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ORIGINAL PAPER

Is male rhesus macaque red color ornamentation attractive to females?

Constance Dubuc · William L. Allen ·
Dario Maestripieri · James P. Higham

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Abstract Male sexually selected traits can evolve through different mechanisms: conspicuous and colorful ornaments usually evolve through intersexual selection, while weapons usually evolve through intra-sexual selection. Male ornaments are rare among mammals in comparison to birds, leading to the notion that female mate choice generally plays little role in trait evolution in this taxon. Supporting this view, when ornaments are present in mammals, they typically indicate social status and are products of male-male competition. This general mammalian pattern, however, may not apply to rhesus macaques (*Macaca mulatta*). Males of this species display conspicuous skin coloration, but this expression is not correlated to dominance rank and is therefore unlikely to have evolved due to male-male competition. Here, we investigate whether male color expression influences female proceptivity toward males in the Cayo Santiago free-ranging rhesus macaque population. We collected face images of 24 adult males varying in dominance rank and age at the peak of the mating season and modeled these to rhesus macaque visual perception. We also recorded female sociosexual behaviors toward these males. Results show that dark red males received more sexual solicitations, by more females, than pale pink ones. Together with previous results, our study suggests that male color ornaments are more likely to be a product of inter- rather than intra-sexual selection. This may especially be the case in rhesus macaques due to the particular characteristics of male-male competition in this species.

Keywords Ornaments · Sexual selection · Female mate choice · Sexual skin · Color · Anthropoid primates

Introduction

Sexual selection theory explains the evolution of traits that improve lifetime reproductive success of the carrier by increasing reproductive rates rather than survival (Darwin 1871). Sexual selection pressures are stronger on males because their reproductive rate is less limited by gamete production and parental investment than in females (Bateman 1948; Trivers 1972). Male sexually selected traits can take several forms depending on the mechanism under which they evolve; while traits such as conspicuous and colorful ornaments that do not serve a direct utilitarian function usually evolve through intersexual selection (female mate choice), weapons and other traits involved in combat evolve through intrasexual selection (male-male contest competition) (Darwin 1871; Andersson 1994). While colorful ornaments are common in several clades such as birds (Darwin 1871; Hill and McGraw 2006), some other groups, including arthropods and mammals, tend to be characterized by weaponry (Emlen 2008; Clutton-Brock and McAuliffe 2009). This difference in the type of sexually selected traits exhibited by different clades has led to the notion that female mate choice plays a much greater role in some groups than others (e.g., in birds more than mammals; Clutton-Brock and McAuliffe 2009).

Primates are mammals characterized by exceptionally slow life history, low reproductive rates, and high maternal investment (Jones 2011), characteristics that have been

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C. Dubuc (✉) · W. L. Allen · J. P. Higham
Center for the Study of Human Origins, Department of Anthropology, New York University, 25 Waverly Place, New York City, NY 10003, USA
e-mail: constance.dubuc@nyu.edu

C. Dubuc · D. Maestripieri
Institute for Mind and Biology, University of Chicago, Chicago, USA

D. Maestripieri
Department of Comparative Human Development, University of Chicago, Chicago, USA

hypothesized to lead to strong female selectivity in mate choice (Trivers 1972; Andersson 1994). Yet, there is little evidence of the importance of female mate choice within this clade (reviewed in Paul 2002). Primates are unique among mammals for the number of species that exhibit conspicuous skin and pelage coloration that is hypothesized to be a product of sexual selection (Bradley and Mundy 2008; Dixson 2012), which may be linked to the evolution of trichromacy in catarrhines (though see Kamilar et al. 2013). In numerous anthropoids, conspicuous red and/or blue skin color ornaments can be exhibited in the face, genitalia, hindquarters, or chest (Dixson 2012), which are generally thought to be a result of female mate choice (e.g., Clutton-Brock and McAuliffe 2009). However, in several of these species, such ornaments have been shown to be a signal of dominance (or badge of status) (drills, *Mandrillus leucophaeus*: Marty et al. 2009; mandrills, *Mandrillus sphinx*: Setchell and Dixson 2001; Setchell and Wickings 2005; geladas, *Theropithecus gelada*: Bergman et al. 2009; crested macaques, *Macaca nigra*: Engelhardt et al. 2008; vervet monkeys, *Chlorocebus aethiops*: Gerald 2001). Such conspicuous signals of dominance may be particularly beneficial in contexts in which group members are limited in their knowledge of alpha male tenure because of large group sizes or dominance instability (Marty et al. 2009; Bergman et al. 2009; Bergman and Sheehan 2013). In contrast, there is no strong evidence that male skin color influences female mate choice in these species (Marty et al. 2009; Gerald et al. 2010; but see below). While females may be more proceptive toward males with intense red coloration in mandrills (Setchell 2005), the fact that coloration and dominance are closely linked in this species may make these two factors difficult to separate. As such, in contrast to ornaments described in birds, skin color ornaments in these anthropoid primate species appear to have evolved largely through intra- rather than intersexual selection.

This general pattern may not apply to all anthropoid primates, however. In rhesus macaques (*Macaca mulatta*), both females and males develop red skin coloration in their face, genitalia, and hindquarters. In females, at least one function of this coloration has been elucidated; female faces darken around ovulation (Dubuc et al. 2009; Higham et al. 2010, 2011). Male sexual skin color also darkens during the mating season (Baulu 1976; Higham et al. 2013), but in some males to a much greater extent than in others. The functional significance of these temporal changes and of interindividual variation in male facial coloration remains unclear. Male sex skin coloration is under the control of testosterone which influences the degree of epidermal blood flow through action on estrogen-dependent receptors (Baulu 1976; Rhodes et al. 1997). Since skin color is directly influenced by blood flow and oxygenation, it can be affected by various other endogenous and exogenous factors such as health, stress, activity, and social interactions (Changizi et al. 2006; Bradley and Mundy 2008; Dixson 2012), and may thus provide reliable information about the signaler's health and condition. While it has been suggested that rhesus males relate red coloration to social status because they avoid humans wearing bright red coloration (Khan et al. 2011), a recent study has revealed no correlation between male skin coloration or darkness and dominance status (Higham et al. 2013), suggesting that male skin ornaments may play a different function in rhesus macaques than in the species mentioned above. Males reach dominance mainly through queuing in this species, leading to high-ranking males being the longest residents of the group and thus highly familiar to all group members. In a context where social knowledge is always sufficient to identify the alpha male, signals of status may be unlikely to evolve.

An alternative possibility is that the ornament was selected through female mate choice, as observed in birds. In an experimental study, Waitt et al. (2003) showed that rhesus macaque females pay more attention to reddened versions of male faces, which suggests that they might prefer males with darker faces as mating partners. However, since the images used to prepare the red and pale stimuli were collected throughout the year in order to maximize color variation, the experimental design actually tested whether the color exhibited by males during the mating season was more attractive to females than the color exhibited in the birth season. As such, the question of whether intermale variation exhibited during the mating season, presumably less pronounced, influences female behaviors remains unsolved. Moreover, the experimental paradigm tested only female looking time, which could reflect many things—not just female sexual preference. For instance, females may have been assessing the risk of aggression from males (or any other characteristic that might be inferred from coloration), or might have been attentive to the manipulated composites of the facial images because they looked unusual.

More recently, Higham et al. (2013) found no evidence that darker rhesus males had higher copulation rates, which may appear to contradict the hypothesis that this facial skin coloration is attractive to females. However, copulation rates are not good estimates of either female preference or male reproductive success in this species. The ability of females to mate with preferred partners might be limited by mate-guarding by high-ranking males (e.g., Muller et al. 2011) and by a lack of interest from males (see Paul 2002; Soltis 2004). Furthermore, our previous studies have shown that there is very little association between male mating effort toward a female and the actual probability of siring an offspring in this population, even when mate-guarding is attempted (Dubuc et al. 2011, 2012). Consequently, studies investigating female proceptive behavior toward males exhibiting different facial skin coloration during the mating season are needed to understand the function of this trait (Higham et al. 2013).

Here, we explore whether intermale variation in sexual skin color as exhibited during the mating season influences the frequency and nature of female sociosexual behaviors toward males in rhesus macaques in a free-ranging setting. We test two alternative hypotheses: (1) increased skin color expression is attractive to females and leads to increased proceptivity toward males and (2) leads to female avoidance of, and submission to, males. In addition, we aim to replicate the results obtained in a previous study (Higham et al. 2013), indicating that male skin characteristics are not linked to male dominance rank and do not influence mating success.

Methods

Field site and subjects

The study was undertaken on Cayo Santiago, a 15.2-ha island located 1 km off the east coast of Puerto Rico managed by the Caribbean Primate Research Center (CPRC) (Rawlins and Kessler 1986). The colony was established in 1938 when approximately 400 monkeys from various locations in India were transferred to the island (Rawlins and Kessler 1986). Since its foundation, individuals have only been added to the population via natural births. Genetic analyses from pedigree data suggest no effect of inbreeding over time (A. Widdig, unpublished data) and pronounced variance in male lifetime reproductive success creates an opportunity for sexual selection in the population (Dubuc et al. 2014). At the time of the study, the population was composed of≈1,000 individuals divided in eight naturally formed multimale-multifemale troops that ranged freely throughout the island. Dates of birth were provided by CPRC. In the Cayo Santiago rhesus population, there is currently a February-July mating season, followed by an August-January birth season (Hoffman et al. 2008). Data collection took place over 3 months during the mating season (February-June 2012) in group R, which consisted of 82 adult females (≥3 years old), 42–45 adult males (≥5.5 years old), 11 subadult males (3–5 years old), and 120 immatures. The investigation was approved by the IACUC of the University of Puerto Rico, Medical Sciences Campus (protocol no. A0100108).

Assessment of male skin color and luminance

Facial images were collected noninvasively for 24 adult males that were regularly observed in the group. These males varied in age (mean ± SEM=12.0±0.8 years; range, 6.2–21.2 years) and dominance rank (mean ± SEM=16.9±2.5; range, 1–40). Male dominance relationships of the core males of the group were already known (Coyne 2011; Dubuc et al. 2013) and were supported by our field observations. Since rhesus macaques are characterized by a dominance system in which males usually queue for high status rather than fight directly to become alpha (Manson 1995; Berard 1999; van Noordwijk and van Schaik 2004), three of the study males that entered the group in 2012 were all considered peripheral and were assigned the same dominance rank at the bottom of the hierarchy.

Skin color images were collected in March 2012, at the peak of the mating season (49.1 % of the group were females and 56.2 % of our female subjects conceived during that month, assuming a 165.5-day gestation length; Silk et al. 1993) when males express sexual skin color at maximal intensity (Baulu 1976). Rhesus macaques live in stable groups in which females are unlikely to reassess the level of attractiveness of the males of the group on every day they are proceptive. Because color characteristics of the face, genitalia, and hindquarters have been shown to covary in males (Higham et al. 2013), we limited image collection to facial skin color.

Multiple images of males and a color standard (X-rite ColorChecker passport) were captured in RAW format from 1–3m away from subjects using a calibrated Canon EOS Rebel T2i camera with a 18-megapixel CMOS APS sensor and an EF-S 55–250 mm f/4–5.6 IS lens following a method previously described elsewhere (Higham 2006; Bergman and Beehner 2008; Dubuc et al. 2009; Stevens et al. 2009; Higham et al. 2013). Immediately after the capture of an image, we took a second photograph of the color standard placed in the same location and photographed under the same lighting as the subjects (i.e., the “sequential method”: Higham 2006; Bergman and Beehner 2008; Dubuc et al. 2009; Stevens et al. 2009; Higham et al. 2013). To improve measurement accuracy, when possible, we used more than one image of the face (mean, 2.4±0.1; range, 1–4) to determine average face color in a series of images and collected multiple series of images for each male (mean, 2.5±0.03; range, 1–5) collected over a period of 6.9±1.1 days (range, 0–18).

Facial skin color was quantified by measuring color values from images converted to 16-bit TIFF files using DCRAW (Dave Coffin). We first took average red (R), green (G), and blue (B) measurements (reflecting the camera sensor stimulation) from the portion of the face, and the neutral gray patches of the color standard illustrated in Fig. 1. The segmented area of the face included the bridge of the nose and all visible skin between the nostrils and the corners of the eyes. Landmarks selected around this area were joined using cubic spline interpolation using a customized MATLAB function. We selected this portion of the face because the color is relatively uniform, and in order to minimize the effect of any local variation, we averaged measurements over a large area and avoided any areas that may have influenced color measurements, such as dirt, dappled light, or shadows.

RGB values for the faces and standards were then transformed from the camera’s color space to rhesus color space. This was achieved by calibrating the camera to determine the

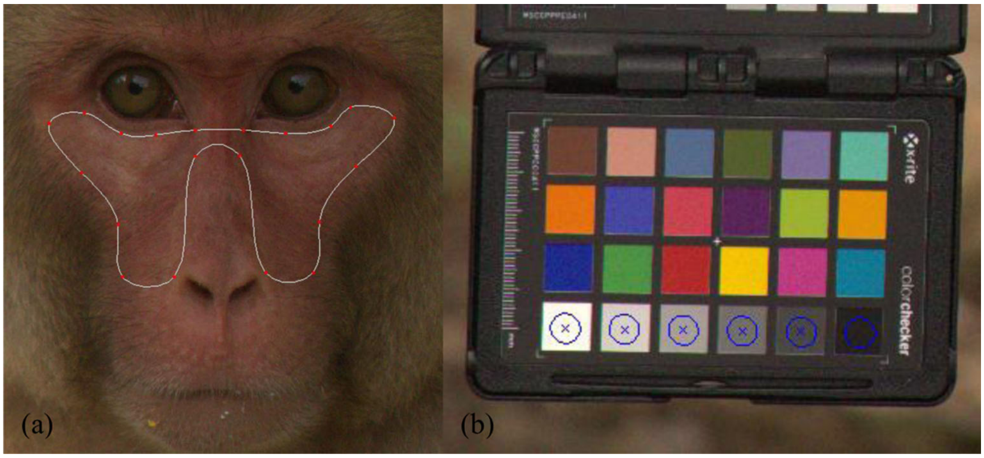


Fig. 1 **a** Segmented area selected for facial R, G, and B measurement. **b** Measurement of the neutral gray patch of the X-rite ColorChecker passport color rendition chart. The RGB values of the *white square* are used to standardize color measurements from associated face images. Credit: Sandra Winters

linearity of the sensors responses to different levels of light intensity and their spectral sensitivity. Linearity was determined by photographing a patch of barium sulphate illuminated by a stabilized tungsten light source through a range of neutral density filters and comparing camera responses to corresponding spectrophotometer measurements. Spectral sensitivity was estimated by imaging the patch through narrow bandpass filters with peaks every 10 nm from 400 to 700 nm and comparing it to spectrophotometer measurements. A linearization equation incorporating modeling of the exposure settings and a polynomial color space transformation from the camera's color space to rhesus color space were calculated using methods described elsewhere (Stevens et al. 2007). Rhesus color space was specified using medium wavelength (MW) and long wavelength (LW) sensitivity curves from Bowmaker et al. (1978) and were set as 535 and 565 nm, respectively. Finally, to standardize skin color values and model color constancy processing, we corrected for variation in lighting by applying the Von-Kries transformation (Ives 1912; reprinted in Brill 1995) using the white patch of the color checker as the white point, after confirming that values were not clipped by examining the relationship between the white patch and the other gray patches.

Measurements from multiple face images taken of the same subject during the same series and multiple accompanying standards were averaged to yield that subject's overall facial skin color phenotype. We calculated male facial color as (LW −MW)/(LW+MW) (the red-green opponency channel, hereafter R-G) and luminance as (LW+MW)/2 (corresponding to luminance vision; Osorio and Vorobyev 2005). The underlying physical basis of variation in redness reflects variation in levels of blood oxygenation, such that redder skin contains more oxygenated blood, while variation in luminance (or darkness) reflects a variation in blood flow (where greater saturation of blood is darker, and thus less luminous) (Changizi et al. 2006; Stephen et al. 2009). Male facial R-G and luminance were calculated based on the average among the series; when more than one series was collected on a given day, we averaged within each series first. The average intraindividual coefficient of variation (CV) between images of the same set was redness, 6.5 % and luminance, 3.0 % and between sets of images was redness, 19.0 % and luminance, 8.5 %. Male facial skin luminance and R-G were significantly negatively correlated (Pearson rho=−0.405, p=0.049, N=24), meaning that darker males were also redder and paler males are also less red (Fig. 2).

Behavioral data collection

Behavioral data were collected 5–6 days a week from 7:30–14:00 (the opening hours of the site) on known individually recognizable individuals, for a total of 363 h of group contact distributed over 60 days (March-May, inclusively). Sociosexual interactions between adult males of the group and 32 parous females of various ages (mean ± SEM, 7.7 years±3.2; range, 4–19) and dominance ranks (41±25; range, 3–76) were recorded by all occurrence sampling (Martin and Bateson 1986; Altmann 1974) by CD with the help of trained assistants. We selected this sampling method because our aim was to assess the frequency and distribution of a specific set of short-term behaviors (rather than their duration) among several group members in a context where up to 20 females could be sexually active per day (average, 5 females/day; range, 0–20). Yet, this method introduces the risk of biasing behavioral data collection toward certain males, e.g., the most central males of the group who are more likely to be observed. Indeed, contrary to females, there is a great variation in centrality among males, with low-ranking males being extremely peripheral, often living at the edge of the group. To control for this, we calculated an estimate of their relative observability, as the number of days of the mating season each subject male was encountered in the group and included this as an offset in the statistical analyses (see below). Observability varied between males (mean ± SEM=44.5± 2.4 days; range, 17–60 days) and was correlated to male dominance rank (Spearman rank correlation: r_s=−0.459,

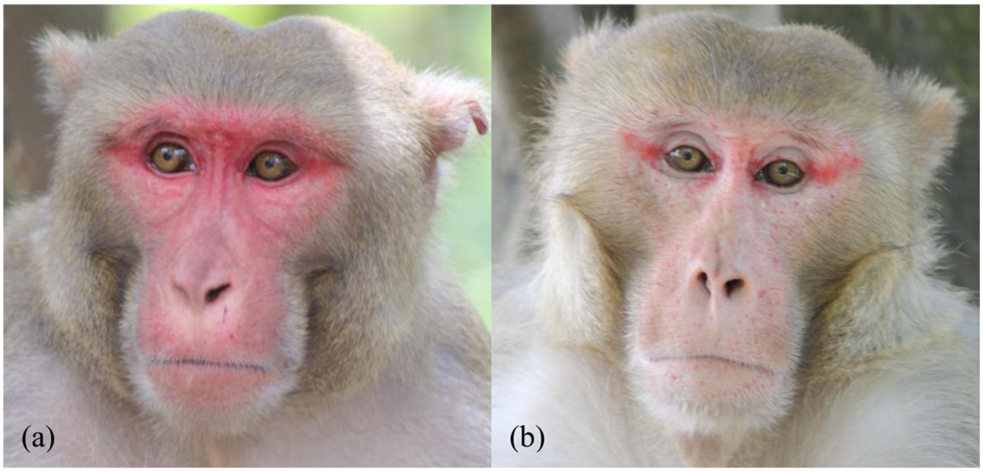


Fig. 2 Illustration of the individual variation in skin color characteristics males can exhibit during the mating season in Cayo Santiago rhesus macaques. The two males were photographed 12 min apart on the same day. The male on the left (**a**) was among the darkest and reddest male of the dataset (i.e., a dark red male), while the male on the right (**b**) was the palest and least red (i.e., a pale pink male)

p=0.024, N=24), such that higher-ranking males were more observable than lower-ranking ones. However, observability was not correlated with skin characteristics (luminance: r_s=−0.020, p=0.928; R-G: r_s=−0.041, p=0.848), indicating that observations were not biased toward darker or paler males.

We assessed female attraction toward males based on the occurrence of the two most frequent proceptive behaviors (i.e., behaviors aimed at soliciting sexual encounters; Michael and Zumpe 1970): (i) presentation of the hindquarters to a male (presentation), complete or partial (hindquarter not facing male completely) and (ii) hand slap (a rapid flexion and extension of the hand and arm that usually leads to it hitting the ground; also known as sporadic arm reflex and hand-reach) (Carpenter 1942; Michael and Zumpe 1970; Wallen et al. 1984; Dixson 2012). These two behaviors have been shown to be expressed in the same context and to have the same function and were thus pooled together to create a measure of proceptivity (for a similar approach, see Zumpe and Michael 1970). When several proceptive behaviors (hereafter, solicitations) were emitted during a sexual interaction, we recorded them only once. Because male rhesus macaques often ejaculate at the end of a mating series that can last as long as 56 min (median of 7 min; Manson 1996) and as the mean inter-ejaculation interval in this species is 26.8 min (Bielert and Goy 1973), we considered two sexual interactions taking place within 30 min as being part of the same event. We also recorded all instances of mating series using this same criterion and considering only mounts with intromissions that took place outside of an agonistic context. We recorded all instances of female submissive behavior (hereafter, submissions) directed toward each group male, including avoidances, displacements, escapes, screams, fear grimaces, and crouches. Submissions were recorded regardless of whether they were unsolicited (i.e., emitted at the sight of the male) or provoked by a threat or aggression from a male. In cases of a series of agonistic interactions between a male and a female, only one instance was recorded.

All behaviors of a same category were combined for analyses (solicitations or submissions). For each male, we calculated the number of females from which they received these behaviors and the total number of times females emitted these behaviors toward them, creating one measure per male for each of these two variables. The same two variables were created for male mating success: the total number of mating series and the total number of mating partners.

Data analyses

We used general linear models (GLMs) to test whether male sexual skin color (R-G) and luminance (fixed effects) influence female behaviors toward males (response variable) while controlling for male dominance rank and age (fixed effects) and observability (offset). We first ran a series of models in which both luminance and R-G were included as continuous predictors and then a second series in which skin color characteristics were set as an ordinal predictor. To do so, we divided males into three categories: (i) males that were both below the median for luminance and above for R-G (hereafter, dark red males; N=8), (ii) males that were both above the median for luminance and below for R-G (hereafter, pale pink males; N=8), and (iii) other males (hereafter, intermediate males; N=8). We then created an ordinal variable with dark red males scoring 1, intermediate males scoring 2, and pale pink scoring 3. We opted for this approach in order to consider the possibility that female perception and decision-making might not be based on differentiation of males on a continuous range of color perception, but through classification of males into categories, e.g., dark red, intermediate, and pale males. Figure 2 illustrates the difference between a dark red male and a pale pink male. We fitted a Gaussian distribution to all models (instead of a Poisson) because these models yielded better fits, better distributions of residuals, and lower Akaike's information criterion (AIC) values. We square root-transformed all behavioral variables related to the number of females emitting the behaviors and log-transformed the ones related to the number of interactions to ensure that models met assumptions on the distribution of residuals. Male dominance rank was not a significant factor in any of the models, but removing it did not affect the models (AIC differences ≤ 2) and was thus kept in models. We also ran GLMs to test whether male dominance rank and age (predictors) influenced male skin luminance and R-G (response variables); here, no data transformation was required to ensure that model assumptions were met. Variance inflation factors (VIF) were below 1.5 in all models, indicating a lack of multicollinearity in the models. GLMs were performed in R 2.15.2, and other statistical analyses were performed in IBM SPSS Statistics 20.0.0. The significance level was set at $\alpha = 0.05$.

Results

Males were solicited on average ± SEM (7.4±1.5) times (range, 0–29) by 4.3±0.7 females (range, 0–13). Dark red males were solicited more often and by more females than males of other categories (Table 1, Figs. 3 and 4). Dark males were solicited 11.2±3.6 times by a total of 6.0±1.5 females, which is twice as frequently as intermediate (6.0±1.6 solicitations by 3.9±0.9 females) and pale males (4.9±1.4 solicitations by 3.0±0.9 females). While models based on continuous or ordinal variables of skin color yield yielded similar results, the effect was stronger and AIC values lower in models using an ordinal variable to describe skin color.

Males received 22.2±3.6 submissions (range, 2–64) from 12.0±1.4 females (range, 2–26). Male skin characteristics did not influence female submissions (Table 1, Fig. 4): dark red males received 26.4±6.5 submissions by 13.5±2.1 females, while intermediate males received 16.3±4.0 submissions by 10.0±1.8 females, and pale males, 25.0±7.4 by 12.9±3.1.

As for other male characteristics, male age, but not rank, affected female behavior, with young males receiving more solicitations and submissions than older males (Table 1; Fig. 5). As predicted, dominance rank and age did not influence male skin color (rank: $t=0.234$, $p=0.817$; age: $t=0.996$, $p=0.331$, $N=24$) or luminance (rank: $t=-0.516$, $p=0.611$; age: $t=0.03$, $p=0.620$), and skin characteristics did not influence the two measures of male mating success, number of mount series and number of mating partners (Table 1). Dark red males were involved in 12.0±5.4 mating series with 3.6±1.2 females, intermediate males in 11.9±4.3 series with 3.0±0.9 females, and pale males in 8.1±3.0 series with 3.8±1.2 females.

Discussion

Our results support the hypothesis that male facial color is attractive to females in a mating context: males with dark red faces were sexually solicited more often by females and by a greater number of females. Females appear to have been attracted to these males in particular, rather than expressing a gradual increase in attraction proportional to intermale variation in skin color. In contrast, there was no support for the hypothesis that male facial sexual skin is associated with female avoidance and submissive responses to males. Therefore, our findings provide evidence that male red skin ornaments play a role in female mate choice in rhesus macaques and extends the findings of Waitt et al. (2003) to show that (i) intermale skin color variation exhibited at the peak of the mating season is sufficient to influence female behavior and that (ii) differential attention toward dark red faces is linked to sexual attraction.

Variation in the expression of sexual skin ornaments did not influence male mating success, as previously reported from analyses using a different dataset from different males and observation years (Higham et al. 2013). Although a trait must influence fitness to evolve through evolutionary processes such as mate choice, we have previously shown that both the frequency of mating and of mate guarding are poor predictors of reproductive success in this population (Dubuc et al. 2011, 2012). This is probably because mating success typically underestimates the importance of sneak copulations and of postcopulatory mechanisms such as sperm competition (e.g., Amos et al. 1993; Inoue et al. 1993; Coltman et al. 1999). Moreover, short-term measures of male reproductive success are known to be poor predictors of longer-term reproductive success in long-lived mammals (Clutton-Brock 1988; Alberts et al. 2006). In this population, male yearly reproductive output is not evenly distributed across a male's reproductive life (Bercovitch et al. 2003; Dubuc et al. 2014), leading cross-sectional approaches to produce inaccurate estimates of inter-individual variation in reproductive output. However, it also remains possible that male skin color variation does not translate into variation in fitness, for example, because female attraction to redness is not adaptive, but a byproduct of sensory biases. A long-term project using genetic paternity data will be needed to explore the question of whether skin color is linked to male lifetime reproductive success.

In contrast to some other animal clades, mammalian males tend to evolve weaponry and fight over access to females rather than exhibit ornaments involved in female mate choice (Emlen 2008; Clutton-Brock and Hichard 2013). The difference between rhesus macaque coloration and the types of color ornaments seen in most mammalian species is likely to be linked to the unusual male-male competitive regime they exhibit. In this species, the monopolization potential of the alpha male is low (Dubuc et al. 2011, 2012), sexual

Table 1 Results of GLM analyses testing the effect of male facial skin characteristics (fixed effect) on the number of females interacting with males and the number of interactions with males for each behavioral category (response variable) accounting for male dominance rank and age (fixed effects). We square root-transformed all variables related to number of females emitting the behaviors and log-transformed the ones related to the number of interactions

		Number of females	Number of interactions
Proceptive behaviors			
Continuous	Model	$F_{4,19}=4.861, p=0.007$*, AIC=60.561	$F_{4,19}=3.001, p=0.045$*, AIC=71.606
	Luminance	$t=-2.124, p=0.047$*	$t=-1.667, p=0.112$
	R-G	$t=-0.369, p=0.716$	$t=-0.403, p=0.692$
	Rank	$t=0.196, p=0.847$	$t=-0.165, p=0.870$
	Age	$t=-2.802, p=0.011$*	$t=-2.056, p=0.054$
Ordinal	Model	$F_{3,20}=7.477, p=0.002$*, AIC=56.817	$F_{3,20}=4.780, p=0.014$*, AIC=67.886
	Skin category	$t=2.741, p=0.013$*	$t=2.236, p=0.037$*
	Rank	$t=0.700, p=0.492$	$t=0.217, p=0.830$
	Age	$t=-3.193, p=0.005$*	$t=-2.391, p=0.027$*
Submissions			
Continuous	Model	$F_{4,19}=5.146, p=0.006$*, AIC=64.094	$F_{4,19}=4.542, p=0.010$*, AIC=57.397
	Luminance	$t=-1.399, p=0.178$	$t=-1.752, p=0.096$
	R-G	$t=-1.636, p=0.118$	$t=-0.545, p=0.139$
	Rank	$t=-1.817, p=0.085$	$t=-0.836, p=0.414$
	Age	$t=-1.669, p=0.112$	$t=-1.781, p=0.091$
Ordinal	Model	$F_{3,20}=5.260, p=0.008$*, AIC=65.045	$F_{3,20}=4.426, p=0.015$*, AIC=58.347
	Skin category	$t=0.751, p=0.467$	$t=1.030, p=0.315$
	Rank	$t=-1.457, p=0.161$	$t=-0.441, p=0.664$
	Age	$t=-1.959, p=0.064$	$t=-2.039, p=0.055$
Copulations			
Continuous	Model	$F_{4,19}=5.730, p=0.003$*, AIC=60.469	$F_{4,19}=4.311, p=0.012$*, AIC=81.436
	Luminance	$t=-1.070, p=0.298$	$t=-1.643, p=0.117$
	R-G	$t=-1.883, p=0.388$	$t=-1.367, p=0.188$
	Rank	$t=-1.882, p=0.389$	$t=-0.887, p=0.386$
	Age	$t=-2.784, p=0.012$*	$t=-2.337, p=0.030$*
Ordinal	Model	$F_{3,20}=6.958, p=0.002$*, AIC=59.865	$F_{3,20}=4.348, p=0.016$*, AIC=82.378
	Skin category	$t=0.375, p=0.711$	$t=-0.717, p=0.481$
	Rank	$t=-0.653, p=0.521$	$t=-0.501, p=0.622$
	Age	$t=-3.034, p=0.007$*	$t=-2.621, p=0.016$*

*$p<0.05$ (significant results)

dimorphism in body size, and canine length is less pronounced compared to many closely related species (Plavcan 2001), while relative testis volume is greater (Bercovitch and Nürnberg 1996). All these factors are suggestive of low male-male direct competition and high indirect competition in this species. Consistent with this, males tend to queue for high rank instead of fighting directly (Berard 1999; van Noordwijk and van Schaik 2004). In such a context, females are not only better able to freely exert direct mate choice because of reduced coercion, but they may also benefit more from investing time and energy in selecting mates based on traits other than dominance rank which, as males have not fought over it directly, is unlikely to represent male quality (see Dubuc et al. 2011, 2012). Further supporting this view, females do not exhibit preferences for high-ranking males in a sexual context in this species (Chapais 1983; Manson 1992) and in our study, actively solicited darker males and young males. A closer look at the data reveals that males that were solicited more than average were all between 6 and 12 years old, the age at which males of the population are the most successful (Bercovitch et al. 2003; Dubuc et al. 2014). Similar work in other species characterized by limited male-male contest competition and reduced male coercion toward females will be needed to assess whether this is a general phenomenon leading to selection for ornaments that function in mate choice rather than dominance signaling.

While this phenomenon may also take place in other animal species, it remains unclear why ornaments involved in

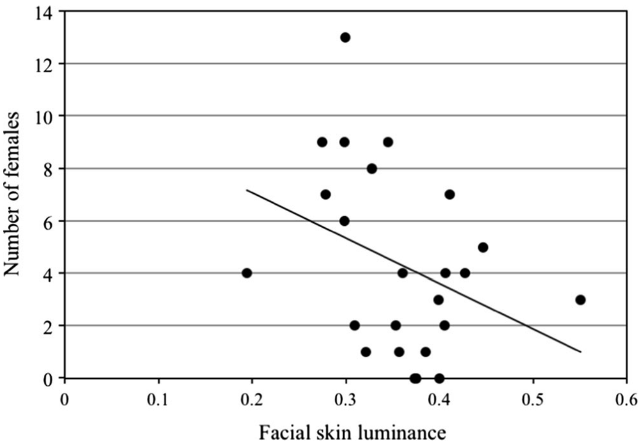


Fig. 3 Relationship between male facial skin luminance and the number of females that solicited them during the mating season for 24 subject males (data presented without transformation). The *regression line* of the relationship between the two variables is displayed. Note that darker skin color leads to lower luminance values

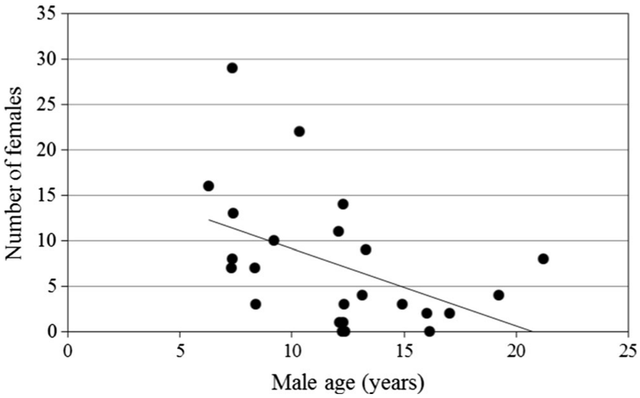
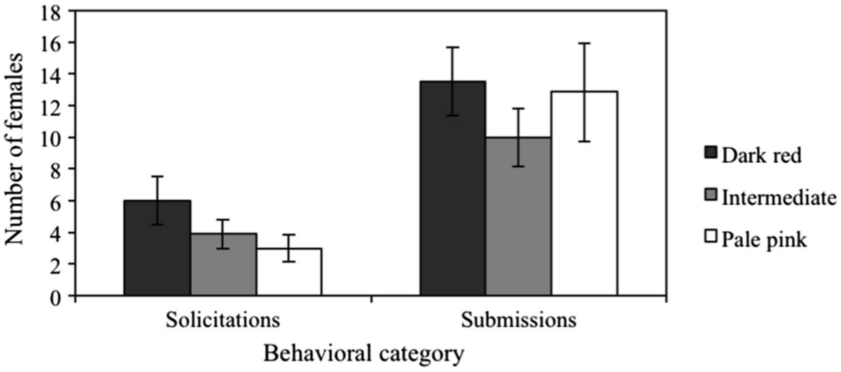


Fig. 5 Relationship between male age and the number of females that exhibited proceptive behaviors toward them during the mating season for 24 subject males. The *regression line* of the relationship between the two variables is displayed

mate choice are so rare in mammalian clades other than anthropoid primates when compared to birds (Clutton-Brock and McAuliffe 2009). Primates might represent a case of convergence with birds in this regard, which could be due to different factors. For instance, it has been proposed that female mate choice might play a larger role in trait evolution in birds than in mammals because in birds, males are limited in their ability to coerce females which can easily escape by flying away (Pradhan and van Schaik 2009). Since primate species are often arboreal, this may (i) facilitate female escapes of male coercion via the canopy and (ii) limit the development of body size dimorphism. Moreover, when compared to mammals, birds have more varied pathways for the production of color patterns (e.g., carotenoids), have better color vision, and are more frequently diurnal. Similarly, the loss of hair on the face and area surrounding the genitalia along with the development of trichromatic color vision in many diurnal anthropoid primates might make the evolution of such ornaments more likely.

The next step will be to establish why rhesus macaque males with darker faces are more attractive to females, a question that remains open for most colorful ornaments observed in the animal kingdom. Red skin ornaments may be an example of condition-dependent ornament providing females with honest and reliable information about male quality. Indeed, skin color change is linked to variation in blood flow and oxygenation (reviewed in Bradley and Mundy 2008; Dixson 2012), which are in turn likely to be associated to health (see Changizi et al. 2006; Stephen et al. 2009). Moreover, intra-male development of rhesus male skin coloration during the mating season is under testosterone control (Vandenbergh 1965; Baulu 1976; Rhodes et al. 1997). Since high testosterone levels may suppress immune function (see Wingfield et al. 1990), it has been proposed that only males of higher quality may be able to develop intense and dark coloration (Folstad and Karter 1992; Clutton-Brock and McAuliffe 2009; see also Waitt et al. 2003). However, the fact that intermale variation in skin color is not linked to variation in testosterone levels in the study population (Higham et al. 2013) does not support this view. It may be that both androgen levels and estrogen receptor expression in the sexual skin need to be assessed at the same time before the function of red skin coloration can be fully understood (Higham et al. 2013). Further studies are also needed to determine which qualities

Fig. 4 Variation among three male categories in the average± SEM number of females that exhibited proceptive and submissive behaviors toward them (data presented without transformation)



male color expression correlates with and understand why females preferentially choose males with these qualities as their mating partners.

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