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Testing for links between face color and age, dominance status, parity, weight, and intestinal nematode infection in a sample of female Japanese macaques

Lucie Rigai¹ · Andrew J. J. MacIntosh^{1,2} · James P. Higham³ · Sandra Winters³ · Keiko Shimizu⁴ · Keiko Mouri¹ · Takafumi Suzumura² · Takeshi Furuichi¹ · Cécile Garcia⁵

Abstract Studies of the role of secondary sexual ornaments in mate choice tend to focus on colorful traits in males, but females of many animal species express colorful ornamentation too. Among non-human primates, investigations into the role of female secondary sexual traits as indicators of life history characteristics, reproductive success, and health status have mostly focused on sexual swellings, whereas only few studies have been conducted on the role of facial color. Recent studies on rhesus macaques and mandrills suggested that female ornamentation might provide information about female life history characteristics, but not on disease resistance factors and parasite infection, which have been shown to affect male ornamentation in some non-primate species. In Japanese macaques (*Macaca fuscata*), females have brightly colored faces that are indicative of their reproductive status. Here, we aimed to determine whether female facial color might also convey information about age, dominance rank, parity, weight, and intestinal nematode infection in free-ranging individuals. We analyzed whether female facial parameters (luminance and redness) were linked to these individual

characteristics, using digital photography and data on intestinal parasite infection collected systematically during 1 month for each of seven free-ranging females. We found no evidence to suggest that female facial color is an indicator of any of these measures in Japanese macaques. Considering our small data set, it is still preliminary to draft any clear conclusions. Future studies combining digital, hormonal, parasitological and behavioral data are needed to assess the possible role of female face color on male preferences and mating choice in Japanese macaques.

Keywords: Sexual selection · Secondary sexual ornaments · Signaling · *Macaca fuscata*

Introduction

In many animal species, both sexes express secondary sexual traits, such as sexual ornaments, which are suggested to improve the carrier's success in reproduction (Darwin 1871). In an honest signaling system, such ornamentation is thought to be linked to indices of individual quality (Zahavi 1975; Hamilton and Zuk 1982). Although it is complicated to assess condition-dependency (Higham 2013; Számadó and Penn 2015), there exists strong evidence of links between ornamentation quality and indices of life history traits and health status (e.g., parasite infection, immunocompetence) (Møller et al. 1999; Amundsen 2000). It is therefore hypothesized that, by signaling individual qualities such as social characteristics, reproductive success, or health status, secondary sexual signals may play an important role in mate attraction and intra-sexual competition (Andersson 1994).

Studies on secondary sexual ornaments mainly focus on colorful traits in males because males often have

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exaggerated trait expression relative to females (Darwin 1871; Andersson 1994). In mammals, the cost of reproduction is generally higher for females due to the production of larger gametes, the energetic costs associated with pregnancy and lactation, and maternal post-natal investment in many species (reviewed in Clutton-Brock 2004). These sex differences in reproductive costs are thought to result in stronger sexual selection pressures on males to express signals that attract females (reviewed in Clutton-Brock 2004; David and Heeb 2009). However, females also express secondary sexual traits and ornaments in many animal species. For example, in some species of fish and lizards, males tend to prefer colorful females (Amundsen and Forsgren 2001; Weiss 2002), perhaps because female ornaments have been found to reflect indices of reproductive success (e.g., clutch or egg size), body condition, or parasite resistance in several species [barn owls (Roulin et al. 2000, 2001); plateau lizards (Weiss 2006); blue tits (Doutrelant et al. 2008)]. Females might develop sexual ornaments in species for which the costs of reproduction are reversed, with males investing more (e.g., paternal care) and therefore showing stronger mate choice than females. In species in which both sexes express some mate choice, females might also inherit the genetic basis from sexual selection for ornamentation in males, since most of the genome is shared between sexes (Amundsen 2000).

Among non-human primates, males tend to show some preferences toward specific females based on their age, dominance rank, and parity (Setchell and Wickings 2006; Muller et al. 2006; Garcia et al. 2009), suggesting that they might discriminate between females based on such characteristics. Most studies of female ornaments in primates have focused on the role of sexual swellings as possible indicators of both intra-individual (e.g., the timing of ovulation), and inter-individual (e.g., female reproductive and life history characteristics) variation (reviewed in Street et al. 2016). Sexual swelling size and/or color might reflect some indices of reproductive quality such as parity or the number of cycles to conception [chimpanzees (Emery and Whitten 2003; Deschner et al. 2004); mandrills (Setchell and Wickings 2004; Setchell et al. 2006a); olive baboons (Higham et al. 2008)], whereas swelling shape seems to be linked to female age in baboons and mandrills (Huchard et al. 2009). However, a few studies have investigated the role of other sexual ornaments such as skin coloration as indicators of individual characteristics, with most work focusing on males [vervet monkeys (Isbell 1995; Danzy Cramer et al. 2013); patas monkeys (Bercovitch 1996); mandrills (Setchell and Dixson 2001; Setchell and Wickings 2005; Setchell et al. 2009); geladas (Bergman et al. 2009); drills (Marty et al. 2009); rhesus macaques (Higham et al. 2013)]. For females, recent findings on rhesus macaques showed that females with

redder faces have higher fecundity (Dubuc et al. 2014b). In mandrills, facial color does not seem to be informative about female social status, body mass, female inter-birth intervals or health (e.g., parasite load, immune-related genetic diversity), but facial color does change with age and parity (Setchell et al. 2006b; 2009).

In Japanese macaques (*Macaca fuscata*), both males and females express red coloration of the face that undergoes seasonal changes through variation in circulating sexual steroids (Fujita et al. 2004; Fooden and Aimi 2005). Lacking sexual swellings, female Japanese macaques advertise their reproductive status through other visual signals, with female facial redness decreasing between the first and the second month of pregnancy and face luminance decreasing from the pre-conceptive month to the pregnancy period (Rigaill et al. 2015). In this seasonal species, males and females mate from autumn to winter, the exact timing depending on the population in question, with food availability and temperature decreasing gradually during the winter (Iwamoto 1982; Fooden and Aimi 2003; Go 2009). During the mating season, females have to balance the costs of mating [e.g., male harassment and increases in the rate of aggression (see Fujita 2010)] with other energetic costs linked to environmental factors, such as thermoregulation and food scarcity. This is particularly the case for the Koshima population, for which the relatively low availability and quality of food resources have been found to impact female reproductive history. This population was provisioned from 1952, but after the end of the intensive provisioning period (1977) the age at first birth increased from around 6–9.2 years, considerably longer than that seen in other natural populations of Japanese macaques [Yakushima 6.1 years, Kinkazan 7.1 years (Takahata et al. 1998)]. Female inter-birth intervals also lengthened after the end of the intensive provisioning (Mori 1979; Watanabe et al. 1992). Moreover, at Koshima, females of smaller body weight (i.e., less than 6.5 kg) are less likely to conceive than females of average body weight (Mori 1979). Finally, like all species, Japanese macaques are also infected by numerous parasites, such as intestinal helminths that are in direct competition with their hosts for energetic resources. Parasite infection rates have been found to be higher in southern populations of Japanese macaques (Gotoh 2000), and degrees of infection vary across seasons, including in relation to reproduction (MacIntosh et al. 2010). However, little is yet known about their potential effects on Japanese macaque reproductive success and, most relevant to the present study, fertility signaling.

We investigated whether facial color is potentially informative about female age, dominance rank, parity, body mass, and parasite infection (here “intestinal helminths”). We test the null hypothesis, that facial color does

not reflect female characteristics in Japanese macaques, against the alternative hypothesis that it does. If facial color acts as an indicator of female characteristics, we would predict older and higher-ranking females, who have experienced successful pregnancies, as well as heavier females presumed to be in better body condition (females of smaller body weight often fail to reproduce), to have faces that differ in their redness and/or luminance when compared to younger, lower-ranking, inexperienced, and thinner females. If intestinal helminth infection is also reflected in female reproductive signaling, we would further expect a difference in facial redness and/or luminance between females with lower levels of infection compared to those with higher levels of infection.

Methods

Study site and subjects

Koshima is a 0.32-km² uninhabited mountainous islet located in Miyazaki prefecture (31°220'N, 131°260'E), Kyushu, Japan. Although Japanese macaques generally mate from autumn to winter, females at Koshima mate during winter from early December to mid-March and deliver mainly between June and August (Mori 1979). Koshima macaques are well habituated to humans and easily identifiable through natural and artificial (tattoos) facial marks. We conducted our study throughout one entire mating season, from December 2013 to mid-March 2014, following the main troop of Koshima macaques. This was composed of 64 individuals: 20 adult (i.e., C6 years old) females (14.2 ± 3.2 years old, range 8–18), seven adult males, 29 subadult and juvenile males and females, and eight infants (≤ 1 year old). During this mating season, we collected data for seven adult females that had the potential to resume cycling (i.e., females older than 8 years old and/or with an infant of more than 2 years). Group composition remained unchanged during the study period.

Female dominance rank, body weight and reproductive history

Female dominance ranks were determined using focal and ad libitum observations during the study period and were assessed by transcribing submissive (avoidances, retreats) and aggressive (attacks, threats and chases) behaviors for which a clear win/loss outcome was identified in an agonistic interaction matrix. We calculated normalized David's scores to assess female rank positions following previously described methods (de Vries et al. 2006; Neumann et al. 2011). Females were weighed every month to the nearest 0.5 kg using analog scales erected at the

provisioning site and baited with wheat. Data on parity (number of successful pregnancies) were provided by the Wildlife Research Center of Kyoto University.

Fecal sample collection

For hormonal analysis, we collected 138 fecal samples from the seven focal females (mean \pm SD per female = 14.3 ± 1.8 fecal samples, range = 13–18). Fecal collection was carried out during the morning focal observations between 8:00 a.m. and 12:00 p.m., as well as opportunistically when defecation was observed. Samples were collected in their entirety, bagged and labeled immediately after defecation. Approximately 2 g of each sample was then stored in 50-mL plastic tubes, mounted on a wire mesh insert placed above 35 mL of silica gel for complete desiccation of the pellet. Samples were transported to the Endocrinology Laboratory of the Department of Ecology and Social Behavior at Kyoto University's Primate Research Institute for subsequent analysis.

For parasitological analysis, we collected at least two fecal samples per month for each individual to estimate intestinal helminth infection, although only one sample could be collected during February for three females due to exceptionally bad weather conditions that hindered fieldwork. During the study period, we collected and analyzed 95 fecal samples from our seven focal females (mean \pm SD = 3.4 ± 1.4 samples/month per female, range = 2–6). Fecal samples were collected immediately following defecation and stored in labeled plastic bags. They were then homogenized and 2 g of feces was placed in 15-ml plastic tubes with 10 % buffered formalin solution within 12 h of collection. Samples were transported to the Parasitology Laboratory of the Department of Ecology and Social Behavior at Kyoto University's Primate Research Institute for subsequent analysis.

Hormonal analyses

Fecal samples were analyzed for estrone conjugates and pregnanediol-3-glucuronide (PdG) using previously described and validated enzyme immunoassays, with a few modifications (Shimizu et al. 2003; Shimizu 2005; details in Rigai et al. 2015). The presumed days of ovulation and conception were defined using PdG profiles. Following previous studies (e.g., Engelhardt et al. 2004; Heistermann et al. 2007; Brauch et al. 2007), the onset of the luteal phase was defined as the sample with a fecal PdG concentration which was at least 2 SDs greater than the mean PdG concentration of the three to four preceding baseline values. Because of the time lag between circulating hormones and the fecal rise in PdG concentration [2–3 days (see Fujita et al. 2001)], we determined a 2-day

periovulatory period as days 2 and 3 relative to the fecal PdG rise. The fertile phase was then defined as the 5-day period covering these 2 days plus the 3 preceding days to account for the life span of sperm in the female tract (Behboodi et al. 1991; Wilcox et al. 1995). We considered the latest possible day of fertilization, i.e., the last day of the fertile phase, as the onset of pregnancy. Five of our focal females became pregnant from their first cycle during the study period.

Estimation of intestinal helminth infection

We used a modified formalin-ethyl acetate sedimentation protocol to concentrate and extract helminth eggs from feces (Young et al. 1979; MacIntosh et al. 2010). After processing, fecal sediment was resuspended in approximately 30 ml of 10 % formalin for analysis. We used a volumetric method based on McMaster microscopy to estimate the size (intensity) of parasitic infection in each subject through assessment of the number of eggs observed per gram of fecal sediment (EPG). We drew aliquots from this fecal suspension, which was kept homogeneous during analysis using a magnetic stirrer, and viewed them in a McMaster chamber at 100 \times magnification. We repeated this procedure five times and used the mean count to calculate EPG based on the amount of sediment viewed per volume of suspension. While EPG has been criticized as a proxy for actual parasite intensity (e.g., Gillespie 2006), it remains a common approach, and numerous studies have identified a linear relationship between EPG and true worm intensity (Roberts and Swan 1981; Stear et al. 1995; Seivwright et al. 2004). In addition, a recent study of wild chimpanzees demonstrated that nodular worm EPG was a good indicator of the number of nodules observed at necropsy (Terio et al. 2016). While caution should be exercised when interpreting variation in raw EPG counts, we feel that our repeated sampling design and reliance on mean EPG from multiple rather than individual samples should reflect a biological difference in the extent to which infection varied across individuals.

In addition to estimating the size of each individual's infection, separately for each parasite species observed, we also recorded parasite species richness across samples, i.e., the total number of intestinal helminth species detected in each sample, which we used to calculate the maximum observed species richness in each individual. According to previous studies, four gastrointestinal nematode parasites are known to infect Koshima macaques: *Streptopharagus pigmentatus* (Spirurida), *Oesophagostomum aculeatum* (nodular worm, Strongylida), *Strongyloides fuelleborni* (threadworm, Rhabditida), and *Trichuris* sp. (whipworm, Enoplida) (Horii et al. 1982; Gotoh 2000). We focused on these four species in our study. Eggs of each parasite were

easily identified through differences in size and morphology, with some already having been molecularly assigned to the species level in Japanese macaques (Arizono et al. 2012). Due to their rarity in our samples (observed in only three of seven subjects), we did not include *Streptopharagus pigmentatus* and *Strongyloides fuelleborni* EPG in our analyses presented below. However, both were included in our assessment of maximum parasite richness. The indices of the intestinal helminth infection of our focal females for the 1-month period of interest was estimated from 45 samples (mean \pm SD = 6.4 \pm 2.4, range = 2–9).

To date, very little is known about the effects of these intestinal helminths on Japanese macaques, or indeed primates in general. Recent studies have highlighted behavioral alterations associated with increasing nodular worm infection in Japanese macaques (MacIntosh et al. 2011) and whipworm infection in red colobus monkeys (Ghai et al. 2015). Nodular worm infection is also associated with the formation of nodules (cysts) in the lining of the large intestine, in which the larvae develop into adult stages before entering the intestinal lumen. Such nodules, a pathological manifestation of oesophagostomiasis, have been observed previously in non-human primates (Krief et al. 2008; Terio et al. 2016), although the degree to which the animals suffer from this condition is unknown. There is also some evidence that Japanese macaques inhabiting regions with greater parasite richness ingest proportionately more plants containing secondary compounds with antiparasitic properties (MacIntosh and Huffman 2010).

Finally, unpublished work suggests that removal of intestinal helminths via anthelmintic treatment can benefit body mass maintenance and does impact reproductive success in female Japanese macaques at Koshima (MacIntosh et al., unpublished data). Taken together, while we do not expect dramatic effects of infection with any of the parasites examined, it is unlikely that infection, at least at higher intensities, is entirely benign.

Assessment of female facial redness and luminance

Objective collection of facial redness (chromatic) and luminance (achromatic) data followed the method described in Rigai et al. (2015). Briefly, images of female faces were taken in the morning between 8:00 a.m. and 12:00 p.m. in an open area. 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. Images were standardized 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). Female

facial parameters (redness and luminance) were assessed by extracting reflectance spectra using the Colourworker software (Stevens et al. 2009) and these spectra were then converted into quantal catches using equations given elsewhere (Stevens et al. 2009; Higham et al. 2010; see also Rigaiil et al. 2015 for more details). We used pictures from the cycling period, i.e., 1-month period which ended with the estimated conception day for pregnant females or with the latest day of the fertile phase for non-pregnant females. In total we used 42 images for color analyses (mean \pm SD per female = 6.0 ± 1.6 images). Because we tested the hypothesis that facial color provides information about female characteristics that might influence male mating decisions, pictures from the pregnancy period were not included in analyses. The present analyses focus on assessing inter-individual differences in facial redness and luminance. Intra-individual differences related to hormonal concentrations and reproductive status have been published elsewhere (Rigaiil et al. 2015).

Statistical analyses

Our statistical approach was designed to test whether female facial redness and luminance were related to individual age, dominance rank, parity, body weight, and intestinal helminth infection (restricted to EPG for nodular worm and whipworm, as well as intestinal nematode species richness). We constructed two general linear mixed-effects models fitted by maximum likelihood to examine variation in luminance and redness separately using the lme4 package in R version 3.2.3 (Bates et al. 2015). 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. All fixed effects were scaled and centered prior to model fitting to facilitate interpretation of the parameter estimates.

Before running our models, we first checked for correlations between our predictor variables to avoid potential confounding effects of multi-collinearity. Female parity (i.e., the number of successful pregnancies) was correlated with female age ($q = 0.64$) and dominance rank ($q = -0.61$), with older and high-ranking females having higher parity. Female age and body weight were also correlated ($q = -0.62$), with younger females in our sample set being heavier than older females. Note that these relationships result from our small sample of females and should not therefore be used to infer population-level relationships. Nodular worm EPG was also highly correlated with whipworm EPG ($q = 0.82$) and intestinal nematode species richness ($q = 0.80$). With these relationships in mind, we constructed two different models and present here the averaged results, i.e., the parameter estimates for all model

terms that appeared in more than one model (dominance rank, body weight, and intestinal nematode species richness) were averaged to avoid multiple testing issues (Burnham and Anderson 2004). We accounted for temporal variation and pseudo-replication in each model by setting the date on which each picture was taken and the focal individual's identity as crossed random effects.

We then ensured that all relevant model assumptions were met by visually inspecting histograms of the residuals and plots of the residuals against fitted values. Each fitted model was then compared via a likelihood ratio test with a null model in which all predictor variables were removed but the random effects structure was maintained. We also calculated the conditional (variance explained by fixed factors; R^2_c) and marginal (variance explained by both fixed and random factors; R^2_m) coefficients of determination using the package MuMIn (Nakagawa and Schielzeth 2013). We report all parameter estimates with their respective 95 % confidence intervals.

Results

Descriptive results for female age, dominance rank, parity, body weight, nodular worm EPG, whipworm EPG, and intestinal nematode species richness used in the analyses can be found in Table 1. The coefficients of determination were 0.10 (R^2_c) and 0.47 (R^2_m) for redness, and 0.04 (R^2_c) and 0.40 (R^2_m) for luminance, suggesting that the random factors explained around 40 % of the observed variance in the data, with fixed effects explaining very little. Comparisons between fitted and null models suggest that neither redness (likelihood ratio test, $\chi^2 = 4.24$, $Ddf = 3$, $P = 0.52$) nor luminance ($\chi^2 = 1.57$, $Ddf = 3$, $P = 0.90$) were related to any of the tested female parameters. Full statistical results, including parameter estimates and their associated 95 % confidence intervals for each factor, can be found in Table 2 (redness) and Table 3 (luminance).

Discussion

Female Japanese macaques in Koshima undergo energetic costs linked to low food availability during the mating season that are suggested to relate to body weight losses and peculiar reproductive characteristics, e.g., delayed sexual maturation and age at first birth, and increased inter-birth intervals (Mori 1979; Iwamoto 1982; Watanabe et al. 1992; Go 2009). Data from non-human primates have shown that female facial color is linked to long-term patterns of fecundity in rhesus macaques, and related to parity and age in mandrills (Setchell et al. 2006a; Dubuc et al. 2014b). However, in our sample, we did not find evidence

Table 1 Female age, parity, dominance rank, body weight and indices of intestinal helminth infection [i.e., mean \pm SD for nodular worm eggs observed per gram of fecal sediment (EPG) and whipworm EPG, and maximum parasite species richness]

Identity	Age	Parity ^a	Rank	Body weight	Nodular worm EPG	Whipworm EPG	Maximum parasite species richness	Number of fecal samples collected
Kizu	8	0	8	7.025	1897.60 \pm 1779.91	710.80 \pm 1397.29	3	2
Kinu	17	4	11	6.500	4112.61 \pm 2585.16	4762.64 \pm 3275.74	4	7
Side	9	0	1	7.300	1515.51 \pm 860.80	126.15 \pm 151.27	2	8
Sone	14	2	14	6.875	2513.94 \pm 1535.72	167.05 \pm 284.92	4	5
Muku	10	1	17	6.725	189.44 \pm 55.70	156.63 \pm 122.36	1	8
Omoto	11	1	6	7.050	2272.04 \pm 1174.85	961.34 \pm 856.64	2	6
Asa	14	0	5	5.475	1369.22 \pm 1266.24	1504.64 \pm 1501.86	2	9

^a Number of successful pregnancies

Table 2 Results of general linear mixed-effects models examining the relationship between female facial redness ($n = 42$ images), age, parity, dominance rank, body weight, and indices of intestinal nematode infection

Factors	Redness			
	Estimate \pm SE	LCI–UCI ^a	z-value	P (\square z)
Age	-0.014 \pm 0.09	-0.20 to 0.17	0.14	0.89
Parity	-0.010 \pm 0.10	-0.21 to 0.19	0.10	0.92
Rank	0.064 \pm 0.08	-0.09 to 0.22	0.80	0.42
Body weight	0.023 \pm 0.08	-0.14 to 0.19	0.28	0.78
Nodular worm EPG	-0.066 \pm 0.08	-0.23 to 0.10	0.78	0.43
Whipworm EPG	-0.130 \pm 0.07	-0.28 to 0.02	1.70	0.09
Parasite species richness	0.095 \pm 0.07	-0.06 to 0.25	1.21	0.23

Details of the statistical approach can be found in the section Statistical analyses

^a Range from lower confidence interval (2.5 %; LCI) to upper confidence interval (97.5 %; UCI)

Table 3 Results of general linear mixed-effects models examining the relationship between female facial luminance ($n = 42$ images), age, parity, dominance rank, body weight, and indices of intestinal nematode infection

Factors	Luminance			
	Estimate \pm SE	LCI–UCI	z-value	P (\square z)
Age	0.074 \pm 0.12	-0.16 to 0.31	0.62	0.54
Parity	0.091 \pm 0.11	-0.14 to 0.32	0.78	0.43
Rank	0.122 \pm 0.10	-0.08 to 0.33	1.17	0.24
Body weight	-0.020 \pm 0.09	-0.20 to 0.16	0.22	0.83
Nodular worm EPG	-0.091 \pm 0.11	-0.31 to 0.13	0.80	0.42
Whipworm EPG	-0.074 \pm 0.10	-0.28 to 0.14	0.69	0.49
Parasite species richness	0.064 \pm 0.10	-0.14 to 0.26	0.58	0.56

Details of the statistical approach can be found in the section Statistical analyses. For abbreviations, see Tables 1 and 2

that female facial color is linked to female age, parity, dominance rank, or body weight. Temporal and individual parameters explained a great part of the observed variance in our data, suggesting that female identity itself might be a critical factor influencing facial coloration. It is possible that our data set may have been too small to detect any evidence of female signaling. Previous studies of rhesus macaque and mandrill facial coloration as signals of female characteristics have been based on larger data sets (Setchell

et al. 2006b; Dubuc et al. 2014b), whereas we conducted our analyses with 1 month's data from one subset of a particular population of Japanese macaques. Individual and seasonal factors might affect long-term variation in facial coloration that could explain our lack of significant results when looking at predictors related to a short and restricted period.

Among primates, studies have failed to link levels of parasitism with variation in facial (or sexual) color in both

males and females (Bercovitch 1996; Setchell et al. 2009; Danzy Cramer et al. 2013). Similarly, we did not find evidence supporting the hypothesis that facial redness and luminance of female Japanese macaques reflect variation in infection with intestinal helminths. Møller et al. (1999) suggested that it might be more relevant to consider measures of anti-parasite defenses (i.e., genetic or immunological qualities) rather than current parasite infections themselves to investigate the role of parasites in the evolution and expression of secondary sexual traits. Indeed, color might reflect the overall ability to cope with (resist and/or tolerate) diverse infections over long time scales rather than reflect current infections, particularly when such infections may not be overly detrimental (e.g., with common parasites that have little direct health effects on their hosts), although to date, there is no evidence for such a relationship in female primates (see Setchell et al. 2009).

One possible alternative explanation for our results relates to the nature of competition and sexual selection dynamics in Japanese macaques. In this species, there is strong intra-sexual competition between males for access to cycling females during the mating season (Furuichi 1985), and female mate choice has been found to be an active reproductive strategy, with females rejecting unfavorable mates independently of their dominance rank, age, or body weight (Huffman 1991, 1992). Consequently, we can hypothesize that female Japanese macaques may be likely to be the “choosier sex” and might not need to advertize their quality to attract males.

Female coloration might have been inherited from selection for these secondary sexual traits in males (Lande 1980; Amundsen 2000), since recent studies on rhesus macaques show that male facial coloration might play a role in mate attraction (Waite et al. 2003; Dubuc et al. 2014a, 2015). Future studies compiling long-term data on individual characteristics, reproductive success and immune parameters should be carried out to better understand the evolution of sexual ornaments in both male and female Japanese macaques and their implications for mating strategies.

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