



Original Article

Is male rhesus macaque facial coloration under intrasexual selection?

Megan Petersdorf,^a Constance Dubuc,^{a,†} Alexander V. Georgiev,^{b,c} Sandra Winters,^a and James P. Higham^a

^aDepartment of Anthropology, New York University, 25 Waverly Pl, New York, NY 10003, USA,

^bInstitute for Mind and Biology, The University of Chicago, 940 E 57th St, Chicago, IL 60637, USA, and

^cSchool of Biological Sciences, Bangor University, Deiniol Road, Bangor, Gwynedd LL57 2UW, UK

Received 12 December 2016; revised 10 July 2017; editorial decision 18 July 2017; accepted 27 July 2017.

Exaggerated male traits can evolve under intra- or intersexual selection, but it remains less clear how often both mechanisms act together on trait evolution. While the males of many anthropoid primate species exhibit colorful signals that appear to be badges of status under intrasexual selection, the red facial coloration of male rhesus macaques (*Macaca mulatta*) appears to have evolved primarily under intersexual selection and female mate choice. Nonetheless, experiments show that red color is salient to males, raising the question of whether the signal may also be under intrasexual selection. Here, we examine whether males express this signal more strongly in competitive contexts. Facial images were collected on all 15 adult males of a free-ranging social group during the peak of the mating season, and coloration was quantified using visual models. Results show that males more similar in facial redness were more likely to interact aggressively than more dissimilar ones, suggesting that color may be involved in the assessment of rivals. Furthermore, males exhibited darker coloration on days they were observed copulating, and dominance rank predicted facial redness only on copulating days, suggesting that coloration may also advertise motivation to defend a mate. Male rhesus macaque facial coloration may thus mediate agonistic interactions with rivals during competition over reproductive opportunities, such that it is under both inter- and intrasexual selection. However, color differences were small, raising perceptibility questions. It remains possible that color variation reflects differences in male condition, which in turn alter investment towards male–male competition and mating effort.

Key words: color, male–male competition, sexual selection, signaling.

INTRODUCTION

Sexual selection theory explains the evolution of elaborate traits that increase an individual's lifetime reproductive success via 2 main mechanisms: competition between members of the same sex for reproductive opportunities with the opposite sex (intrasexual selection), and mate choice for attractive members of the opposite sex (intersexual selection) (Darwin 1871; Andersson 1994). While it was originally proposed that armaments directly involved in fights have evolved through intrasexual selection and ornaments involved in communication through intersexual selection (Darwin 1871), it is now apparent that the function of male sexually-selected traits is less clear-cut. Competition between members of the same sex may lead to the evolution of armaments that are used to fight directly, but which may also act as a signal of strength to mediate conflicts or intimidate rivals (Bradbury and Vehrencamp 2011; McCullough

et al. 2016). Moreover, there is increasing evidence that such signals can then secondarily be under intersexual selection, with females preferring males that signal their strength and competitive ability (e.g., Berglund et al. 1996; Candolin 1999; Borgia and Coleman 2000; Wong and Candolin 2005). The opposite also appears to occur: ornaments that have primarily evolved through intersexual selection might be secondarily under intrasexual selection if these signals allow same-sex conspecifics to assess the competitiveness of rivals (e.g., Morris et al. 2007). Since male ornaments can serve multiple functions, it is important to examine the current role they may play in both intra- and intersexual selection (Hunt et al. 2009).

One interesting group in which to study these questions are the Primates, which are unique among mammals in that many species exhibit conspicuous coloration of the skin and pelage (Bradley and Mundy 2008). These colorful traits have been proposed to be the product of female mate choice (Clutton-Brock and McAuliffe 2009) similar to how bright colors function to attract mates in birds. In contrast to bird ornaments, however, they appear to instead be “badges of status” in males in most species studied to date, and correlate strongly with dominance rank (e.g., mandrills, *Mandrillus*

Address correspondence to M. Petersdorf. E-mail: megan.petersdorf@nyu.edu.

[†]C. Dubuc is now at the Large Animal Research Group, Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK

sphinx: Setchell and Wickings 2005, Renoult et al. 2011; crested macaques, *Macaca nigra*: Engelhardt et al. 2008; drills, *Mandrillus leucophaeus*: Marty et al. 2009; geladas, *Theropithecus gelada*: Bergman et al. 2009; black-and-white snub-nosed monkeys, *Rhinopithecus bieti*: Grueter et al. 2015). Further, coloration rapidly changes following changes in dominance (e.g., mandrills: Setchell and Dixson 2001, geladas: Bergman et al. 2009). Such conspicuous signals may be particularly likely to evolve when conspecifics do not have social knowledge about dominance status (Bergman and Sheehan 2013).

Unlike these other species studied to date, in the rhesus macaques (*Macaca mulatta*) of Cayo Santiago, male coloration does not correlate with dominance rank (Higham et al. 2013; Dubuc et al. 2014a). Instead, there is evidence that coloration is used in female mate choice, in an analogous way to the male ornaments seen in taxa such as birds (Waite et al. 2003; Dubuc et al. 2014a; Dubuc et al. 2016). Despite this, facial coloration is nonetheless salient to other males. A subset of adult males show an attentional bias toward images of dark red compared to pale pink males, although less pronounced than females' bias (Dubuc et al. 2016), a pattern that cannot be explained by general sensory bias of the species (Hughes et al. 2015; Dubuc et al. 2016). Moreover, rhesus macaque males avoid humans wearing red, such that they are more likely to steal food in an experimental context from a human "competitor" wearing blue or green (Khan et al. 2011), suggesting that red coloration may be intimidating to them. This raises the question of whether sex skin coloration may function to mediate aggressive interactions in reproductive contexts, even if it is not correlated with dominance status.

There might be good reasons why red skin coloration could be involved in intrasexual selection without being a signal of status in Cayo Santiago rhesus macaques. Males of this population mainly queue for dominance, such that dominance rank is best predicted by tenure length (Manson 1995; Berard 1999). In such a context, group stability might make badges of status obsolete (cf. Bergman and Sheehan 2013). However, since dominance rank is not a reliable social cue of physical strength (van Noordwijk and van Schaik 2004), males might nonetheless gain by signaling their competitiveness through red skin coloration in order to avoid costly conflicts. One reason to expect links between male facial redness and condition relate to the mechanisms underlying color expression. Unlike carotenoid-based skin color changes seen in many animal species, facial skin color changes in rhesus macaques are related to blood flow, as well as the relative proportion of oxygenated to deoxygenated blood. These changes are under the control of estrogen in females, and testosterone in males, which is converted to estrogen by aromatase in the skin. Skin coloration is thus influenced by blood flow and oxygenation, and may as such be related to underlying health and condition.

Here, we aim to examine whether male red facial coloration is under intrasexual selection in rhesus males. Based on findings in other primate species in which dominance rank is linked to color expression, we predict that male facial coloration is more strongly expressed in contexts generating intense competition. After controlling for dominance rank and age, we predict that: 1) darker/redder males are more aggressive and less submissive than paler/less red males; and that 2) facial coloration mediates dyadic male–male interactions. In particular, we expect that: 2.1) facial coloration will predict the occurrence of agonistic encounters in which the winner in the interaction is lower ranking than the loser but expresses darker/redder coloration; and 2.2) males similar in color will interact more aggressively whereas males markedly different in color will

avoid conflict. Finally, we predict that 3) males will express signals in response to mating activity to advertise motivation to defend a female against other males. Specifically, 3.1) males will express a darker and/or redder signal on days observed copulating with females; 3.2) and/or when more females in the group are mating on a given day.

METHODS

Study site and subjects

This study was conducted on the free-ranging rhesus macaques of Cayo Santiago, a 15.2-hectare island located 1 km off the eastern coast of Puerto Rico. The current population of the island is descended from 409 rhesus macaques that were introduced from India in 1938 (Rawlins and Kessler 1986), and is currently managed by the Caribbean Primate Research Center of the University of Puerto Rico. During the study period, the population consisted of approximately 1300 individuals divided into 9 naturally-formed social groups. All individuals range freely, but are provisioned with commercial monkey chow and ad libitum access to clean water. Reproduction is seasonal, with a 6-month mating season currently occurring between February and July, followed by a 6-month birth season between August and January (Hoffman et al. 2008; Hernández-Pacheco 2016). Data for this study were collected in Group S between 21 February 2013 and 12 April 2013, encompassing the peak of the mating season, when males express the maximal intensity of sexual skin coloration (Baulu 1976). At that time, group S consisted of 128 individuals, including 15 adult males (≥ 5 years old) and 42 adult females (≥ 3 years old) (Georgiev et al. 2015, 2016). All subjects are individually recognizable from ear notches and tattoos. Dates of birth are known from long-term records of the population; as of 1 March 2013, the study subjects ($N = 15$ adult males) had a mean age of 8.4 years (SEM ± 0.7 ; range: 5.3–13.3).

Collection and measurement of sexual skin color and luminance

Rhesus macaques exhibit sexual skin coloration of the face, hind-quarters, and genitals, which has been shown to significantly positively correlate across regions in males (Higham et al. 2013). Digital photographs of the faces of study males were collected across the study period. Images were taken when subjects were 1–3 m away, and captured in RAW format using a color-calibrated Canon EOS Rebel T2i camera with an 18-megapixel CMOS APS sensor and an EF-S 55–250 mm f/4–5.6 IS lens. To standardize images for ambient light and camera settings, the "sequential method" (Higham 2006; Bergman and Beehner 2008) was used, in which immediately after a facial photograph was taken, a second photograph of a color standard (X-Rite ColorChecker Passport) was taken in the same location as the subject. If possible, multiple images of the face (mean \pm SEM 2.75 ± 0.06 , range 1–4) were taken to determine average face color measurements in a series of images at a given time point. Multiple series of images for each male (6.8 ± 0.75 , range 1–11) were taken across the study period, every 5.2 ± 0.48 days (range 0–16). We have previously undertaken analyses of within- and between- series repeatability of these measurements using the same camera and on the same population. We found that the intraindividual coefficient of variation (CV) between images of the same set was redness 6.5%, and luminance 3.0%, and between different sets of images was redness 19.0%, and luminance 8.5% (Dubuc et al. 2014a).

Skin coloration was quantified using methods previously described elsewhere (Dubuc et al. 2014a). Briefly, images were converted to 16-bit TIFF files using DCRRAW (Coffin 2015), and average red (R), green (G), and blue (B) measurements were taken from a fixed portion of the face and the neutral gray patches from the color standard. RGB values were computationally transformed from the camera's color space to rhesus color space using standard visual modeling methods (Stevens et al. 2007, 2009), resulting in estimates of rhesus long (LW, 565 nm), medium (MW, 535 nm), and short (SW, 431 nm) wavelength photoreceptor catches (data from Bowmaker et al. 1978, Hárosi 1987). Two measures of facial coloration were then calculated: the red-green opponency (R-G) channel $(LW-MW)/(LW+MW)$, and the luminance channel $(LW+MW)/2$ (Osorio and Vorobyev 2005). Both R-G and luminance were calculated for every image, averaged within a series of images at a given time point, and averaged across series within a day when applicable. Color measures were further averaged weekly for a subset of analyses (see Statistical Analyses for details). As in previous studies (Dubuc et al. 2014a), male facial skin R-G and luminance are inversely related: redder males (greater R-G) are generally darker (lower luminance), and less red males (lower R-G) are generally paler (higher luminance) (linear mixed model with response R-G, fixed effect luminance, random effect male ID: $F_{1,74.9} = 6.354$, $P = 0.01$). However, as the 2 measures may be related to different aspects of condition, with R-G variation more related to the proportion of oxygenated to deoxygenated blood, and luminance to blood flow, we analyzed both measures separately.

Behavioral data collection

Data were collected between 7:30 and 14:00 by trained observers 5 days a week for a total of 195 group contact hours across 30 days. Restrictions on observation time are a constraint of needing boat captains to arrive on and leave the island, but observations made by one of us (J.P.H.) up to 17:00 h during 2009 suggest that agonistic and mating behaviors observed prior to 14:00 h each day are representative of those later in the day. Focal and ad libitum sampling (Altmann 1974) of study males was used to record all occurrences of agonistic and/or submissive interactions between males and of copulations with adult females (Georgiev et al. 2015, 2016). Agonism included displays, aggression (threaten, displace, charge, chase, physical attack), and submission (avoid, fear grin, cower, flee, scream) directed at another individual. Submissions were restricted to those unprovoked by another male. Focal samples were short (5 min in duration) but frequent (every 1–2 h) in order to sample the focal subject's activity throughout the day. A total of 1534 focal samples were conducted (mean \pm SEM: 102.3 ± 15.5 per male, range: 34–195) during the study period.

Dominance rank

Dominance rank was calculated using the outcome of dyadic agonistic interactions between all males in the study period from focal and ad libitum observations ($N = 226$). Males were assigned as the winner or loser of each interaction based on displacement (winner is the displacer), threats (winner threatens), charge/chase (winner is charger/chaser), physical attack (winner is the attacker), avoidance (winner is the avoided animal), fear grin (winner receives fear grin), cower (winner is cowered at), flee (winner is fled from), and scream (winner is the animal screamed at). The dominance hierarchy was calculated using the I&SI method, which minimizes the number (I) and strength (SI) of inconsistencies between dyads to

find the rank order most consistent with a linear hierarchy (de Vries 1998, Schmid and de Vries 2013). Four optimal hierarchies (I = 1, SI = 2) were found that correlated most strongly with David's Scores (a complementary ranking method, Gammell et al. 2003; $r_s = 0.988$). The hierarchies only differed in positions 12–14 (of 15 rank positions) and the most parsimonious hierarchy was selected. The hierarchy was significantly linear (Landau's $h = 0.854$, de Vries $h' = 0.555$, $P < 0.01$) with high directional consistency (DCI = 0.964). The I&SI method was employed using the software package DomiCalc (Schmid and de Vries 2013); linearity and DCI were calculated with the R package "compete" (Curley et al. 2015).

Statistical analyses

All statistical analyses were run in R version 3.1.3 (R Core Team 2015).

Overall agonism

To examine whether darker/redder males were more aggressive, received less aggression, and received more submissions, agonistic behavioral observations from focal samples were collapsed into 5 different categories for analysis: aggression given and received, submission given and received, and display given. Focal observations consisted of 237 instances of agonism from 14 of the 15 study males (aggression given: $n = 25$, aggression received: $n = 30$, submission given: $n = 87$, submission received: $n = 48$, display given: $n = 47$). Some of these variables are correlated, with aggression given positively correlated to submission received (Poisson generalized linear mixed model [GLMM] with male ID as random effect: $z = 4.425$, $P < 0.001$) and submission given positively correlated with aggression received (Poisson GLMM $z = 5.883$, $P < 0.001$). We nonetheless analyzed these variables separately, because the tendency to undertake aggression, or to submit, are potentially separate behavioral mechanisms that might link coloration to dyadic outcomes. Not all males had both agonistic behaviors and luminance/R-G scores collected within the same week for each of the 5 weeks of the study (median: 4, range: 1–5). There were 57 unique "male weeks" (unique male-week combinations) out of a possible 75 that included weekly counts of agonistic behaviors, total number of weekly focal samples, and weekly averages of facial skin luminance and R-G.

To investigate whether sexual skin luminance and R-G are associated with the frequency of aggressive/submissive behavior given or received by males, we used zero-inflated GLMMs. We determined that dependent behavioral variable counts were zero-inflated based on comparisons of the number of observed versus expected zeros under a standard Poisson distribution. Zero-inflated Poisson GLMMs were run using the R package "MCMCglmm" (Hadfield 2010). Following Hadfield (2010), and online responses and comments to queries regarding priors, we fixed the residual variance to 1, used inverse Wishart distributions for the random effects, and defined multivariate normal distributions for the fixed effects. Response variables were weekly frequencies for each male: aggression given, aggression received, submission given, submission received, and display given. Fixed effects were dominance rank, age, and either average weekly luminance or R-G, with an offset for the number of weekly focal observations to account for differences in observation time between males. Random effects were male ID and week. Zero-inflated Poisson models assess 2 separate processes: the binomial process, which models the probability that the zeros are inflated (false zeros, due to observer error, etc.) versus true data (true zeros and counts), and the count process, which models the

probability of the behavior fit using a Poisson distribution with a log-link function (Zuur et al. 2009). Models were fit using Markov chain Monte Carlo (MCMC) simulation methods that result in a posterior distribution for each model parameter that is used to generate parameter estimates, as well as test statistics indicating the statistical significance of each fixed effect, with results generated for both parts of the model. Models were run for 2,550,000 iterations with a burn-in of 50,000 iterations, and the MCMC chain sampled every 2000 iterations thereafter. Each model was run 3 times to verify model convergence on qualitatively similar results, and Gelman diagnostics for model runs were all less than 1.1 (Gelman and Rubin 1992). Across all models, visual inspection of all MCMC trace plots revealed no aberrant behavior, and non-zero autocorrelation within the MCMC chain was minimal to none. We present results from the first model runs.

Dyadic agonistic interactions

To examine whether facial color mediated agonistic interactions within dyads, we used a total of 179 dyadic interactions involving aggression or submission between males recorded during focal samples. Color measurement (R-G and luminance) scores were not available for every male every day that agonism was observed, and were therefore applied to each male from the closest day they had a color measurement (mean = 1.5 days, range: 0–5 days). While this may introduce some small error of mismatch between coloration and behavior as male color values do vary within individuals, the timescale of intraindividual change is usually over weeks rather than within hours or 1–2 days. A daily approach was chosen rather than using weekly average scores to minimize the number of missing data points. Using this method, color scores were available for both males in the dyad for 138 of the interactions. Each dyadic interaction was categorized based on whether the subordinate individual won or not (i.e., 1: the winner in the interaction is lower ranking than the loser, $N = 23$; 0: the winner in the interaction is higher ranking than the loser, $N = 156$). For each dyad, differences in facial skin R-G and luminance were calculated by subtracting the loser's color from the winner's color. The absolute value of the difference in dominance rank and age between the 2 individuals was calculated to determine how close in rank and age the dyadic individuals are, as conflicts resulting in the subordinate opponent winning might be more common between individuals of similar rank and/or age. We used GLMMs with a binomial error structure and a logit link function (using the Laplace approximation for parameter estimation) to test whether differences in the males' facial skin R-G or luminance and distance between their dominance ranks (fixed effects) influenced the occurrence of the subordinate winning conflicts over the dominant. We controlled for both individual IDs and dyad ID by fitting them as random effects. To select the optimal model, we compared models with different combinations of fixed effects (R-G or luminance difference only, rank distance only, age distance only, all three variables, and a null model with no fixed effects) and compared models with likelihood-ratio tests and AICc (Akaike Information Criterion corrected for small sample sizes) values (models with AICc differences greater than 3 were determined as better fits). Models were fit using the R package "lme4" (Bates et al. 2015).

Binomial GLMMs were also used to determine whether, when a dyadic agonistic interaction occurred ($N = 138$), the likelihood of aggressive or submissive behavior is related to similarity in male coloration. For these models, we collapsed the agonistic behavior into the presence or absence of aggression ($N = 45$) or unprovoked

submission ($N = 93$). We modeled the occurrence of aggression or submission as a function of absolute value of the R-G or luminance difference (color distance between males in each agonistic dyad), controlling for dominance rank and age distance (set as fixed effects) and the male IDs and dyad ID (set as random effects). This full model was compared to a model without the variable of interest (R-G or luminance distance) with likelihood ratio tests and AICc values to determine if the inclusion of R-G or luminance distance improved model fit. Variance inflation factors (VIFs) for all GLMMs were less than 1.5, indicating no collinearity in the fixed effects.

Mating

For every day of the study ($N = 30$ days), each male was assigned a binary value based on if they had been observed copulating with adult females that day based on focal and ad libitum observations. Additionally, for each day of the study the number of sexually active adult females (i.e., observed copulating with any adult male) was calculated. As in the dyadic analyses, color scores were applied to males based on their closest color measurement (mean = 1.36 days, range: 0–4 days), resulting in a subset of 308 "male days" (20.5 ± 7.6 days per male, range: 1–30) out of the possible 450 days. These 308 "male days" were used in models testing the number of females mating, whereas male copulation models were restricted to study days in which males had color scores for both copulating and not-copulating days ($N = 257$ "male days," $N = 11$ males) to ensure that a within-individual comparison of color was undertaken.

Linear mixed models (LMMs) were fit to test whether the number of sexually active females or observed copulation (binary fixed effect) influenced male R-G or luminance, controlling for dominance rank and age (fixed effects), and multiple observations on the same date and of the same individual by incorporating these as random effects. Model selection was determined with likelihood ratio tests with models refitted using maximum likelihood estimates. The significance of fixed effects was determined with Type II Wald chi-squared tests (R package "car," Fox and Weisberg 2011). Models met assumptions of normality and distribution of residuals, and VIFs were less than 1.5 in all models indicating a lack of collinearity in the fixed effects. LMMs were fit using R package "lme4" (Bates et al. 2015).

RESULTS

Overall agonism

Neither luminance nor R-G was related to any of the tested agonistic behaviors (Table 1). There were, however, relationships between some of the tested behaviors and both dominance rank and age (Table 1).

Dyadic agonistic interactions

None of the models examining the occurrence of subordinates winning over dominants performed better than the null model, suggesting that no combination of difference in R-G, luminance, rank, or age distance between the 2 males influences the occurrence of subordinates winning over dominants.

When looking at all bouts of dyadic agonism (with or without a subordinate win), aggressive interactions were more likely to occur between males that were similar to each other in R-G than in more dissimilar dyads (Table 2; Figure 1), whereas distance in

Table 1

Results of zero-inflated Poisson models testing how dominance rank, age, and average luminance (A) or R-G (B) influences weekly probability (logistic process) and rates (Poisson process) of agonistic behaviors, controlling for male ID and study week

(A)	Logistic		Poisson		(B)	Logistic		Poisson	
	β	pMCMC	β	pMCMC		β	pMCMC	β	pMCMC
Aggression Given (DIC = 91.19)					Aggression Given (DIC = 91.81)				
Rank	-0.320	0.776	-0.218	0.043	Rank	-0.419	0.605	-0.225	0.029
Age	-0.699	0.166	-0.139	0.146	Age	-0.804	0.146	-0.138	0.126
Luminance	0.027	0.987	-0.296	0.789	R-G	0.044	0.978	-0.095	0.923
Aggression Received (DIC = 91.78)					Aggression Received (DIC = 91.54)				
Rank	-0.309	0.730	-0.029	0.840	Rank	-0.361	0.733	-0.037	0.795
Age	-0.819	0.150	-0.315	0.003	Age	-0.922	0.109	-0.326	0.005
Luminance	0.030	0.995	-0.388	0.701	R-G	-0.012	0.984	-0.037	0.969
Submission Given (DIC = 161.57)					Submission Given (DIC = 161.84)				
Rank	-0.586	0.387	0.018	0.778	Rank	-0.642	0.402	0.010	0.832
Age	-0.977	0.070	-0.182	0.032	Age	-0.957	0.041	-0.184	0.030
Luminance	-0.004	0.976	-0.307	0.734	R-G	0.004	0.978	-0.129	0.896
Submission Received (DIC = 127.42)					Submission Received (DIC = 127.46)				
Rank	-0.430	0.566	-0.223	0.006	Rank	-0.403	0.629	-0.221	0.006
Age	-0.866	0.038	-0.137	0.131	Age	-0.896	0.051	-0.139	0.115
Luminance	-0.034	0.962	-0.056	0.936	R-G	0.000	0.971	-0.167	0.880
Display Given (DIC = 134.04)					Display Given (DIC = 133.67)				
Rank	-0.427	0.670	-0.126	0.078	Rank	-0.387	0.662	-0.129	0.102
Age	-0.789	0.061	-0.205	0.029	Age	-0.767	0.075	-0.207	0.009
Luminance	-0.015	0.963	-0.180	0.837	R-G	-0.019	0.998	-0.062	0.954

Statistically significant results are in bold.
 Logistic model parameters are on a logit scale and Poisson parameters are on a log scale.
 DIC = Deviance Information Criterion.

Table 2

Results of binomial GLMMs testing the effects of rank distance, age distance, and luminance distance or R-G distance on the likelihood of aggression or unprovoked submission within agonistic interactions, controlling for both male IDs in the dyad (N = 138)

	Estimate	Standard error	z-value	P
Aggression (luminance)				
Intercept	-0.589	0.529	-1.12	0.266
Rank Distance	-0.028	0.058	-0.495	0.621
Age Distance	-0.133	0.099	-1.344	0.179
Luminance Distance	7.917	5.581	1.419	0.156
Aggression (R-G)				
Intercept	0.102	0.481	0.212	0.832
Rank Distance	0.020	0.056	0.356	0.722
Age Distance	-0.108	0.093	-1.163	0.245
R-G Distance	-33.317	14.256	-2.337	0.019
Submission (luminance)				
Intercept	0.580	0.524	1.106	0.269
Rank Distance	0.042	0.058	0.722	0.470
Age Distance	0.091	0.095	0.957	0.339
Luminance Distance	-7.289	5.499	-1.326	0.185
Submission (R-G)				
Intercept	-0.051	0.478	-0.107	0.915
Rank Distance	-0.004	0.055	-0.071	0.944
Age Distance	0.070	0.091	0.766	0.443
R-G Distance	30.555	13.805	2.213	0.027

Statistically significant results are in bold.

dominance rank and age had no influence (Table 2). The inclusion of R-G distance improved model fit (likelihood ratio test: $\chi^2 = 6.27(1)$, $P = 0.01$; $dAICc > 4$), further showing the importance of this fixed effect. Similarly, dyadic interactions characterized by unprovoked submission were more likely between males more different to each other in R-G than those more similar to each other (binomial GLMM: $z = 2.21$, $P = 0.03$; Figure 2), with no

significant influence of dominance rank or age (Table 2). Again, the inclusion of R-G distance improved model fit (likelihood ratio test: $\chi^2 = 5.49(1)$, $P = 0.02$; $dAICc > 4$). Luminance distance had no effect on the likelihood of aggression or submission in the interaction (Table 2).

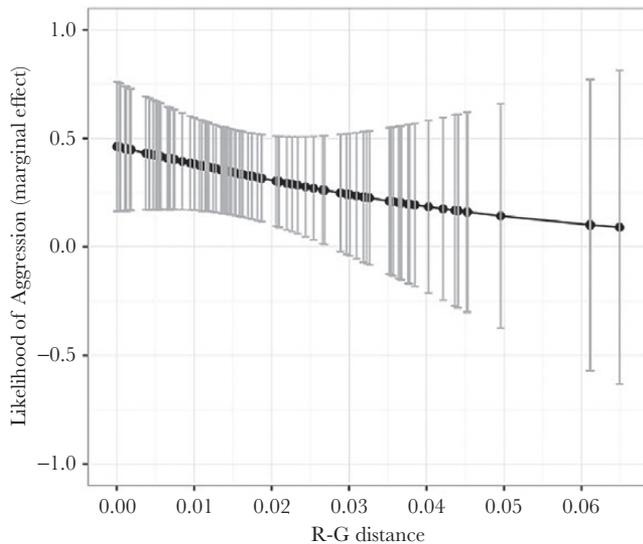


Figure 1
Marginal effect of the likelihood of aggression in agonistic dyadic interactions (bars represent \pm standard errors of mean-fitted values) for different R-G distances between males ($N = 138$).

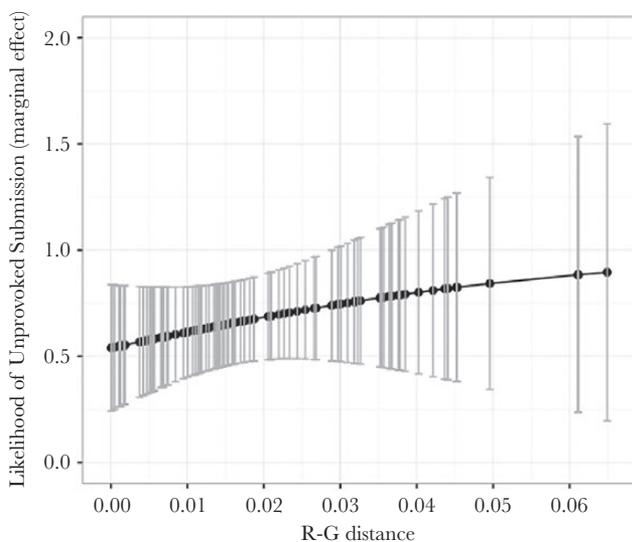


Figure 2
Marginal effect of the likelihood of unprovoked submission in agonistic dyadic interactions (bars represent \pm standard errors of mean-fitted values) for different R-G distances between males ($N = 138$).

Mating

On average, male facial luminance was lower (facial skin coloration was darker) on days they were seen copulating (mean: 0.307, range: 0.233–0.356) compared to days when they were not (mean: 0.310, range: 0.245–0.359) (Table 3, Figure 3). The inclusion of copulation in the model improved model fit compared to the model including only rank and age (likelihood ratio test: $\chi^2 = 5.95(1)$, $P = 0.01$). In contrast, the R-G LMM including copulation did not improve model fit compared to a model with just dominance rank and age (likelihood ratio test: $\chi^2 = 1.04(1)$, $P = 0.31$), suggesting that copulation activity may not influence R-G. Dominance rank was the only significant predictor of R-G; higher-ranking males had redder facial coloration (Table 3). Note however that this term is nonsignificant in all other models.

Female mating behavior varied across study days, with an average of 2.8 ± 1.8 adult females (range: 0–6) observed copulating with study males per day. The number of females mating each day did not influence daily male luminance or R-G. The luminance and R-G models with and without the number of females mating were not significantly different (luminance likelihood ratio test: $\chi^2 = 1.196(1)$, $P = 0.2741$; R-G likelihood ratio test: $\chi^2 = 0.112(1)$, $P = 0.738$), suggesting that males do not collectively increase trait expression when more females are mating on a given day.

DISCUSSION

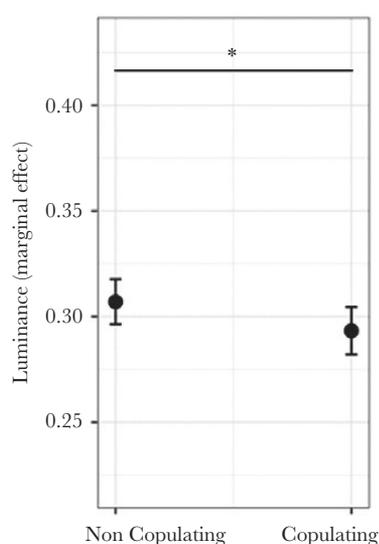
We sought to clarify the role of intrasexual selection on the sexual skin coloration of male rhesus macaques. Overall, male facial coloration did not reflect individual rates of agonistic behaviors. However, males more similar in facial redness (R-G scores) engaged in more aggressive and less submissive interactions, suggesting that facial coloration does function in mediating male–male interactions in rhesus macaques. Moreover, males were darker (expressed lower luminance scores) on days they were seen copulating, but not when more females were sexually active. In contrast to previous findings (Higham et al. 2013; Dubuc et al. 2014a), our results show that facial R-G also positively correlated with dominance rank in the analyses examining the association between coloration and mating activity. Interestingly, however, it appears that dominance was a predictor of male R-G mainly on days when they were seen copulating, further supporting the view that the signal is expressed when required, such as, when trying to intimidate an opponent.

One important caveat with our results is that the predicted model values for R-G and luminance in our significant results are very small. This raises questions over the likely perceptibility of the variation as predicted by the model output. In prior studies we have shown that genital and hindquarter coloration in males shows greater variation in expression than the variation in the face, but that nonetheless expression in the 3 regions is correlated (Higham et al. 2013). In this study, we did not collect genital and hindquarter images reliably in large numbers, as good standardized images of these regions are much more difficult to obtain. However the correlation between face coloration and coloration in other regions that show more variation, creates the possibility that our results might be reflective of overall signal changes, including some of greater magnitude. An alternative interpretation of our results, is that the differences in facial coloration might indeed be too small to be involved in signaling, and that coloration differences detecting in the present study represent health/condition differences between males, given that the signal is linked to blood flow and the degree of blood oxygenation. These condition differences might then be important in determining dyadic interactions, hence explaining the present results. Under this scenario, coloration differences between 2 males might be viewed simply as a proxy for condition differences between those 2 males that predict the likelihood of fighting, whereby 2 males more evenly matched in current condition are more likely to fight. Nonetheless, these color differences could influence males if they can be perceived. In this case, the interpretation would be that these subtle color differences might be cues to (rather than signals of) male condition that might influence the likelihood of aggression and submission. Another possible alternative explanation for our results is that, since a portion of coloration expression is heritable (Dubuc et al. 2014b), differences between individuals actually reflect interindividual differences in other characteristics of males, not measured in the present study.

Table 3**Results of LMMs testing the effects of dominance rank, age, and daily presence of copulation on luminance or R-G, controlling for male ID and date ($N = 257$)**

	Coefficient	Standard error	<i>t</i> -value	chi-square (df) ^a	<i>P</i> ^a
Luminance					
Intercept	0.333	0.042	7.871		
Dominance Rank	0.000	0.002	-0.192	0.037 (1)	0.847
Age	-0.002	0.004	-0.713	0.5079 (1)	0.476
Copulating	-0.014	0.005	-2.535	6.425 (1)	0.011
R-G					
Intercept	0.084	0.011	7.365		
Dominance Rank	-0.002	0.001	-2.565	6.578 (1)	0.010
Age	0.001	0.001	0.723	0.422 (1)	0.469
Copulating	0.001	0.002	0.700	0.489 (1)	0.484

Statistically significant results are in bold.

^aType II Wald chi-square tests**Figure 3**

Male luminance marginal effects (fitted model values, bars represent \pm standard errors) for days males were observed copulating or not ($N = 257$). Males had significantly lower luminance scores (they were darker) on days observed copulating. Y axis reflects the maximum and minimum luminance scores found in the dataset.

Badges of status are hypothesized to have evolved across animal taxa via intrasexual selection to advertise an individual's competitive ability to avoid costly aggressive interactions between males of different abilities (Andersson 1994; Bradbury and Vehrencamp 2011). In many primate species, competitive ability is directly correlated with dominance rank, and subsequently colorful male sexual signals advertise social status (e.g., mandrills: Setchell and Wickings 2005, Renoult et al. 2011; crested macaques: Engelhardt et al. 2008; drills: Marty et al. 2009; gelada: Bergman et al. 2009; black-and-white snub-nosed monkeys: Grueter et al. 2015). Rhesus macaque males express colorful sexual signals, but a series of projects has suggested a more important role of inter- rather than intrasexual selection, as coloration does not usually correlate with dominance rank (Higham et al. 2013; Dubuc et al. 2014a) and is attractive to females (Dubuc et al. 2014b; Dubuc et al. 2016). Here, however, we show that at the behavioral level facial coloration may in fact mediate male–male interactions similarly to other primate species with colorful badges of status, in addition to the role it plays in intersexual selection.

If variation in coloration reflects variation in a male's competitive ability or his motivation to fight and defend a resource, rather than primarily reflecting his dominance rank, then individuals can use this signal to avoid costly interactions that they may lose. If 2 individuals are similar in color, regardless of their absolute color, the outcome of the interaction might be unknown and they may fight to determine who gains access to fertile females. For example, in black-and-white snub-nosed monkeys, red lip coloration changes in the mating season reflect one-male-unit (OMU) holder's status. This relationship is, however, driven by non-OMU-holders paling in color in the mating season, potentially to signal to OMU-holders their decreased motivation to fight in order to avoid aggression (Grueter et al. 2015). A similar phenomenon may also occur in vervet monkeys; the difference between 2 males in the blue coloration of their scrota predicts the likelihood of aggression in an experimental setting (Gerald 2001), but it is unclear whether dominance rank and/or aggression generally relates to absolute male color intensity (Henzi 1985; Isbell 1995).

The lack of relationship between individual rates of agonism and coloration in the present study may be due to a variety of factors. Rhesus macaque males vary in the maximum intensity of coloration that they express (Higham et al. 2013). By comparing absolute coloration scores across males, we may not capture important relative changes for any one male, such that a male with paler/less red coloration relative to others may in fact be expressing his individual maximum coloration. Rhesus macaques live in stable groups with high familiarity and social knowledge of dominance rank without the need for badges of status (Bergman and Sheehan 2013). Further, discrimination of changes in female facial coloration improves with social familiarity (Higham, Hughes, et al. 2011). It is thus possible that males can learn and remember other males' facial coloration and associated behaviors at different relative intensities, and use this social knowledge to make decisions about their interactions, which would not be reflected simply in absolute color scores. Provisioning in this population may also reduce variation in male condition. Studies of wild rhesus macaques, in which we might expect more interindividual variation in condition, might find a wider range of results linked to male coloration.

In this study, higher-ranking males expressed redder (greater R-G) facial coloration, whereas analyses conducted in a different social group 4 years earlier did not find this relationship (Higham et al. 2013; Dubuc et al. 2014a). Our results do not mean that coloration is a badge of status generally in rhesus macaques. With a hierarchy based mainly on group-tenure length, the characteristics

of high versus low ranking males may change from group to group and year to year (Georgiev et al. 2015, 2016). In some years and groups, high-ranking males may be prime-aged males of high quality and competitiveness, whereas in other years this may not be true. Consistent with this, there is variation in how dominance rank influences reproductive success among groups and across years (reviewed in Widdig et al. 2016). This further supports our hypothesis that males express coloration flexibly and in relation to motivational state (i.e., willingness to defend a mate) rather than at all times.

The inconsistency in the relationship between coloration and dominance rank in rhesus macaques is in contrast to species where the highest-ranking males are consistently the reddest, and who change in coloration after rising or falling in social status (mandrills: Setchell and Dixson 2001; gelada: Bergman et al. 2009). These species are in a constant state of reproductive competition and may need to express maximal signals of competitive ability at all times, as evidenced by maximum color expression year-round despite reproductive seasonality (Setchell and Dixson 2001). Male rhesus macaques only express sexual skin coloration during the mating season, with intramale variation in levels of expression throughout, suggesting that their competition is more nuanced and related to, rather than being defined by, their dominance hierarchy. Male rhesus macaque facial coloration may thus function similarly to other closely related species with color signals despite not consistently advertising social status, likely due in part to the differences in how rhesus macaques generally acquire dominance rank and their associated competitive regime.

While males also expressed darker coloration (lower luminance scores) on days they were observed mating, they did not do so when more females were sexually active. Since females find males that express darker/redder facial coloration more attractive (Dubuc et al. 2014a; Dubuc et al. 2016), one would have expected males to express coloration at higher intensities when females were sexually active as a means to attract them. As such, our results raise the question of whether male coloration's primary function is to advertise motivation to defend a mate rather than to attract females, particularly since dominance rank is related to coloration only when considering these mating days. An alternative possibility is that since rhesus males are selective (e.g., Manson and Perry 1993) and males who invest the most in mating incur energetic costs (Bercovitch 1997; Higham, Heistermann, et al. 2011), males may express the signals only when they are motivated to mate with and defend access to a currently receptive female. A more detailed study on intramale sexual skin color variation will be needed to disentangle the relationship between mating and coloration.

In conclusion, in addition to its role in female mate choice, male facial coloration appears to mediate male–male agonistic interactions in rhesus macaques, similarly to how it functions in other species with typical badges of status. Badges of status reflect competitive ability of an individual and when individuals fight over social status, this competitive ability is reflected in both dominance rank and sexual signals. In contrast, rhesus macaques in this population have a different competitive regime, whereby they enter the dominance hierarchy at the bottom and rise in rank over time rather than fighting over social status, such that the highest-ranking male is not necessarily the most competitive or brightest in color. Coloration may reflect male condition since it is attractive to females, and condition may influence a male's competitive ability, resulting in a sexual signal that is informative in both intra- and intersexual contexts. Male–male interactions thus appear

to reflect a nuanced decision-making process based on dominance rank, competitive ability, current mating status and motivational state, and social knowledge, and are at least partially mediated by differences in facial coloration between males. This adds further evidence to support that male facial coloration may have evolved under both inter- and intrasexual selection. Further studies need to investigate whether variation in color expression is linked to physiological aspects of male condition, such as immune activation and oxidative stress.

FUNDING

This work was supported by a MacCracken Fellowship from New York University (NYU) to M.P., a fellowship from the Fonds Québécois de la Recherche sur la Société et la Culture to C.D., by NIH to Prof. Dario Maestripieri, by the NSF IGERT program (grant number 0966166) and an NYU MacCracken Fellowship to S.W., and by intra-mural funds from NYU to J.P.H. The Cayo Santiago population is currently supported by the University of Puerto Rico (UPR) and the Office of Research Infrastructure Programs (ORIP) of the National Institutes of Health (grant number 2P40OD012217).

We thank CPRC staff for facilitating work on Cayo Santiago. We thank Julie Cascio, Diana Christie, Sam Schulte, Duncan Schulte, Amauri Michel, Clement Ludcher, and Jesus Madrid for assistance in the field, Paul Brown and Kevin Rosenfield for assistance in measuring skin coloration, and Rafael Maia for help with priors. We are also very grateful to Louise Barrett and 2 anonymous reviewers for constructive comments on a previous version of the manuscript. The content of this publication is solely the responsibility of the authors and does not necessarily represent the official views of the UPR or ORIP.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Petersdorf et al. (2017).

Handling editor: Louise Barrett

REFERENCES

- Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour*. 49:227–267.
- Andersson M. 1994. Sexual selection. Princeton (NJ): Princeton University Press.
- Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw*. 67:1–48.
- Baulu J. 1976. Seasonal sex skin coloration and hormonal fluctuations in free-ranging and captive monkeys. *Horm Behav*. 7:481–494.
- Berard J. 1999. A four-year study of the association between male dominance rank, residency status, and reproductive activity in rhesus macaques (*Macaca mulatta*). *Primates*. 40:159–175.
- Bercovitch FB. 1997. Reproductive strategies of rhesus macaques. *Primates*. 38:247–263.
- Berglund A, Bisazza A, Pilastro A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol J Linn Soc*. 58:385–399.
- Bergman TJ, Sheehan MJ. 2013. Social knowledge and signals in primates. *Am J Primatol*. 75:683–694.
- Bergman TJ, Beehner JC. 2008. A simple method for measuring colour in wild animals: validation and use on chest patch colour in geladas (*Theropithecus gelada*). *Biol J Linn Soc*. 94:231–240.
- Bergman TJ, Ho L, Beehner JC. 2009. Chest color and social status in male geladas (*Theropithecus gelada*). *Int J Primatol*. 30:791–806.
- Borgia G, Coleman SW. 2000. Co-option of male courtship signals from aggressive display in bowerbirds. *Proc R Soc Lond B*. 267:1735–1740.
- Bowmaker JK, Dartnall HJ, Lythgoe JN, Mollon JD. 1978. The visual pigments of rods and cones in the rhesus monkey, *Macaca mulatta*. *J Physiol*. 274:329–348.

- Bradbury JW, Vehrencamp SL. 2011. Principles of animal communication. 2nd ed. Sunderland (MA): Sinauer Associates.
- Bradley BJ, Mundy NI. 2008. The primate palette: the evolution of primate coloration. *Ev Anth.* 17:97–111.
- Candolin U. 1999. Male-male competition facilitates female choice in sticklebacks. *Proc R Soc Lond B.* 266:785–789.
- Clutton-Brock T, McAuliffe K. 2009. Female mate choice in mammals. *Q Rev Biol.* 84:3–27.
- Coffin D. 2015. DCRAW [2012 November 6]. <https://www.cybercom.net/~dcoffin/dcrawl/>
- Curley JP. 2016. compete: Organizing and Analyzing Social Dominance Hierarchy Data. R package version 0.1 [cited 2015 October 24]. Available from: <https://cran.r-project.org/web/packages/compete/index.html>.
- Darwin C. 1871. The descent of man, and selection in relation to sex. London: John Murray.
- Dixon AF. 2012. Primate sexuality: comparative studies of prosimians, monkeys, apes, and human beings. 2nd ed. Oxford: Oxford University Press.
- Dubuc C, Brent LJN, Accamando AK, Gerald MS, MacLarnon A, Semple S, Heistermann M, Engelhardt A. 2009. Sexual skin color contains information about the timing of the fertile phase in free-ranging *Macaca mulatta*. *Int J Primatol.* 30:777–789.
- Dubuc C, Muniz L, Heistermann M, Engelhardt A, Widdig A. 2011. Testing the priority-of-access model in a seasonally breeding primate species. *Behav Ecol Sociobiol.* 65:1615–1627.
- Dubuc C, Muniz L, Heistermann M, Widdig A, Engelhardt A. 2012. Do males time their mate-guarding effort with the fertile phase in order to secure fertilisation in Cayo Santiago rhesus macaques? *Horm Behav.* 61:696–705.
- Dubuc C, Allen WL, Maestriperi D, Higham JP. 2014a. Is male rhesus macaque red color ornamentation attractive to females? *Behav Ecol Sociobiol.* 68:1215–1224.
- Dubuc C, Winters S, Allen WL, Brent LJ, Cascio J, Maestriperi D, Ruiz-Lambides AV, Widdig A, Higham JP. 2014b. Sexually selected skin colour is heritable and related to fecundity in a non-human primate. *Proc Biol Sci.* 281:20141602.
- Dubuc C, Allen WL, Cascio J, Lee DS, Maestriperi D, Petersdorf M, Winters S, Higham JP. 2016. Who cares? Experimental attention biases provide new insights into a mammalian sexual signal. *Behav Ecol.* 27:68–74.
- Engelhardt A, Neumann C, Heistermann M, Perwitasari-Farajallah D. 2008. Sex skin coloration in male Sulawesi crested black macaques (*Macaca nigra*). *Primate Eye.* 96:337.
- Fox J, Weisberg S. 2011. An {R} companion to applied regression. 2nd ed. Thousand Oaks: Sage.
- Gammell MP, de Vries H, Jennings DJ, Carlin CM, Hayden TJ. 2003. David's score: a more appropriate dominance ranking method than Clutton-Brock *et al.*'s index. *Anim Behav.* 66:601–605.
- Gelman A, Rubin DB. 1992. Inference from iterative simulation using multiple sequences. *Stat Sci.* 7:457–511.
- Georgiev AV, Muehlenbein MP, Prall SP, Emery Thompson M, Maestriperi D. 2015. Male quality, dominance rank, and mating success in free-ranging rhesus macaques. *Behav Ecol.* 26:763–772.
- Georgiev AV, Christie D, Rosenfield KA, Ruiz-Lambides AV, Maldonado E, Thompson ME, Maestriperi D. 2016. Breaking the succession rule: the costs and benefits of an alpha-status take-over by an immigrant rhesus macaque on Cayo Santiago. *Behaviour.* 153:325–51.
- Gerald MS. 2001. Primate colour predicts social status and aggressive outcome. *Anim Behav.* 61:559–566.
- Grueter CC, Zhu P, Allen WL, Higham JP, Ren B, Li M. 2015. Sexually selected lip colour indicates male group-holding status in the mating season in a multi-level primate society. *R Soc Open Sci.* 2:150490.
- Hadfield JD. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J Stat Softw.* 33:1–22.
- Hárosi FI. 1987. Cynomolgus and rhesus monkey visual pigments. Application of Fourier transform smoothing and statistical techniques to the determination of spectral parameters. *J Gen Physiol.* 89:717–743.
- Henzi SP. 1985. Genital signalling and the coexistence of male vervet monkeys (*Cercopithecus aethiops pygerythrus*). *Folia Primatol (Basel).* 45:129–147.
- Hernández-Pacheco R, Rawlins RG, Kessler MJ, Delgado DL, Ruiz-Lambides AV, Sabat AM. 2016. Discovery of a secular trend in Cayo Santiago macaque reproduction. *Am J Primatol.* 78:227–237.
- Higham JP. 2006. The reproductive ecology of female olive baboons (*Papio hamadryas anubis*) at Gashaka-Gumti National Park, Nigeria. London: Roehampton University.
- Higham JP, Hughes KD, Brent LJ, Dubuc C, Engelhardt A, Heistermann M, Maestriperi D, Santos LR, Stevens M. 2011. Familiarity affects the assessment of female facial signals of fertility by free-ranging male rhesus macaques. *Proc Biol Sci.* 278:3452–3458.
- Higham JP, Heistermann M, Maestriperi D. 2011. The energetics of male-male endurance rivalry in free-ranging rhesus macaques, *Macaca mulatta*. *Anim Behav.* 81:1001–1007.
- Higham JP, Pfeifferle D, Heistermann M, Maestriperi D, Stevens M. 2013. Signaling in multiple modalities in male rhesus macaques: sex skin coloration and barks in relation to androgen levels, social status, and mating behavior. *Behav Ecol Sociobiol.* 67:1457–1469.
- Hoffman CL, Ruiz-Lambides AV, Davila E, Maldonado E, Gerald MS, Maestriperi D. 2008. Sex differences in survival costs of reproduction in a promiscuous primate. *Behav Ecol Sociobiol.* 62:1711–1718.
- Hughes KD, Higham JP, Allen WL, Elliot AJ, Hayden BY. 2015. Extraneous color affects female macaques' gaze preference for photographs of male conspecifics. *Evol Hum Behav.* 36:25–31.
- Hunt J, Breuker CJ, Sadowski JA, Moore AJ. 2009. Male-male competition, female mate choice and their interaction: determining total sexual selection. *J Evol Biol.* 22:13–26.
- Isbell LA. 1995. Seasonal and social correlates of changes in hair, skin, and scrotal condition in vervet monkeys (*Cercopithecus aethiops*) of Amboseli National Park, Kenya. *Am J Primatol.* 36:61–70.
- Khan SA, Levine WJ, Dobson SD, Kralik JD. 2011. Red signals dominance in male rhesus macaques. *Psychol Sci.* 22:1001–1003.
- Manson JH. 1995. Do female rhesus macaques choose novel males. *Am J Primatol.* 37:285–296.
- Manson JH, Perry SE. 1993. Inbreeding avoidance in rhesus macaques: whose choice? *Am J Phys Anthropol.* 90:335–344.
- Marty JS, Higham JP, Gadsby EL, Ross C. 2009. Dominance, coloration, and social and sexual behavior in male drills *Mandrillus leucophaeus*. *Int J Primatol.* 30:807–823.
- McCullough EL, Miller CW, Emlen DJ. 2016. Why sexually selected weapons are not ornaments. *Trends Ecol Evol.* 31:742–751.
- Morris MR, Tudor MS, Dubois NS. 2007. Sexually selected signal attracted females before deterring aggression in rival males. *Anim Behav.* 74:1189–1197.
- van Noordwijk MA, van Schaik CP. 2004. Sexual selection and the careers of primate males: paternity concentration, dominance acquisition tactics and transfer decisions. In: Kappeler PM, van Schaik CP, editors. Sexual selection in primates: new and comparative perspectives. Cambridge: Cambridge University Press. p. 208–229.
- Osorio D, Vorobyev M. 2005. Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and colour vision. *Proc Biol Sci.* 272:1745–1752.
- Petersdorf M, Dubuc C, Georgiev AV, Winters S, Higham JP. 2017. Data from: is male rhesus macaque facial coloration under intra-sexual selection? Dryad Digital Repository. <http://dx.doi.org/10.5061/dryad.696js>
- R Core Team. 2015. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing [cited 2014 April 14]. <https://www.R-project.org/>.
- Rawlins RG, Kessler MJ. 1986. The Cayo Santiago macaques: history, behavior, and biology. Albany (NY): SUNY Press.
- Renoult JP, Schaefer HM, Sallé B, Charpentier MJE. 2011. The evolution of the multicoloured face of mandrills: insights from the perceptual space of colour vision. *PLoS One.* 6:e29117.
- Schmid VS, de Vries H. 2013. Finding a dominance order most consistent with a linear hierarchy: an improved algorithm for the I&SI method. *Anim Behav.* 86:1097–1105.
- Setchell JM, Dixon AF. 2001. Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. *Horm Behav.* 39:177–184.
- Setchell JM, Wickings EJ. 2005. Dominance, status signals, and coloration in male mandrills (*Mandrillus sphinx*). *Ethology.* 111:25–50.
- Stevens M, Parraga CA, Cuthill IC, Partridge JC, Troscianko TS. 2007. Using digital photography to study animal coloration. *Biol J Linn Soc.* 90:211–237.
- Stevens M, Stoddard MC, Higham JP. 2009. Studying primate color: towards visual system-dependent methods. *Int J Primatol.* 30:893–917.

- de Vries H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Anim Behav.* 55:827-843.
- Waitt C, Little AC, Wolfensohn S, Honess P, Brown AP, Buchanan-Smith H, Perrett DI. 2003. Evidence from rhesus macaques suggests that male coloration plays a role in female primate mate choice. *Proc R Soc Lond B.* 270(Suppl 2):144.
- Widdig A, Kessler MJ, Bercovitch FB, Berard JD, Duggleby C, Nürnberg P, Rawlins RG, Sauermaun U, Wang Q, Krawczak M, Schmidtke J. 2016. Genetic studies on the Cayo Santiago rhesus macaques: a review of 40 years of research. *Am J Primatol.* 78:44–462.
- Wong BBM, Candolin U. 2005. How is female mate choice affected by male competition? *Biol Rev.* 80:559–571.
- Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. *Mixed effects models and extensions in ecology with R.* New York: Springer-Verlag.