females. We further hypothesised that the relationship between male response and female coloration should vary according to a) intra-cycle (timing of the fertile phase), b) inter-cycle (number of consecutive cycles and conceptive nature of the cycles),

and/or c) inter-individual (age, social rank, weight, and parity) variation. If so, we predicted a positive relationship between male sexual behaviours and darker/redder female coloration a) when the likelihood of ovulation is the highest (i.e., during the fertile phase vs. prefertile and post-fertile phases), b) during cycles that lead to conception (i.e., during conceptive cycles and the first cycles of a given mating season), and/or c) with older, higher ranking, heavier, and possibly multiparous females.

Methods

Ethical note

Our research protocol was reviewed and approved by the Center for Human Evolution Modeling Research of the Primate Research. Our methods are in agreement with the Guidelines for the Care and Use of Nonhuman Primates of the Kyoto University Primate Research Institute.

Subjects

We conducted our data collection during the 2011-2012 mating season, from early November to late January. We collected data from a captive social group of 39 Japanese macaques living in a 1,210 m² outdoor enclosure at Kyoto University Primate Research Institute (KUPRI, Inuyama, Japan). Group composition was as follow: 13 adult females (> five years, mean $\pm$ SD = 10.64 ± 6.84 years, range = 5-27), 6 sexually immature females (2.79 ± 0.81 years, range = 1-4), 3 adult males (> six years, 10.67 ± 3.06 years, range = 8-14), 12 sexually immature males (2.99 ± 1.05 years, range = 1-4), and 5 infants less than one year old. We only selected all sexually active adults as focal subjects to limit the potential effects of maturational age on traits, ovarian cyclicity, and mating decisions (see Table A1 for female characteristics). The group composition is similar to other captive and wild populations from studies of sexual behaviours and mating strategies (Fooden & Aimi, 2005; Fujita, 2010). The Center for Human Modeling

Research of KUPRI provided data on female age and weight calculated at the beginning of the mating season (to the nearest 100g). Parity was calculated by dividing the total number of infants born by the number of years post-adulthood. Animals had *ad libitum* access to water and were provided with food twice a day.

Behavioral observations

One observer collected behavioural data using 30-min continuous focal samples every day for 3 months (7:00 AM to 5:00 PM). We used a female-centered approach because of the need to assess female trait variation in order to address the question of male responses. We equally distributed focal samples across days and between females to follow each focal female 2 hours per week. We recorded all occurrence social and sexual behaviours directed by the focal female and received from any identified adult male: i.e., female presentations, female approaches, female mounts, female vocalisations (oestrus and copulation calls), male approaches, male holding behaviours, male inspections of female genitals (i.e., visual and/or tactile and/or olfactory inspections of the female anogenital area), and male mounts (i.e., ejaculatory and non-ejaculatory). The number of observed records for each behaviour is given in Table 1. Each clear win/loss outcome of an agonistic interaction was recorded into an agonistic interaction matrix (541 female-female interactions, mean $\pm$ SD per female = 38.64 ± 11.93 , range = 17-76). Female social rank positions were calculated using Normalized David's Score (NDS) (de Vries et al., 2006) (Table A1). Given that there were only three adult males in the group, male ranks were assessed as alpha (winning all agonistic interactions), beta (defeating all males except the alpha male), and gamma (losing all agonistic interactions) directly from the agonistic interaction matrix (data provided by the Center for Human Modeling Research of KUPRI).

Female coloration

Data collection and analyses are extensively described in Rigai et al. (2019). Briefly, one experimenter took digital images of female face and hindquarters every two days using a Canon EOS 350D camera with an 8 megapixel CMOS sensor and an EF28–135 mm f/3.5–5.6 IS USM lens. The experimenter standardized data collection daily using white balance and colour standards (GretagMacbeth ColorChecker). Colour standards were photographed in the exact same conditions as those for the subject (i.e., camera settings and distance, orientation from the camera). For each female's photo, colour was assessed separately from the face and hindquarter skin. A technician who was blind to females' identity and characteristics extracted reflectance spectra using Colourworker software (Chrometics Ltd. Website, available: <http://www.chrometrics.com>). These spectra were converted into quantal catches, i.e., the stimulation of Japanese macaque photoreceptors, for the longwave and mediumwave photoreceptors using macaque cone ratio and spectral sensitivity values given elsewhere (Higham et al., 2010; Stevens et al. 2009). Based on the quantal catch data for both face and hindquarter coloration, variation in luminance $((LW+MW) / 2)$ and redness $((LW-MW) / (LW+MW))$ was calculated as perceived by the macaque visual system (Higham et al., 2010; Stevens et al., 2009; data from Rigai et al., 2019).

Female reproductive status

To accurately determine each female's ovarian cycle, we collected a total of 381 faecal samples (mean $\pm$ SD per female = 29.31 ± 3.17 , range = 24–34, between 8:00 AM and 12:00 PM mainly) on average every 1.59 days (range = 0–4 days) (Hodges & Heistermann, 2011). We followed the enzyme immunoassays method described by Garcia et al. (2009) to analyse concentration of pregnanediol-3-glucuronide (PdG) and estimate the day of ovulation of each ovarian cycle. Briefly, we determined the onset of the luteal phase as the sample with a sustainable increase in faecal PdG concentration compared to the preceding 3–4 mean baseline values (threshold:

two standard deviations greater than the mean) (Hodges & Heistermann, 2011). We determined the 2-day window for ovulation as days -2 and -3 relative to the faecal PdG rise. The fertile phase corresponds to the five-day period that covers the two-day window for ovulation plus the three preceding days (Behboodi et al., 1991). The five-day period preceding and following the fertile phase represented the prefertile phase and the post-fertile phase respectively. Twenty-four ovarian cycles were recorded (mean $\pm$ SD per female = 2.0 ± 0.83 , range = 1-3, 19 conceptive cycles). We excluded one female from our analyses as she failed to cycle during the study.

Data analysis

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

We conducted our analyses in R version 3.3.3. Before running the statistical analyses, we checked for correlations between our variables of interest. None of the female behaviours (i.e., presentations, approaches, and mounts) were correlated with each other (all $P > 0.05$). None of the male behaviours (i.e., approaches, holding behaviours, genital inspections, and mounts) were correlated with each other (all $P > 0.05$). Redness and luminance co-varied; females with redder hindquarters also had darker hindquarters and females with redder faces also had darker faces (from Rigai et al., 2019).

We aimed at testing whether the likelihood of a male behavioural response (binary variable: 1 = occurrence, 0 = non-occurrence) toward a female was predicted by female coloration, i.e., whether males were more likely to engage in or maintain sexual interactions

with darker/redder females. The few occurrences of copulatory events alone prevented us from analysing the effect of female coloration on this behaviour only. We thus computed a binary response variable that corresponded to a male behavioural response as the occurrence of at least one of the behaviours involved in establishing and maintaining consortship that were displayed by the interacting male of the dyad (i.e., approaches, holding behaviours, genital inspections, and copulations). Similarly, we also computed a binary variable that corresponded to a female behavioural display (hereafter, *female behaviours*), as the occurrence of at least one of the behaviours involved in establishing and maintaining consortship that were displayed by the interacting female of the dyad (i.e., presentations, approaches, and mounts).

We built a series of generalized linear mixed models with a binomial error structure and logit link function with the function `glmer` from the `lme4` package (Bates et al., 2015) to investigate the relationship between male behavioural response (binary variable) and female coloration (continuous variables). Hindquarter luminance followed a normal distribution, face luminance, face redness, and hindquarter redness followed a lognormal distribution. We first constructed three different models to test the relationship between male behaviours and female face coloration (luminance and redness), male behaviours and female hindquarter coloration (luminance and redness), and male behaviours and female face and hindquarter coloration (luminance and redness). To account for a) intra-cycle, b) inter-cycle, and c) inter-individual effects on the potential relationship between female coloration and male response, our three models included interactions between female coloration and a) the cycle phase (categorical variable, three levels: pre-fertile, fertile, and post-fertile phases), b) the number of consecutive cycles (continuous variable) and the conceptive nature of the cycle (binary variable: 1 = conceptive, 0 = non-conceptive cycles, hereafter *conception*), and c) female social rank (continuous variable) and parity (continuous variable). We also included female behaviours (binary variable) and male social rank (categorical variable, three levels: alpha, beta, gamma)

as covariates to account for the potential effects of female direct solicitation and male social attributes on mating decisions. Finally, we included the following random factors: date of the focal and the identity of the male-female pair. We also constructed a null model, i.e., we removed all predictor variables and covariates but maintained the random effects structure. All continuous variables were standardized (mean = 0, SD = 1) to improve model performance and facilitate interpretability (Harrison et al., 2018). We checked for variance inflation ($\text{GVIF}^{(1/(2 \times \text{Df}))} < 3$) using the car package (Fox & Weisberg, 2019); we excluded female age, weight, and the number of consecutive cycles from the models due to variance inflation. We inspected the histograms of the residuals and plots of residuals against fitted values to check the homogeneity of the residuals and the stability of the estimates (Figure A1).

We used an information-theory approach to objectively compare and rank the four candidate models (i.e., null model, face coloration model, hindquarter coloration model, and face and hindquarter coloration model) in terms of how well one or more models among the candidates is/are best supported by the data (Burnham et al., 2011; Symonds & Moussalli, 2011). Candidate models were ranked based on their respective Akaike's information criterion corrected for small sample size (AICc values) (MuMIn package, function: model.sel, Barton, 2020). We considered models with ΔAICc (the difference in AICc values between the smallest AICc and the other AICc values) below four as competitive models with the plausibly higher-ranked model among candidates (Burnham & Anderson, 2002). We reported the weight of the models which indicates the probability that one candidate model is more likely than others to provide a reasonable explanation of the variance in the data. We also extracted evidence ratio (ER) which provides a measure on the likelihood that the higher-ranked model is more parsimonious than another model in the candidate set. We then calculated for each model their marginal (R^2_m) and conditional (R^2_c) coefficients of determination (function: r.squaredGLMM, Nakagawa & Schielzeth, 2013). We presented the weighted parameter estimates (β) of model

intercepts and predictors along with their standard errors (SE) and 95% confidence intervals (95% CIs) of the higher-ranked model or alternatively, the conditional averaging of the competitive candidate models (function: model.avg).

Results

Among the candidate models, the model including female hindquarter coloration (luminance and redness) and covariates had the highest weight (0.999) and more than 999 times more empirical support than the competing models (face coloration: $\Delta\text{AICc} = 13.98$; face and hindquarter coloration: $\Delta\text{AICc} = 18.09$; null model: $\Delta\text{AICc} = 38.10$, Table 2). We thus present results for the higher-ranked model only (see Table A2 for the results of the other candidate models). The fixed and random effects accounted for around 35% of the observed variance in the occurrence of male behavioural responses.

a) Intra-cycle effect

We found a slight tendency for a higher probability of male behavioural responses when hindquarter luminance was low (i.e., stronger signal) only during the post-fertile phase compared with the fertile phase ($\beta = -0.80 \pm 0.45$ SE, $P = 0.075$, 95% CI = -1.68; 0.08, Table 3, Figure 1a). However, there was no general effect of cycle phase on the occurrences of male behaviour (fertile vs. pre-fertile and post-fertile phases, all $P > 0.50$, Table 3).

b) Inter-cycle effect

There was a slight tendency for a higher probability of male behavioural responses when hindquarter luminance was low in conceptive vs. non-conceptive cycles ($\beta = -1.03 \pm 0.58$ SE, $P = 0.076$, 95% CI = -2.17; 0.11, Table 3, Figure 1b). However, the conceptive nature of the cycle did not influence the occurrence of male behaviours ($\beta = -0.26 \pm 0.64$ SE, $P = 0.68$, 95% CI = -1.52; 0.99, Table 3).

c) Inter-individual effect

There was no effect of a female's hindquarter redness or luminance *per se* on male behavioural response (all $P > 0.50$, Table 3). Males were more likely to display sexual behaviours toward females of lower parity ($\beta = -1.28 \pm 0.62$ SE, $P = 0.039$, 95% CI = -2.49; -0.06, Table 3), but independently of their hindquarter coloration (all $P > 0.05$, Table 3). Female social rank did not strongly explain the occurrence of male behavioural response ($\beta = 0.59 \pm 0.34$ SE, $P = 0.082$, 95% CI = -0.07; 1.25, Table 3) or the interaction between male behavioural response and hindquarter redness ($\beta = 0.40 \pm 0.23$ SE, $P = 0.084$, 95% CI = -0.05; 0.85, Table 3).

Males were more likely to display sexual behaviours toward females that have solicited or interacted with them ($\beta = 3.07 \pm 0.49$ SE, $P < 0.001$, 95% CI = 2.11; 4.03, Table 3). Male social rank was not strongly related to the occurrence of male sexual behaviours (alpha vs. beta: $\beta = -1.14 \pm 0.72$ SE, $P = 0.11$, 95% CI = -2.55; 0.27, alpha vs. gamma: $\beta = -1.35 \pm 0.72$ SE, $P = 0.059$, 95% CI = -2.76; 0.05, Table 3).

Discussion

We examined male choice toward a non-sex-specific colourful ornament in a promiscuous primate species with traditional sex roles and demonstrated that male Japanese macaques did not bias their sexual behaviours toward darker/redder females (luminance and redness of the face and hindquarters). Our results also showed that males did not use coloration as a signal to selectively choose females based on a) intra-cycle, b) inter-cycle, and c) inter-individual variation.

This was unexpected since previous studies suggested a potential role of female coloration on male mate choice in Japanese macaques (face redness: Pflüger et al., 2014; face and hindquarter luminance and redness: Rigai et al., 2019). While we investigated changes in male sexual behaviours toward group-member females varying in skin coloration and characteristics, Pflüger et al. (2014) investigated male responses toward two visual stimuli of

an unknown female face. A red effect may have been over-estimated due to the binary choice, the lack of familiarity with the stimuli which is important in communication (e.g., visual trait: Higham et al., 2011; odorant trait: Setchell et al., 2010; auditory trait: Townsend et al., 2011), or the lack of a precise measure of attention such as tracking fine-scale eye movements (Hopper et al., 2020; Yorzinski et al., 2013). Our present study demonstrated that female coloration is unlikely to be a sexually selected trait since males did not appear to use this trait to discriminate when, and with whom to mate, to reproduce efficiently. It is possible that males do use colour in mating decisions in this species, as suggested by Pflüger's (2014) study, but our data failed to capture it. It could also be argued that males of this group may not rely – or need to rely – on coloration to make their mating decisions due to the lack of peripheral males and low levels of male-male competition. However, if female coloration indeed plays a role in male sexual strategies in this species where females vary in quality and female-female competition is high, one may have expected the alpha male to express mate choice as he has priority of access to mating (Altmann, 1962). However, the alpha male did not appear to do so (Table A3).

Males in our study did not appear to use female coloration to focus their effort on periods of highest fertility within (the fertile phase) or between (conceptive cycles) cycles. This suggests that ovulation is concealed or, at least, not advertised through multiple female traits in this species (Garcia et al., 2009; O'Neill et al., 2004; Rigai et al., 2019). Does this mean that males mate randomly? This is highly unlikely considering the energetic costs of extended sperm production, prolonged consortship, and male-male competition (Matsubara, 2003; Thomsen et al., 2006). While female coloration may not inform males about the probability of ovulation, this trait appears to be involved in the communication of pregnancy status (information content: Rigai et al., 2015). Males have been found to reduce or avoid mating with pregnant females in populations facing higher energetic constraints (Fujita, 2010; Rigai et al., 2015). However, whether males indeed use female coloration to avoid wasting energy in post-conceptive mating

calls for further investigation. We also found that males were more likely to respond to female solicitations and thereby apportion their mating effort toward receptive females vs. non-cycling females. Males may adapt their mating strategies according to female behaviour and increase their access to mates by either intensifying mate guarding (higher-ranking males) or seizing a mating opportunity (lower-ranking males). Monitoring female behaviours would ultimately benefit to both higher- and lower-ranking males by balancing the costs and benefits of mate searching, direct competition, and mating.

Males did not discriminate between females based on their coloration. However, males appeared to bias their mate choice toward females that had relatively fewer infants during post-adulthood, independently of their coloration. This contrasts with previous findings in primates (rhesus macaques: Dubuc et al., 2016; Higham et al., 2011, 2021) and non-primate species (blue tits: Mahr et al., 2012; rock sparrows: Pilastro et al., 2003; Griggio et al., 2009; blue-footed boobies: Torres & Velando, 2005) where female colourful traits positively correlate with reproductive history or success and are attractive to males. It is complicated to interpret this result. It is possible that preferences by males for females that had relatively fewer infants during post-adulthood may reflect preferences based on age or experience rather than on parity *per se*, as in this study older females tended to have lower parity (Table A1). More precise and long-term data on the interaction between male mate choice and inter-individual variation in female coloration and reproductive success (e.g., interbirth intervals, offspring survival rate, inclusive fitness) are needed to clarify this point.

Studies of the role of non-sex-specific colourful ornaments displayed on feather or skin have been relatively limited in comparison with sex-specific colourful ornaments in both males and females. From this rather incomplete picture, it appears that male choice and preferences for female traits may evolve because of the costs associated with reproduction. One factor may be the cost of sexual signalling itself, when female ornamentations are costly to produce or

maintain and thus impact the energy allocated to reproduction and ultimately, offspring quality and survival (blue tits: Doutrelant et al., 2008, 2012; Peters et al., 2011; rock sparrow: Griggio et al., 2009; Pilastro et al., 2003). However, assessing such signalling costs is difficult. Another factor may be the shared costs of rearing offspring in socially monogamous species displaying extra-pair copulations (rock sparrow: Griggio et al., 2005; blue tits: Mahr et al., 2012; blue-footed boobies: Torres & Velando, 2005). Under such conditions, both males and females would benefit from traits indicative of one's fecundity to adjust their mating and parental effort according to the costs and prospective benefits of signalling to, and reproducing with, a particular mate. Alternatively, male choice for a colourful trait may also evolve in promiscuous species with traditional sex roles to maximize reproductive success when mating decisions are limited or constrained (e.g., territorial agamid lizards: LeBas & Marshall, 2000).

To our knowledge, our study is among the few to report an absence of male mate choice based on female coloration (sockeye salmons: Foote et al., 2004; threespine sticklebacks: Wright et al., 2015). One possible explanation may be that in seasonal breeders the operational sex ratio becomes more male-biased as the season progresses, favouring male-male competition and female choice (T. H. Clutton-Brock & Parker, 1992). It is likely that the number of cycling, receptive, and defendable females within a group or location decreases rapidly during the mating season as a consequence of reproductive synchrony (Ims, 1990; Thompson, 2018). Increased male-male competition for mating opportunities would select for male ornaments, especially in species where the cost of reproduction is heavier on females than males. Such scenario may explain the lack of male choice for female coloration in Japanese macaques. Females are indeed more likely to conceive at the beginning of the mating season and to invest high energy on gestation and maternal care while facing energetic stress from decreased food availability and thermoregulation (Fujita, 2010; Garcia et al., 2010, 2011). Thus, female coloration may only represent a genetical by-product of selection for male ornamentation

(Lande, 1980). The signalling function of male coloration and its role on mate choice in Japanese macaques is still unknown. However, evidence from other primate species suggests that male coloration can vary according to male social characteristics (geladas, *Theropithecus gelada*: Bergman et al., 2009; snub-nosed monkeys, *Rhinopithecus bieti*: Grueter et al., 2015; drills, *Mandrillus leucophaeus*: Marty et al., 2009; rhesus macaques: Petersdorf et al., 2017; mandrills: Setchell & Dixon, 2001) and may influence female mating decisions (rhesus macaques: Dubuc, Allen, et al., 2014; Dubuc et al., 2016; Waitt et al., 2003). Nonetheless, it should be noted that promiscuous mating, female reproductive synchrony, and strong intra-sexual competition have been recently suggested to explain the evolution of female (and male) colourful and attractive ornaments in another primate species (rhesus macaques: Higham et al., 2021). Clearly, further studies are needed to better understand the role of socio-sexual and environmental pressures on the evolution and signalling function of both female-specific and mutual ornamentations across taxa.

In conclusion, we found no clear evidence that female coloration (luminance and redness of the face and hindquarters) influences male mate choice in Japanese macaques. Skin coloration may thus correlate with intra-cycle, inter-cycle, and inter-individual variation in female fertility without having a signalling function (correlation without causation). This highlights the importance of studying traits suspected to have a role in sexual signalling and mating decisions from both signaller (what information may be contained) and perceiver (how the trait may affect behaviours) perspectives. Future studies on both primates and non-primate species should examine the potential role of both female and male coloration in the communication of reproductive status (i.e., not only the timing of ovulation or a female's receptivity), reproductive history, and its function in intra- and inter-sexual selection. Only then can any definitive conclusions be drawn about the evolution of non sex-specific colourful ornaments, especially in species facing different reproductive constraints (e.g., reproductive

seasonality, challenging environments, variation in food availability or predictability, styles of parental care). Whether reproductive seasonality and reproductive costs have a role into the evolution of male mate choice and female traits remains an open question, especially in primates for which little data is available.

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744

Table 1. Total number of female behaviours, male behaviours, and female vocalisations recorded.

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

750 **Table 2.** Characteristics of candidate models

Models	k	logLik	AICc	ΔAICc	weight	ER	R²m - R²c
Hindquarter coloration	23	-133.0	314.3	0.0	0.999	-	0.26 - 0.35
Face coloration	23	-140.0	328.3	13.98	0.001	999	0.18 - 0.29
Face and hindquarter coloration	35	-128.6	332.4	18.09	0.00	-	0.27 - 0.37
Null	3	-173.2	352.4	38.10	0.00	-	0.00 - 0.24

751 k: number of predictors, AICc: Akaike's information criterion corrected for small sample size,
752 Δ AICc: the difference in AICc values between the smallest AICc and the other AICc values,
753 weight: model's probability, ER: evidence ratio, and R²m – R²c: marginal and conditional
754 coefficients of determination.

755

756 **Table 3.** Result of the higher-ranked generalized linear mixed model predicting the
757 occurrence of male behavioural response.

	β	SE	z-value	P	95% CI
Intercept	-1.47	0.70	-2.10	0.036	-2.85; -0.10
Hindquarter luminance	0.54	0.40	1.34	0.18	-0.25; 1.32
Hindquarter redness	-0.47	0.42	-1.13	0.26	-1.29; 0.35
Female behaviour	3.07	0.49	6.27	< 0.001	2.11; 4.03
Cycle phase (fertile vs. prefertile)	-0.13	0.44	-0.29	0.77	-0.99; 0.74
Cycle phase (fertile vs. post-fertile)	-0.29	0.42	-0.68	0.50	-1.11; 0.54
Conception	-0.26	0.64	-0.41	0.68	-1.52; 0.99
Parity	-1.28	0.62	-2.06	0.039	-2.49; -0.06
<i>Female rank</i>	<i>0.59</i>	<i>0.34</i>	<i>1.74</i>	<i>0.082</i>	<i>-0.07; 1.25</i>
Male rank (alpha vs. beta)	-1.14	0.72	-1.58	0.11	-2.55; 0.27
<i>Male rank (alpha vs. gamma)</i>	<i>-1.35</i>	<i>0.72</i>	<i>-1.89</i>	<i>0.059</i>	<i>-2.76; 0.05</i>
Interaction: hindquarter luminance x					
Cycle phase (fertile vs. prefertile)	0.31	0.48	0.64	0.52	-0.64; 1.26
<i>Cycle phase (fertile vs. post-fertile)</i>	<i>-0.80</i>	<i>0.45</i>	<i>-1.78</i>	<i>0.075</i>	<i>-1.68; 0.08</i>
<i>Conception</i>	<i>-1.03</i>	<i>0.58</i>	<i>-1.77</i>	<i>0.076</i>	<i>-2.17; 0.11</i>
Parity	0.05	0.40	0.12	0.90	-0.74; 0.84
Female rank	0.08	0.22	0.39	0.69	-0.34; 0.51
Interaction: hindquarter redness x					
Cycle phase (fertile vs. prefertile)	-0.53	0.53	-1.00	0.32	-1.58; 0.51
Cycle phase (fertile vs. post-fertile)	-0.47	0.46	-1.02	0.31	-1.37; 0.43
Conception	0.44	0.69	0.64	0.52	-0.92; 1.80
Parity	0.05	0.44	0.10	0.92	-0.82; 0.91

Female rank *0.40* *0.23* *1.73* *0.084* *-0.05; 0.85*

758 Parameters estimates (β) $\pm$ adjusted standard errors (SE), z-value, probability (P), and
 759 confidence intervals (95% CIs) of the higher-ranked model. For each categorical comparison,
 760 the first level indicate baseline. Results are presented in bold when CI does not include zero,
 761 trends in italic.
 762

763 **Table A1.** Female characteristics.

Female	Age	Weight	Parity	Social rank
female 1	21.46	14.4	0.30	0.538
female 2	14.48	10.0	0.42	0.231
female 3	12.44	12.4	0.40	0.846
female 4	10.22	10.5	0.58	0.154
female 5	8.42	11.4	0.88	0.00
female 6	7.37	9.0	0.85	1.00
female 7	7.27	11.3	0.00	0.769
female 8	6.55	9.4	0.00	0.615
female 9	6.38	6.9	1.45	0.692
female 10	5.54	10.0	0.00	0.308
female 11	5.41	9.1	2.43	0.077
female 12	5.37	8.8	2.68	0.462

764

765 **Table A2.** Result of the generalized linear mixed models model predicting the occurrence of
766 male behavioural response.

	β	SE	z-value	P	95% CI
Null model					
Intercept	-2.96	0.53	-6.51	< 0.001	-3.85; -2.07
Face coloration model					
Intercept	-1.43	0.68	-2.10	0.036	-2.77; -0.09
Face luminance	0.25	0.45	0.57	0.57	-0.63; 1.15
Face redness	0.43	0.63	0.68	0.50	-0.81; 1.66
Cycle phase (fertile vs. prefertile)	-0.11	0.43	-0.26	0.80	-0.96; 0.74
Cycle phase (fertile vs. post-fertile)	-0.37	0.45	-0.82	0.41	-1.24; 0.51
Conception	-0.28	0.61	-0.46	0.65	-1.49; 0.92
Parity	-1.08	0.53	-2.03	0.042	-2.12; -0.04
Female rank	0.30	0.33	0.93	0.35	-0.33; 0.94
Female behaviour	2.93	0.46	6.33	< 0.001	2.02; 3.84
Male rank (alpha vs. beta)	-1.11	0.73	-1.51	0.13	-2.56; 0.33
<i>Male rank (alpha vs. gamma)</i>	<i>-1.29</i>	<i>0.73</i>	<i>-1.77</i>	<i>0.078</i>	<i>-2.72; 0.14</i>
Interaction: face luminance x					
Cycle phase (fertile vs. prefertile)	-0.51	0.48	-1.06	0.29	-1.45; 0.43
Cycle phase (fertile vs. post-fertile)	-0.35	0.49	-0.71	0.48	-1.31; 0.61
Conception	-0.54	0.49	-1.09	0.27	-1.50; 0.42
Parity	0.24	0.43	0.57	0.57	-0.60; 1.09
Female rank	0.13	0.22	0.60	0.55	-0.30; 0.56
Interaction: face redness x					
Cycle phase (fertile vs. prefertile)	0.22	0.57	0.38	0.70	-0.89; 1.33

Cycle phase (fertile vs. post-fertile)	-0.05	0.54	-0.08	0.93	-1.00; 1.01
Conception	-0.45	0.50	-0.90	0.37	-1.44; 0.53
Parity	-0.07	0.44	-0.15	0.88	-0.93; 0.80
Female rank	0.25	0.22	1.14	0.26	-0.18; 0.69
Face and hindquarter coloration model					
<i>Intercept</i>	<i>-1.33</i>	<i>0.75</i>	<i>-1.78</i>	<i>0.075</i>	<i>-2.80; 0.13</i>
Face luminance	-0.08	0.59	-0.14	0.89	-1.24; 1.07
Face redness	0.26	0.69	0.38	0.70	-1.09; 1.62
Hindquarter luminance	0.53	0.49	1.08	0.28	-0.43; 1.48
Hindquarter redness	-0.47	0.46	-1.02	0.31	-1.38; 0.43
Cycle phase (fertile vs. prefertile)	-0.14	0.49	-0.29	0.78	-1.09; 0.81
Cycle phase (fertile vs. post-fertile)	-0.43	0.49	-0.88	0.38	-1.38; 0.52
Conception	-0.24	0.71	-0.33	0.74	-1.63; 1.16
Parity	-1.50	0.74	-2.03	0.042	-2.94; -0.05
Female rank	0.53	0.36	1.47	0.14	-0.18; 1.25
Female behaviour	3.13	0.51	6.11	< 0.001	2.13; 4.13
Male rank (alpha vs. beta)	-1.18	0.75	-1.58	0.11	-2.65; 0.29
<i>Male rank (alpha vs. gamma)</i>	<i>-1.37</i>	<i>0.75</i>	<i>-1.83</i>	<i>0.068</i>	<i>-2.83; 0.10</i>
Interaction face luminance x					
Cycle phase (fertile vs. prefertile)	-0.29	0.58	-0.50	0.62	-1.43; 0.85
Cycle phase (fertile vs. post-fertile)	-0.19	0.58	-0.33	0.74	-1.32; 0.94
Conception	-0.34	0.58	-0.59	0.55	-1.47; 0.79
Parity	0.42	0.50	0.84	0.40	-0.56; 1.39
Female rank	0.03	0.25	0.11	0.91	-0.46; 0.52
Interaction face redness x					

Cycle phase (fertile vs. prefertile)	0.49	0.63	0.79	0.43	-0.74; 1.73
Cycle phase (fertile vs. post-fertile)	0.19	0.60	0.31	0.75	-0.98; 1.35
Conception	-0.36	0.54	-0.66	0.51	-1.42; 0.71
Parity	-0.14	0.52	-0.27	0.79	-1.17; 0.89
Female rank	0.30	0.24	1.22	0.22	-0.18; 0.78
Interaction hindquarter luminance x					
Cycle phase (fertile vs. prefertile)	0.47	0.53	0.87	0.38	-0.57; 1.50
Cycle phase (fertile vs. post-fertile)	-0.63	0.50	-1.26	0.21	-1.61; 0.35
<i>Conception</i>	<i>-1.23</i>	<i>0.67</i>	<i>-1.85</i>	<i>0.065</i>	<i>-2.54; 0.07</i>
Parity	-0.03	0.48	-0.05	0.96	-0.97; 0.92
Female rank	0.13	0.24	0.54	0.59	-0.34; 0.60
Interaction hindquarter redness x					
Cycle phase (fertile vs. fertile)	-0.48	0.60	-0.81	0.42	-1.66; 0.69
Cycle phase (fertile vs. post-fertile)	-0.75	0.53	-1.40	0.16	-1.79; 0.30
Conception	0.33	0.80	0.42	0.68	-1.23; 1.90
Parity	0.11	0.55	0.19	0.85	-0.97; 1.18
Female rank	0.29	0.25	1.15	0.26	-0.20; 0.78

Models parameters estimates (β) $\pm$ adjusted standard errors (SE), z-value, probability (P), and confidence intervals (95% CIs) from each 4 candidate models. For each categorical comparison, the first level indicate baseline. Results for which CI does not include zero are presented in bold, trends are presented in italic.

772 **Table A3.** Result of the generalized linear mixed models model predicting the occurrence of
773 male behavioural response in relation to their rank.

	β	SE	z-value	P	95% CI
Intercept	-2.19	0.63	3.49	< 0.001	-3.41; -0.96
Face luminance	-0.14	0.26	0.55	0.59	-0.65; 0.37
Face redness	-0.03	0.23	0.12	0.90	-0.48; 0.42
Hindquarter luminance	0.37	0.23	1.61	0.11	-0.08; 0.82
<i>Hindquarter redness</i>	<i>-0.46</i>	<i>0.26</i>	<i>1.80</i>	<i>0.072</i>	<i>-0.96; 0.04</i>
Male rank (alpha vs. beta)	-1.42	0.91	1.56	0.12	-3.20; 0.36
Male rank (alpha vs. gamma)	-1.07	0.87	1.22	0.22	-2.77; 0.64
Face luminance x Male rank (alpha vs. beta)	0.32	0.45	0.72	0.47	-0.56; 1.22
Face luminance x Male rank (alpha vs. gamma)	-0.07	0.41	0.17	0.86	-0.89; 0.74
<i>Face redness x Male rank (alpha vs. beta)</i>	<i>0.78</i>	<i>0.42</i>	<i>1.86</i>	<i>0.063</i>	<i>-0.04; 1.61</i>
Face redness x Male rank (alpha vs. gamma)	0.18	0.38	0.48	0.63	-0.56; 0.92
Hindquarter luminance x Male rank (alpha vs. beta)	0.05	0.43	0.13	0.90	-0.79; 0.90
Hindquarter luminance x Male rank (alpha vs. gamma)	-0.43	0.38	1.15	0.25	-1.17; 0.31
Hindquarter redness x Male rank (alpha vs. beta)	0.00	0.49	0.01	0.99	-0.96; 0.97

Hindquarter redness x Male

rank (alpha vs. gamma) 0.39 0.42 0.94 0.34 -0.42; 1.21

774 Models parameters estimates (β) $\pm$ adjusted standard errors (SE), z-value, probability (P), and
775 confidence intervals (95% CIs). For each categorical comparison, the first level indicate
776 baseline. Results for which CI does not include zero are presented in bold, trends are presented
777 in italic.

778

779 **Figure 1.** Interaction plot of the generalized linear mixed model exploring the relationship
780 between male behavioural response and female hindquarter luminance (log) (a) across cycle
781 phases and (b) between conceptive vs. non-conceptive cycles.

782

783 **Figure A1.** Residuals plots of the (a) null model, (b) face coloration model, (c) hindquarter
784 coloration model, and (d) face and hindquarter coloration model.