

1 **Female ornaments: is red skin color attractive to males and related to condition in**
2 **rhesus macaques?**

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25 LAY SUMMARY

26 Sexual selection produces traits that are advantages in competition, or that are attractive
27 to the opposite sex. We studied the bright red facial coloration of 32 female rhesus
28 monkeys. We found that males preferred females with more colourful faces. When
29 combined with other lines of evidence, our study suggests that the colorful face of female
30 rhesus monkeys may have evolved by male mate choice.

31

32 ABSTRACT

33 Sexual selection produces extravagant male traits, such as colorful ornaments, via female
34 mate choice. More rarely, in mating systems in which males allocate mating effort
35 between multiple females, female ornaments may evolve via male mate choice. Females
36 of many anthropoid primates exhibit ornaments that indicate intra-individual cyclical
37 fertility, but which have also been proposed to function as inter-individual quality signals.
38 Rhesus macaque females are one such species, exhibiting cyclical facial color variation
39 that indicates ovulatory status, but in which the function of inter-individual variation is
40 unknown. We collected digital images of the faces of 32 rhesus macaque adult females.
41 We assessed mating rates, and consortship by males, according to female face coloration.
42 We also assessed whether female coloration was linked to physical (skinfold fat, BMI) or
43 physiological (fecal glucocorticoid metabolite fGCM, urinary C-peptide concentrations)
44 condition. We found that redder-faced females were mated more frequently, and
45 consorted for longer periods by top-ranked males. Redder females had higher fGCM
46 concentrations, perhaps related to their increased mating activity and consequent energy
47 mobilization, and blood-flow. Prior analyses have shown that female facial redness is a

48 heritable trait, and that redder-faced females have higher annual fecundity, while other
49 evidence suggests that color expression is likely to be a signal rather than a cue.
50 Collectively, the available evidence suggests that female coloration has evolved at least
51 in part via male mate choice. Its evolution as a sexually-selected ornament attractive to
52 males is probably attributable to the high female reproductive synchrony found in this
53 species.

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57 INTRODUCTION

58 Sexual selection explains the prevalence of traits that influence the reproductive rates of
59 carriers, sometimes at a detriment to their survival (Darwin 1872; Andersson 1994). This
60 evolutionary process is thought to be usually stronger on males than on females, because
61 their reproductive rate is less constrained by gamete production and parental investment
62 (Bateman 1948; Trivers 1972). This typically produces extravagant male traits, such as
63 armaments via direct male-male competition, and ornaments via female mate choice
64 (Clutton-Brock and McAuliffe 2009). However, stronger sexual selection on males is not
65 always the case, and females of some species exhibit extravagant conspicuous sexually-
66 selected traits (Clutton-Brock 2009). This occurs most commonly in species with sex-role
67 reversal, where extensive paternal care limits the reproductive success of males, leading
68 males to be highly choosy in their mate choices, and to female traits which males use to
69 select mates (Clutton-Brock 2009; Edward and Chapman 2011).

70 Female ornamentation can also occur without any sex-reversal. For example
71 many Anthropoid primates exhibit conspicuous signals in females, despite the absence of
72 sex-role reversal (Dixson 1983; Dixson 2012) – indeed, anthropoid females are thought
73 to expend some of the highest levels of maternal investment in the animal kingdom (Lee
74 1987). One set of anthropoid traits that have long been of interest to evolutionary
75 biologists is the colorful red skin ornaments exhibited by females of several anthropoid
76 species, which includes sexual swellings of the anogenital area of species such as
77 baboons (Domb and Pagel 2001; Higham et al. 2008; Fitzpatrick et al. 2014) and
78 chimpanzees (Emery and Whitten 2003; Deschner et al. 2004), the red facial coloration
79 of Japanese (Fujita 2010; Rigaiil et al. 2015; Rigaiil et al. 2019) and rhesus macaques

80 (Dubuc et al. 2009; Dubuc, Winters, et al. 2014), and the red chest patch of geladas
81 (Bergman et al. 2009) (reviewed in Dixson (2012) Chapter 7). Most hypotheses and
82 empirical studies surrounding such female signals focus on the function of conspicuous
83 sexual swellings, but may also be applied to signals such as facial and chest coloration
84 too. There are many hypotheses related to the function of sexual swellings, which try to
85 explain 3 types of variation: i) intra-cycle variation, in which swelling sizes change
86 across the menstrual cycle; ii) intra-female inter-cycle variation, in which swelling sizes
87 differ between cycles of the same female; and iii) inter-female variation, in which
88 swelling sizes differ between different females (Zinner et al. 2002). One well studied
89 hypothesis to explain intra-cycle variation, proposes that this correlates with conceptive
90 probability across the cycle, with swellings being larger when conceptive probability is
91 high, and small when it is low (the graded signal hypothesis, (Nunn 1999). Studies of
92 multiple species have generally supported this hypothesis, although there is a great
93 variation in the extent of to which swelling size correlates with conceptive probability
94 among anthropoids (e.g. macaques, Higham & Dubuc (2015)). One well-studied
95 hypothesis that proposes to explain inter-individual signal variation is the reliable
96 indicator hypothesis (Pagel 1994) which proposes that sexual swelling expression
97 represents variation in female quality, allowing males to choose between females of
98 different quality by choosing the female with the largest swelling (i.e. exhibiting the
99 greatest signal expression).

100 Under the reliable indicator hypothesis (Pagel 1994), the conspicuous traits
101 exhibited by anthropoid primate females have evolved via male mate choice, paralleling
102 the function of male conspicuous traits that are selected via inter-sexual selection.

103 Nonetheless, a weakness of the hypothesis is that it did not address the benefits that
104 females might accrue, such as paternal care, which would be necessary for selection to
105 act on the signaller (Alberts and Fitzpatrick 2012). Although many studies have tested
106 whether such signals covary with intra-cycle differences in fertility (e.g. long-tailed
107 macaques, Engelhardt et al. (2005); chimpanzees, Deschner et al. (2004); olive baboons,
108 Higham et al. (2008)), very few studies of sexual swellings have tested whether such
109 signals are potentially informative about inter-individual differences in female quality, as
110 proposed by the reliable indicator hypothesis. While one study of olive baboons claimed
111 that sexual swelling size did indeed indicate female reproductive value (Domb and Pagel
112 2001), the study was criticized for a flawed analysis (Zinner et al. 2002). A study of
113 chacma baboon sexual swellings suggested that swellings may have initially evolved as
114 signals of intra-individual fertility, and then have secondarily evolved into inter-
115 individual quality signals over time (Huchard et al. 2009). Similar analyses have not been
116 conducted in other anthropoid genera, and it remains unclear whether signals that are
117 attractive to males within cycles might also be used by males to select among different
118 females. While these hypotheses were formulated for sexual swellings, they may
119 nonetheless also be applied to analogous female fertility signals exhibited on other parts
120 of the body, such as the red chest patches of female gelada (Dixon 2012).

121 One strong candidate for a female signal that could be sexually-selected as both
122 an intra- and inter-female signal of reproductive value, is the red facial coloration of
123 female rhesus macaques. In parous adult females, facial skin intensity varies over the
124 course of the ovarian cycle with the greatest expression around the timing of ovulation,
125 such that it is covaries with intra-cycle variation in fertility (Dubuc et al. (2009); Higham

126 et al. (2010)). Such variation is perceived by males (Waite et al. (2006), Higham et al.
127 (2011)). Rhesus facial and hindquarter skin redness is under the control of targeted
128 estrogen-receptors only present in bare skin areas, and not found in adjacent skin (Rhodes
129 et al. 1997), which suggests that there has been selection on the color-change for its
130 communicative value – i.e. that the color change is a signal rather than a cue. Inter-
131 female red-faced coloration is heritable, and females with redder faces exhibit higher
132 reproductive rates (Dubuc, Winters, et al. 2014). Behavioural evidence shows that males
133 of this species are selective (reviewed in Paul (2002)). For instance, higher-ranking males
134 appear to prefer higher-ranking and parous females. Male selectivity is likely to be a
135 response to the high level of synchrony in female mating activity in this seasonally
136 breeding species forming large multimale-multifemale groups (Higham and Maestriperi
137 2014). While these are necessary conditions for intersexual selection to act on the trait,
138 there is as yet no observational evidence of whether males prefer to mate with redder-
139 faced faces – a key piece of evidence that is required to argue that female coloration itself
140 is under sexual selection via male mate choice.

141 There are also other mechanisms aside from sexual selection that could be
142 invoked to explain how such female traits might evolve. For instance, the trait may be
143 exhibited in females because it is exhibited in males, and it may be co-expressed in
144 females without being selected against as long as the cost to its expression in females is
145 low (Kraaijeveld et al. 2007). Evidence that rhesus macaque facial coloration is under
146 sexual selection in males is quite strong. There is both observational (Dubuc, Allen, et al.
147 2014) and experimental (Dubuc et al. 2016) evidence that dark redder-faced males are
148 preferred by females, and the trait is heritable (Dubuc, Winters, et al. 2014), with

149 selection gradients demonstrating that higher-ranked males with dark redder faces have
150 higher fecundity (Dubuc, Winters, et al. 2014). However, since females with redder facial
151 skin color have higher fecundity (Dubuc, Winters, et al. 2014), males starting to select
152 females with redder faces in the population would start to outcompete males without this
153 preference. When combined with the other existing data on female facial redness outlined
154 above, evidence for such a preference would suggest facial redness is under inter-sexual
155 selection in females in addition to males, but such evidence is currently lacking.

156 Understanding the extent to which underlying physiological condition may be
157 associated with trait variation is also informative for understanding the selection
158 pressures that might be acting on the trait, in addition to the extent to which it might be
159 considered a signal versus a cue, influencing male behaviour. Since skin color is
160 determined by blood-flow in the capillaries, the degree of expression of coloration might
161 be influenced by blood oxygenation (skin redness) and flow (skin darkness), and hence
162 directly related to physiological condition (Changizi et al. 2006; Stephen et al. 2009).
163 Intensity of signal expression may also be limited by the consequence of male behaviors:
164 female attractiveness in mammals is often accompanied with harassment and coercion as
165 well as high mating activity, which could lead to increased energetic expenditure. As
166 such, redder females may be in better physical or physiological condition overall, but also
167 may be in worse energetic condition due to increased mating and other activity, leading
168 us to make no prediction as to whether redder females are in better or worse physical or
169 physiological condition.

170 In the present study, our objectives are to ask: **1) Do males prefer females with**
171 **redder and/or darker faces? And; 2) Is face redness or darkness linked to physical**

172 **or physiological condition?**, in the Cayo Santiago free-ranging population of rhesus
173 macaques (*Macaca mulatta*). Due to large group sizes and hence a large number of
174 cycling females per group, combined with breeding seasonality, this population shows a
175 high degree of synchrony in female mating activity (e.g. Dubuc et al. (2011)), requiring
176 males to choose between multiple mating females. Large group sizes and seasonal
177 breeding are thought to be found among truly wild rhesus populations, too (Southwick
178 and Siddiqi 2011).

179

180 METHODS

181 *Data accessibility statement*

182

183 Analyses reported in this article can be reproduced using the data, which will be available
184 on datadryad.org on publication, and which are available during peer-review here:

185 <https://www.dropbox.com/sh/1s03ymeq2kakqwy/AAB1FPY4fFVTDefowJPQoUM6a?dl>

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188 *Study population and subjects*

189 The study took place on the free-ranging population of Cayo Santiago, a 15.2 ha island
190 located 1km off the East coast of Puerto Rico, which is managed by the Caribbean
191 Primate Research Center (CPRC) and was established in 1938. We studied group R,
192 which consisted of 82 adult females (≥ 3 yrs old), 42-45 adult males (≥ 5.5 yrs old), 11
193 sub-adult males (3-5 yrs old), and 120 immatures. Data collection focused on the 32
194 females who had given birth in the previous mating season, i.e., that all had offspring of
195 similar age at the beginning of the study. Subject females varied in age (mean +/- SEM

196 7.69 +/- 0.07 years). Thirty (30) out of the 32 females in our sample conceived during the
197 study period, precluding us from conducting any analyses focused on color and
198 conception likelihood. Subjects were captured during the yearly trapping period (mid-
199 January to mid-March 2012) immediately prior to the mating season (mid-February to
200 mid-June), and all non-invasive data (behavior, urine, fecal samples) were collected 5
201 days per week at the peak of the mating season (11 March to 18 May 2012). The
202 investigation was approved by the IACUC of the University of Puerto Rico, Medical
203 Sciences Campus (protocol No. A0100108).

204

205 *Assessment of skin redness and darkness*

206 Images were collected 2-3 times per week for all 32 females (mean +/- SEM 19.81 +/-
207 1.01 images per female). Details of image collection and measurements can be found in
208 Dubuc et al. (2014). Briefly, multiple images of males and a color standard (X-rite
209 ColorChecker passport) were captured in RAW format from 1-3 meters away from
210 subjects using a calibrated Canon EOS Rebel T2i camera with an 18 megapixel CMOS
211 APS-sensor and an EFS55-250mm f/4-5.6 IS lens. Immediately after the capture of an
212 image, we took a second photograph of the color standard placed in the same location and
213 photographed under the same lighting and camera settings as the subject (i.e. the
214 “sequential method”: Higham (2006); Bergman and Beehner (2008); Stevens (2009)).
215 Facial skin color was quantified by measuring color values from images converted to 16-
216 bit TIFF files using DCRAW (Coffin 2008). We first took average red (R), green (G),
217 and blue (B) measurements (reflecting the camera sensor stimulation) from a portion of
218 the face which included the bridge of the nose and all skin between the nostrils and the

219 corners of the eyes, avoiding areas of dirt, dappled light, or shadows, and the neutral grey
220 patches of the color standard. Landmarks selected around this area were joined using
221 cubic spline interpolation using a customized MATLAB function. RGB values were
222 transformed to rhesus color space via a polynomial colorspace transformation (Stevens et
223 al. 2007), corrected for variation in lighting by applying the Von-Kries transformation
224 (Ives (1912); reprinted in Brill (1995)) using the white patch of the color checker.
225 Measurements from multiple successive face images taken of the same subject with
226 multiple corresponding standard images were averaged to yield that subject's overall
227 facial skin color phenotype for that day. We calculated female facial redness as $(LW-$
228 $MW)/(LW+MW)$ (the Red-Green Opponency Channel, hereafter "Redness") and
229 luminance as $(LW+MW)/2$, hereafter "Darkness" (Osorio and Vorobyev 2005). We
230 describe higher Red-Green Opponency values as "redder", and lower luminance values as
231 "darker". We present summary statistics for Redness and Darkness values in Table 1.

232

233 *Behavioral data collection and definitions*

234 Behavioral data was collected by two trained observers who have collected behavioral
235 data together on multiple studies (Dubuc, Hughes, et al. 2012; Dubuc, Muniz, et al. 2012;
236 Dubuc, Allen, et al. 2014). Data collection focused on male-female socio-sexual
237 interactions. All occurrences of male-female interactions were recorded (Altmann 1974).
238 We recorded female proceptive behaviors (presentation of hindquarters and hand slaps
239 (Carpenter 1942; Michael and Zumpe 1970; Wallen et al. 1984; Dixson 2012)), plus all
240 mounts and intromissions. We considered as *proceptive* females that were: observed
241 mating, exhibiting a sperm plug, receiving or emitting sexual solicitations, or consorting

242 with a male. Consecutive proceptive days (with gaps of 1-2 days) were considered as
243 being part of the same proceptive period or behavioral oestrus. *Mating* was considered to
244 take place when a mount with penetration and pelvic thrusts occurred outside the context
245 of social tension and conflicts. Since rhesus macaques are multiple-mounters, two
246 observed mounts were considered part of the same *mating series* if they took place ≤ 30
247 min apart from each other, unless an ejaculation pause or a new sperm plug was observed
248 (Dubuc et al. 2011). *Consortships* were defined as sexual associations where a male and a
249 female maintained proximity and synchronized their activity, regardless of who was
250 mainly in charge of such maintenance. No evidence of mating between the male and the
251 female was required for them to be considered as forming a consortship, but the female
252 did need to be considered to be behaving proceptively.

253

254 *Dominance rank*

255 For females, we used previously-calculated dominance ranks from Mandalaywala et al.
256 (2014), which were determined based on the outcome of dyadic agonistic interactions
257 between females in Group R. Dyadic interactions were placed into a winner-loser matrix
258 and MatMan was used to generate linear dominance hierarchies (cf. Higham &
259 Maestripiéri (2014)). Following 10,000 iterations, significant linear hierarchies were
260 produced (linearity test using Landau's linearity index corrected for unknown
261 relationships, $P = 0.03$). For males, we used previously-calculated dominance ranks from
262 Dubuc et al. (2013; 2014). Briefly, male dominance ranks were calculated for all males
263 resident in group R in 2011 using agonistic interactions; this hierarchy was then modified
264 to include three males that immigrated into group R in 2012. Since rhesus macaque males

265 “queue” for dominance, such that males enter a new group at the bottom of the hierarchy
266 and rise in rank over time (Manson 1995), all three of these new males were assigned the
267 lowest rank in the hierarchy. We defined *top-ranked* males as the males with the four
268 highest dominance ranks. In studies of species with largely asynchronous female fertile
269 phases, it is common to independently assess the mate choice preferences of the alpha
270 male (e.g., Bradley et al. (2005), Setchell et al. (2005)), who should have priority of
271 access to the fertile female on any given day (Altmann 1962). However, due to the high
272 female reproductive synchrony in our study population, assessing the choices of several
273 top-ranked males seems more appropriate. In our sample, 2.48 females from the 32 study
274 subjects were seen in consort with males per day (range 0-9) across all observation days.
275 This translates to 3.49 females in consort on an average observation day across the whole
276 study group (45 females). We therefore reasoned that the mate choices of the 4 top-
277 ranked males were important to assess independently of those of all males.

278

279 *Female attractiveness and male mating effort*

280 We used two measures to assess female attractiveness to males: (i) the number of mating
281 series in which females were involved; and (ii) the dominance rank of male consortship
282 partners, i.e. the ones that have priority-of-access to females. We calculated each measure
283 for each observation day of the study (i.e. for the entire dataset).

284

285 *Physical condition*

286 All subjects except one were captured and anesthetized with ketamine by trained CPRC
287 employees. Body mass was measured using a hanging scale. Body length (top of head to

288 tail base) and skinfold fat above and below the navel were measured with electronic
289 calipers by CD. Each measurement was taken two times and averaged. Body-mass-index
290 (BMI) was calculated as kg/m^2 (Campbell and Gerald 2004) and skinfold fat as the
291 average of both measurements.

292

293 *Physiological condition*

294 Fecal samples were collected opportunistically during fieldwork for measurement of
295 glucocorticoid metabolites, break-down products of metabolic hormones associated with
296 energy allocation in response to the physical and social environment. Special effort was
297 invested in collecting samples from females for which no recent (within the last 1-2
298 weeks) samples had been collected, if needed. Samples were kept in a cooler with ice
299 while in the field and then put in a -20°C freezer upon return from the field. Fecal
300 samples were shipped to the German Primate Center (DPZ) on ice for analysis using a
301 previously-validated glucocorticoid metabolite assay (Hoffman et al. 2011). All fecal
302 samples arrived at the DPZ frozen, and were subsequently prepared for enzyme-immuno
303 assay (EIA) by being lyophilized and pulverized. An aliquot (50 – 70 mg) of the resulting
304 fecal powder was extracted with 3 ml of 80% methanol by vortexing for 15 min
305 (Heistermann, Finke, & Hodges (1995)). Samples were analysed for 11β -
306 hydroxyetiocholanolone, a major metabolite of cortisol in primate faeces (e.g.,
307 Heistermann, Palme, & Ganswindt (2006)) using an EIA that has been biologically
308 validated for use in rhesus macaques (see Hoffman et al. (2011) for validation, and
309 Heistermann, Ademmer, and Kaumanns (2004) for a detailed description of the EIA).
310 High and low concentration standards were assayed across plates to assess measurement

311 variation, which demonstrated inter-assay variation of below 15%, and intra-assay
312 variation of below 10%. Assay results are standardized for differences in fecal weight and
313 are expressed as fGCM concentration (ng) per dry fecal weight.

314 Urine samples were collected opportunistically for measurement of urinary C-
315 peptide (UCP) of insulin. This biomarker is a measure of energetic status, and in rhesus
316 macaques has been shown to be primarily influenced by whether an individual is in
317 overall positive or negative energy balance (Girard-Buttoz et al. 2011). Sampling effort
318 was again invested in collecting samples from females when no samples had been
319 collected in the previous 1-2 weeks. Samples were not collected if contamination with
320 faeces or blood was suspected. In order to remove substrate from the sample, we allowed
321 each sample to settle and pipetted off the clean urine from the top, transferring the urine
322 into a new tube every minute or so until the sample was completely clean (Higham,
323 Heistermann, et al. 2011). Samples were kept in a cooler on ice while in the field and
324 then put in a -20° C freezer upon return from the field. Samples were shipped to New
325 York University (NYU) for analyses using a previously-validated assay (Girard-Buttoz et
326 al. 2011; Higham, Girard-Buttoz, et al. 2011; Higham, Heistermann, et al. 2011). High
327 and low concentration standards assayed across plates to assess measurement variation
328 demonstrated inter-assay variation of below 15%, and intra-assay variation of below
329 10%. Assay results were indexed for differences in urine concentration by creatinine
330 measurement via the Jaffe reaction.

331

332 *Statistical analyses*

333 All statistical analyses were performed in R version 4.0.1 (R Development Core Team
334 2020). We removed outlying values prior to analyses ($n = 3$ fGCM measures). These data
335 points were greater than three standard deviations above the mean and may represent
336 methodological errors. Some fecal samples contain large amounts of undigested fecal
337 matter. Removing the undigested matter leads to a low fecal dry weight, and results in a
338 very high hormone-per-weight concentration. While fGCM concentrations can increase
339 and decrease, it is unlikely that a fGCM measure, which is an integrated measure of
340 fGCM production over a few days, should show very high one-off spikes, leading us to
341 question whether strongly outlying values were likely to be physiologically valid. In
342 addition, we also reasoned that we were in any case more interested in baseline effects
343 than one-off responses to acute stressors. We did not remove any other values from the
344 dataset.

345

346 **1) Do males prefer females with redder and/or darker faces?**

347 First, we explored whether female color predicted patterns of investment among males
348 using Generalized Linear Mixed Models (GLMMs). We ran a total of eight models. First,
349 we examined patterns of male investment across our entire dataset (four models). We
350 tested whether redder (one model) and/or darker females (a second model) were involved
351 in more mating series per day using GLMMs with a negative binomial error structure,
352 setting the number of mating series as the response variable, with color, age, and rank
353 (fixed effects), and female ID and study week (to control for changes across the mating
354 season) (random effects) as predictors, and the number of observations per female per

355 day as an offset. Age and rank were coded as numerical predictors, and study week was
356 coded as a categorical predictor. We also tested whether on a daily basis, the 4 top-ranked
357 males were more likely to consort redder (one model) and/or darker females (a second
358 model) using GLMMs with a binomial error structure, setting whether or not a female
359 was consorted by a top male as the response variable, with color, age, and rank (fixed
360 effects), and female ID and study week (random effects) as predictor variables, and the
361 number of observations per female per day as an offset. As above, we coded age and rank
362 as numerical predictors and study week as a categorical predictor. Including female ID as
363 a random effect allowed us to control for uneven sampling across females and generate
364 more robust estimates for each female. Nevertheless, to further ensure to that our
365 analyses focused on interindividual variation, we ran a second set of analyses (four
366 models) using only data collected on females when they were recorded as exhibiting
367 proceptive behaviors towards males (hereafter: *proceptive-only dataset*), using the same
368 model structures outlined above. We log-transformed the number of observations (offset)
369 in all models. Several females were observed in consort but were not formally focused on
370 a given day. We excluded these cases from the models ($n = 32$ for redness, $n = 33$ for
371 darkness) because zeroes (for the observation time offset) cannot be log-transformed.
372 Proceptive-only dataset models that analysed whether color influenced consortship by
373 top-ranked males did not meet assumptions regarding the distribution of residuals as
374 originally structured, so we also ran a second set of these models, dropping the random
375 ID term representing the study week. Results were qualitatively the same, so we present
376 results from models including the week random ID term. All GLMM analyses were run

377 in the R package “glmmTMB” (Brooks et al. 2017), and residuals were visualized using
378 the R package “DHARMA” (Hartig 2017).

379

380 **2) Is face redness or darkness linked to physical or physiological condition?**

381 Next, we used two approaches to test whether skin redness or darkness was linked to
382 physical or physiological condition (estimated based on BMI, skinfold fat, fGCM
383 concentrations, and UCP concentrations). Since we had only one measure of BMI and
384 skinfold fat from just before the mating season, we first conducted analyses across the
385 whole dataset using color values averaged across the mating season and single
386 measurements of BMI and skinfold fat, using GLMs, controlling for age and sex (fixed
387 effects). GLMs were implemented using the glm function using log-transformed
388 measures for all variables. Secondly, since we had more regular fGCM and UCP
389 measurements, we used LMMs to test for the effect of fGCM and UCP by week. We ran
390 four models in total. We set color (either Redness or Darkness) as the response variable,
391 and either fGCM or UCP as a numerical predictor variable, controlling for dominance
392 rank and age (fixed effects) and female ID (random effect) in all models. Dominance
393 rank and age were coded as continuous predictor variables. In our UCP models we
394 included collection time, since exploratory analysis revealed a strong effect of collection
395 time on UCP concentrations. We log-transformed dominance rank and age, but we used
396 untransformed values for redness and darkness because weekly-averaged values of
397 redness and darkness were normally distributed. LMMs were run in the R package
398 “lme4” (Bates et al. 2015), and significance of fixed effects was tested using type II Wald
399 chi-square tests implemented using the R package “car” (Fox and Weisberg 2011). For all

400 models, we visually assessed residual plots to verify that residuals were normally
401 distributed and uncorrelated with fitted values.

402

403 RESULTS

404 **1) Do males prefer redder and/or darker females?**

405 Across the entire dataset, the females who engaged in the highest number of mating
406 series across all males were both darker and redder (Table 2a; Figure 1). However, when
407 only the proceptive period of the ovarian cycle is considered, only redder (but not darker)
408 females engaged in more mating series (Table 2b; Figure 1). Models of daily data
409 revealed that top-ranked males formed consortships with redder, but not darker females
410 more often across the whole dataset (Table 3a; Figure 2); this difference is not detected in
411 the proceptive-only dataset (Table 3b; Figure 2). Overall, results suggest that males bias
412 mating effort towards redder females.

413

414 **2) Is face redness or darkness linked to physical or physiological condition?**

415 There was a significant positive association between female redness and fGCM
416 concentrations, but not between female darkness and fGCM concentrations (Table 4;
417 Figure 3). No association was found for UCP concentrations (Table 4), BMI (Table 5) or
418 skinfold fat (Table 5). Results suggest that, overall, redder females have higher
419 concentrations of fGCM during the mating season.

420

421

422

423 DISCUSSION

424 Our results show that female skin redness and darkness are associated with male mating
425 activity. Specifically, males mated more with females with redder and darker faces, and
426 the top-ranked males, who have priority-of-access, preferentially consort redder-faced
427 females. The fact that only skin redness, but not darkness, is associated with interfemale
428 variation in sexual activity when the analyses are limited to proceptive periods of the
429 ovarian cycles, suggest that color (i.e. blood oxygenation; Changizi et al. (2006); Stephen
430 et al. (2009)) rather than darkness (i.e. blood flow; Changizi et al. (2006); Stephen et al.
431 (2009)) is the more important variable in determining male preference.

432 Cumulative evidence strongly suggests that facial skin coloration is most likely to
433 be a signal under sexual selection in both females and males in rhesus macaques. Results
434 to date do not support the view that trait expression in females could be a non-adaptive
435 by-product of the evolution in males: the trait is heritable in females, is related to higher
436 reproductive success, with redder-faced females having higher annual fecundity (Dubuc,
437 Winters, et al. 2014), and males prefer to consort and mate with these females (this
438 study). Our conclusion that the trait is a sexually-selected signal rather than a cue is
439 further supported by what is known about the mechanism by which the facial skin
440 reddens. The redness of rhesus macaque facial skin is caused by the binding of estrogen
441 to estrogen receptors, which are expressed in far greater concentration in the face than in
442 adjacent skin on the body (Rhodes et al. 1997). Targeted tissue-specific estrogen-receptor
443 expression in the bare-skin the facial and hindquarter area, which is not present in
444 adjacent areas of the skin covered in fur, shows that facial skin has become specialized
445 and targeted to create dark red color, and hence the visual signaling effect. Therefore, it is

446 unlikely that facial skin color could be a mere cue of female quality that correlated
447 directly with female physiological condition and hence fecundity, while not being under
448 selection for its communicative value. Even if a redder face was originally a cue to
449 female fecundity, perhaps initially because it is linked to the flow of oxygenated blood
450 and indicates female health, then any male that started using facial redness to choose
451 females - a preference we found in the present study would start to do better than males
452 not doing so. This preference for the trait among males will start to select for greater
453 expression of it in females for its communicative value, as long as females gain fitness
454 benefits from increasing expression and their attractiveness to males (see below).

455 Collectively then, our results are consistent with the idea that female facial
456 coloration acts as an ornament, indicating a female's reproductive potential and value as a
457 mate, with females being preferentially selected by males according to their degree of
458 color expression. This would suggest that inter-female color variation is a classical inter-
459 sexually selected ornament, but of an unusual kind, being exhibited by females of a large
460 mammal species in the absence of sex-role reversal. Combined with results of prior
461 studies, these results suggest that inter-female differences in redness may reflect inter-
462 female differences in quality, while skin darkness is more linked to intra-female variation
463 in the probability of conception (Higham et al. 2010).

464 One key question to address relates to the fitness benefits that females might
465 obtain by signaling their quality, since such benefits must manifest for the signal to be
466 selected. Often, such benefits are framed in the context of "good genes" explanations, but
467 the theoretical basis for expecting such effects, and the extent of the supporting empirical
468 evidence available, continues to be the source of much debate (Møller and Alatalo 1999;

469 Alonzo and Servedio 2019). In our system, males are highly variable in their reproductive
470 success (Dubuc, Ruiz-Lambides, et al. 2014) and males who combine both high
471 dominance rank and dark red face coloration have the greatest annual fecundity (Dubuc,
472 Winters, et al. 2014). Females are preferentially proceptive to such males – those with
473 redder, darker, facial coloration (Dubuc, Allen, et al. 2014), and prefer to look at such
474 males when tested experimentally (Dubuc et al. 2016). This evidence is consistent with
475 the idea that females do exhibit mate choice preferences. In a context where females
476 exhibit mate choice preferences for specific males, and in which many females are
477 synchronously fertile and sexually active at the same time such that males must choose
478 which female to mate with (Dubuc et al. 2011) selection should favour signals in females
479 that increase mating interest from desirable males. Since such males sire more offspring,
480 this provides mechanisms by which females accrue benefits from mating with such males
481 – females may themselves have increased fecundity by mating with such males, and will
482 also give birth to sons who may inherit these favourable traits from their fathers.

483 We expect an inter-female quality ornament to be particularly likely to evolve in a
484 species such as rhesus macaques, for multiple reasons. Rhesus macaques live in very
485 large groups (as many as >400 individuals) on Cayo Santiago, and are thought to live at
486 least facultatively in very large groups in the wild too (Southwick and Siddiqi 2011).
487 They are also seasonal breeders; large group sizes and seasonal breeding are typically
488 considered to be the two primary factors determining the likelihood of female
489 reproductive synchrony (Kutsukake and Nunn 2006; Ostner et al. 2008; Gogarten and
490 Koenig 2013). Consistent with this, the Cayo Santiago rhesus macaque population has an
491 unusually high degree of female fertile phase and birth synchrony (Dubuc et al. 2011;

492 Hernández-Pacheco et al. 2016). This high degree of fertile phase synchrony means that
493 there are often multiple females fertile on the same day. Given low degrees of body and
494 canine size dimorphism in this species (Plavcan 2004), males cannot monopolize multiple
495 females. Moreover, sperm competition is extremely strong, as indicated by large relative
496 testis volume (Bercovitch and Rodriguez 1993), and despite increased investment in
497 production, sperm may be a limited resource for promiscuously mating males.
498 Collectively, these factors should select for male choosiness when selecting mates, and
499 when allocating mating effort. Males may be able to parse out variation in different
500 dimensions of female coloration – intra-cycle vs inter-female color variation. In support
501 of this, males who are familiar with specific females prefer looking at images of those
502 females when they exhibit their red fertile faces, while the same preferences are not
503 shown across all males (Higham, Hughes, et al. 2011). Mathematical modelling has
504 shown that learning the intra-cycle variation for specific females has significant fitness
505 benefits for males (Ma and Higham 2018).

506 We made no prediction about whether females who were redder and/or darker
507 would be in better or worse physiological condition with respect to our available
508 measures (i.e. via measures of energetic status, such as body fat and BMI; urinary C-
509 peptide of insulin concentrations (Girard-Buttoz et al. 2011; Higham, Girard-Buttoz, et
510 al. 2011); and glucocorticoids (Dallman et al. 1993; Beehner and Bergman 2017)). Our
511 finding that females who are redder have higher fGCM concentrations could be explained
512 in two different ways. Firstly, since redder-faced females have higher fecundity, they
513 may differ in energetic condition, energy mobilization, and blood-flow relative to other
514 females. Under this scenario, these females are in different physical or physiological

515 condition, which manifests itself in both the expression of redder-faces, indicating higher
516 rates of oxygenated blood-flow, and higher fecundity. A second, non-mutually exclusive
517 alternative, is that the relationship is not directly related to underlying properties, but
518 instead reflects the higher energetic burden of a lot of mating and constant attention,
519 coercion, and harassment by males. This additional mating and other associated physical
520 activities, may lead to higher levels of energy mobilization among these females, who
521 hence exhibit higher fGCM concentrations. This seems likely to be the case in rhesus
522 macaques, because proceptive females appear restless, and active (C. Dubuc, personal
523 observation). Further studies will be needed to examine the extent to which skin color is
524 directly affected by levels of physical activity.

525 The data presented here, combined with our results from prior studies showing
526 that female signal expression indicates female fecundity (Dubuc, Winters, et al. 2014),
527 are consistent with the reliable indicator hypothesis (Pagel 1994). Originally developed
528 for understanding the function of female sexual swellings, we suggest it can also explain
529 the function of inter-individual variation in female face coloration in rhesus macaques, a
530 species in which sexual swellings are absent. While it remains unclear whether sexual
531 swelling size is acting as a reliable indicator of female quality in most species (though see
532 Huchard et al. (2009) for chacma baboons) our results shed new light on the comparative
533 function of sexual signals in primates. Indeed, sexual swellings are found in species
534 where females are aseasonal breeders (Nunn 1999), and among Papionins have their
535 strongest degree of expression in species with the least amount of female reproductive
536 synchrony, such as crested macaques (Higham et al. 2012). It therefore seems less likely
537 that the reliable indicator hypothesis will apply to sexual swellings compared to signals

538 found in species in which many females are fertile at the same time, and in which males
539 choose between multiple fertile females. There may also be substantive differences in the
540 function of sexual swellings across species given extensive comparative variation in the
541 socioecology and mating systems of primates that exhibit such swellings (for baboons,
542 see Petersdorf et al. (2019), especially given that sexual swellings have evolved at least
543 twice independently (Nunn 1999).

544 Our results support adding inter-individual variation in female rhesus macaque
545 facial coloration to the list of signals thought to represent female ornaments used by
546 males in mate choice. Other examples of evidence for such ornaments include: male
547 tropidurid lizards, which prefer females with white over red throat patches (Watkins
548 1997); house finches, in which males prefer females with redder plumage (Hill 1993);
549 bluethroats, in which males prefer females with more colorful throat patches (Amundsen
550 et al. 1997); and blue-footed boobies, in which males prefer females with bluer feet
551 (Torres and Velando 2005). However, rhesus macaque female coloration has some
552 elements of added complexity, in that it is also an intra-individual signal of variation in
553 fertility and conceptive probability. It may represent an example of an intra-individual
554 signal of fertility, which has secondarily evolved to become an inter-individual signal of
555 quality, as outlined in the evolutionary model of Huchard et al. (2009). It is also one of
556 the only known color ornaments functioning as an inter-individual signal indicator for
557 females of any large mammal species. This is likely to be attributable to the relatively
558 unusual (for a large mammal) sexual selection pressures experienced by rhesus
559 macaques, in which large group sizes, reproductive seasonality, and a polygynandrous
560 mating system cause reduced direct, and increased indirect, forms of male-male

561 competition, while increasing female-female competition and direct female mate choice
562 for the best males.

563

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805 **Table 1.** Summary statistics for facial Redness and Darkness.

ID	mean Redness (min – max)	mean Darkness (min – max)	CV Redness (%)	CV Darkness (%)
1	0.095 (0.082 - 0.110)	0.252 (0.196 - 0.335)	7.425	12.349
2	0.087 (0.065 - 0.110)	0.283 (0.206 - 0.431)	14.079	21.949
3	0.082 (0.050 - 0.101)	0.362 (0.233 - 0.489)	15.019	20.124
4	0.091 (0.060 - 0.127)	0.287 (0.175 - 0.591)	15.030	28.788
5	0.081 (0.062 - 0.104)	0.295 (0.238 - 0.403)	14.545	14.439
6	0.092 (0.076 - 0.115)	0.285 (0.208 - 0.405)	12.304	15.766
7	0.072 (0.057 - 0.082)	0.337 (0.285 - 0.447)	8.349	12.260
8	0.089 (0.073 - 0.110)	0.311 (0.252 - 0.411)	12.216	13.716
9	0.081 (0.066 - 0.097)	0.289 (0.220 - 0.396)	11.708	13.990
10	0.091 (0.074 - 0.113)	0.292 (0.195 - 0.475)	12.247	23.030
11	0.084 (0.055 - 0.112)	0.252 (0.186 - 0.338)	16.441	16.894
12	0.091 (0.068 - 0.113)	0.293 (0.213 - 0.401)	9.318	16.910
13	0.084 (0.060 - 0.105)	0.319 (0.251 - 0.483)	12.553	22.799
14	0.099 (0.083 - 0.126)	0.221 (0.160 - 0.282)	10.862	18.621
15	0.110 (0.095 - 0.129)	0.284 (0.182 - 0.363)	9.930	18.296
16	0.089 (0.060 - 0.127)	0.300 (0.215 - 0.412)	19.469	15.202
17	0.084 (0.060 - 0.108)	0.316 (0.241 - 0.429)	19.095	20.942
18	0.084 (0.066 - 0.114)	0.278 (0.185 - 0.389)	13.374	19.179
19	0.074 (0.065 - 0.084)	0.309 (0.224 - 0.353)	8.481	13.239
20	0.075 (0.056 - 0.094)	0.303 (0.233 - 0.462)	11.254	19.569
21	0.090 (0.079 - 0.100)	0.281 (0.188 - 0.370)	6.762	14.923
22	0.084 (0.069 - 0.098)	0.305 (0.216 - 0.501)	10.874	28.885
23	0.089 (0.073 - 0.114)	0.244 (0.187 - 0.304)	12.232	11.967
24	0.084 (0.062 - 0.105)	0.299 (0.231 - 0.398)	12.214	15.284
25	0.087 (0.073 - 0.112)	0.315 (0.253 - 0.505)	11.720	18.695
26	0.071 (0.047 - 0.091)	0.320 (0.208 - 0.416)	18.032	20.770
27	0.085 (0.073 - 0.098)	0.285 (0.215 - 0.361)	8.056	14.013
28	0.092 (0.079 - 0.113)	0.258 (0.156 - 0.324)	11.443	16.990
29	0.087 (0.072 - 0.108)	0.277 (0.206 - 0.340)	9.594	13.813
30	0.081 (0.075 - 0.084)	0.284 (0.248 - 0.348)	4.331	14.689
31	0.081 (0.052 - 0.099)	0.320 (0.173 - 0.584)	13.108	28.047
32	0.077 (0.057 - 0.097)	0.328 (0.233 - 0.422)	14.217	16.568
Total			14.964	20.470

808 **Table 2a.** Results of negative binomial GLMMs testing the effects of redness or
 809 darkness, age, and rank on the number of mating series in which a female participated,
 810 controlling for female ID and study week, with an offset for the number of observations
 811 per female per day. Analyses shown are across the whole dataset.

	Estimate	Standard error	z-value	p
Number of mating series				
(Redness; daily)				
n = 602 female days				
Intercept	-7.569	0.978	-7.737	< 0.001
Redness	52.602	8.790	5.984	< 0.001
Age	-0.126	0.065	-1.932	0.053
Rank	0.011	0.008	1.336	0.182
Number of mating series				
(Darkness; daily)				
n = 602 female days				
Intercept	-1.811	0.810	-2.236	0.025
Darkness	-4.394	1.884	-2.333	0.020
Age	-0.086	0.051	-1.668	0.095
Rank	0.009	0.007	1.397	0.163

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814 **Table 2b.** Results of negative binomial GLMMs testing the effects of redness or
 815 darkness, age, and rank on the number of mating series in which a female participated,
 816 controlling for female ID and study week, with an offset for the number of observations
 817 per female per day. Analyses shown are for proceptive females only.

	Estimate	Standard error	z-value	p
Number of mating series				
(Redness; daily)				
n = 252 female days				
Intercept	-4.793	0.678	-7.068	< 0.001
Redness	27.756	7.065	3.929	< 0.001
Age	-0.076	0.033	-2.314	0.021
Rank	0.013	0.004	3.289	0.001
Number of mating series				
(Darkness; daily)				
n = 252 female days				
Intercept	-1.680	0.605	-2.776	0.006
Darkness	-2.562	1.590	-1.611	0.107
Age	-0.053	0.031	-1.716	0.086
Rank	0.012	0.004	3.057	0.002

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820 **Table 3a.** Results of binomial GLMMs testing the effects of redness or darkness, age,
 821 and rank on the likelihood of a female being consorted by a top-ranked male, controlling
 822 for female ID and study week, with an offset for the number of observations per female
 823 per day. Analyses shown are across the whole dataset.

	Estimate	Standard error	z-value	P
Consort by top-ranked male				
(Redness; daily)				
n = 602 female days				
Intercept	-28.067	6.870	-4.085	< 0.001
Redness	116.735	43.369	2.692	0.007
Age	0.106	0.383	0.278	0.780
Rank	0.026	0.054	0.480	0.631
Consort by top-ranked male				
(Darkness; daily)				
n = 602 female days				
Intercept	-13.523	4.467	-3.027	0.002
Darkness	-7.912	9.095	-0.870	0.384
Age	0.130	0.342	0.379	0.705
Rank	0.012	0.046	0.268	0.789

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826 **Table 3b.** Results of binomial GLMMs testing the effects of color (Redness or
827 Darkness), age, and rank on the likelihood of a female being consorted by a top-ranked
828 male, controlling for female ID and study week, with an offset for the number of
829 observations per female per day. Analyses shown are for proceptive females only

	Estimate	Standard error	z-value	p
Consort by top-ranked male				
(Redness; daily)				
n = 252 female days				
Intercept	-42.774	13.271	-3.223	0.003
Redness	64.671	95.369	0.678	0.498
Age	0.065	0.585	0.110	0.912
Rank	0.014	0.100	0.143	0.886
Consort by top-ranked male				
(Darkness; daily)				
n = 252 female days				
Intercept	-34.803	13.947	-2.495	0.013
Darkness	-6.702	24.345	-0.275	0.783
Age	0.060	0.586	0.103	0.918
Rank	0.008	0.101	0.082	0.935

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832 **Table 4.** Results of LMMs for weekly non-invasive measurements of skin color and
 833 physiological measurements, controlling for female ID as a random effect. In UCP
 834 models we also included collection time as a fixed effect.

	Estimate	Standard error	chi-square	p
			(df)	
fGCM (Redness)				
n = 137 female				
weeks				
Intercept	0.065	0.009		
fGCM	< 0.001	< 0.001	5.270 (1)	0.022
Age	0.008	0.004	4.289 (1)	0.038
Rank	-0.001	0.001	0.448 (1)	0.503
fGCM (Darkness)				
n = 137 female				
weeks				
Intercept	0.325	0.040		
fGCM	< 0.001	<0.001	<0.001 (1)	0.989
Age	-0.016	0.016	0.978 (1)	0.322
Rank	-0.001	0.006	0.031 (1)	0.861
UCP (Redness)				
n = 79 female weeks				
Intercept	0.074	0.013		
UCP	< 0.001	< 0.001	0.073 (1)	0.787

Sample Collection	< -0.005	0.012	0.150(1)	0.699
Time				
Age	0.007	0.005	2.312 (1)	0.129
Rank	-0.001	0.002	0.099 (1)	0.753

UCP (Darkness)

n = 79 female weeks

Intercept	0.336	0.045		
UCP	0.003	0.002	3.154 (1)	0.076
Sample Collection	< -0.011	0.051	0.046 (1)	0.830
Time				
Age	-0.027	0.016	2.924 (1)	0.087
Rank	0.004	0.007	0.345 (1)	0.557

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837 **Table 5.** Results of GLMs testing relationships between average Redness or Darkness,
 838 BMI, and skinfold fat (n = 31 females)

	Estimate	Standard error	t-value	p
BMI (Redness)				
Intercept	-2.736	0.426	-6.423	<0.001
BMI	0.044	0.116	0.379	0.708
Age	0.078	0.046	1.711	0.099
Rank	-0.009	0.017	-0.516	0.610
BMI (Darkness)				
Intercept	-1.835	0.467	-3.933	<0.001
BMI	0.209	0.127	1.649	0.111
Age	-0.039	0.050	-0.774	0.446
Rank	-0.017	0.019	-0.915	0.368
Skinfold Fat (Redness)				
Intercept	-2.576	0.101	-25.389	< 0.001
Skinfold Fat	-0.007	0.021	-0.359	0.722
Age	0.081	0.047	1.715	0.098
Rank	-0.008	0.017	-0.501	0.621
Skinfold Fat (Darkness)				
Intercept	-1.100	0.114	-9.680	< 0.001
Skinfold Fat	0.028	0.023	1.191	0.244
Age	-0.064	0.053	-1.212	0.236
Rank	-0.015	0.019	-0.765	0.451

839 FIGURE LEGENDS

840 **Figure 1.** Marginal effects of Redness (left column) and Darkness (right column) values
841 on the number of mating series per day for all females (top row, $n = 602$ female days for
842 Redness, 602 female days for Darkness) and for proceptive females (bottom row, $n = 252$
843 female days for both Redness and Darkness). The shaded area represents 95% confidence
844 bands of mean-fitted values.

845

846 **Figure 2.** Differences in Redness (left) and Darkness (right) values for females when
847 they were consorted by low and top-ranked males. Smaller values indicate darker skin
848 color. Top-ranked males consorted redder females more often ($p = 0.007$, $n = 634$ female
849 days, but not darker females $p = 0.384$, $n = 634$ female days) across the full dataset (top
850 row), but not the proceptive-only dataset (redness $p = 0.498$, $n = 257$ female days, or
851 darkness $p = 0.783$, $n = 257$ female days) (bottom row). Note that sample sizes for the
852 figures produced here directly from the raw data are slightly larger than for the models
853 (Table 2, see Methods for details).

854

855 **Figure 3.** Weekly measures of fGCM and Redness values ($n = 137$).

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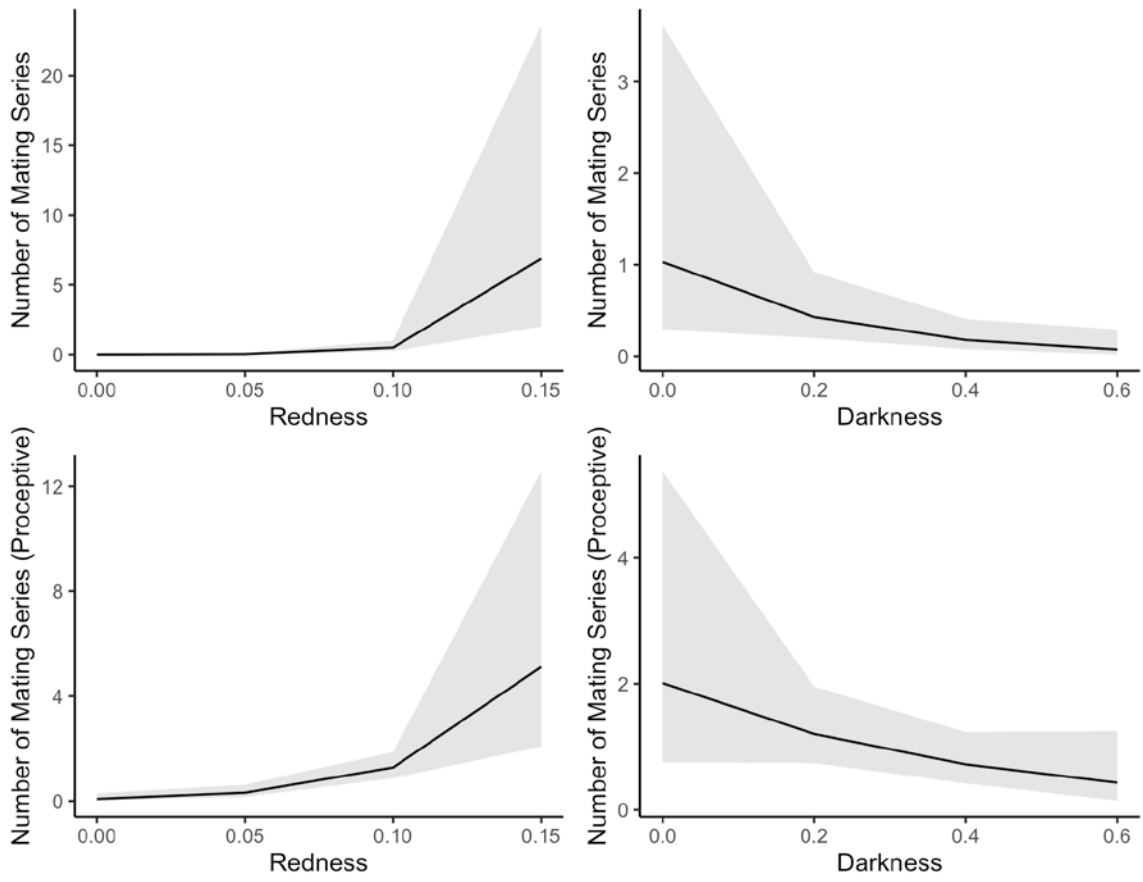
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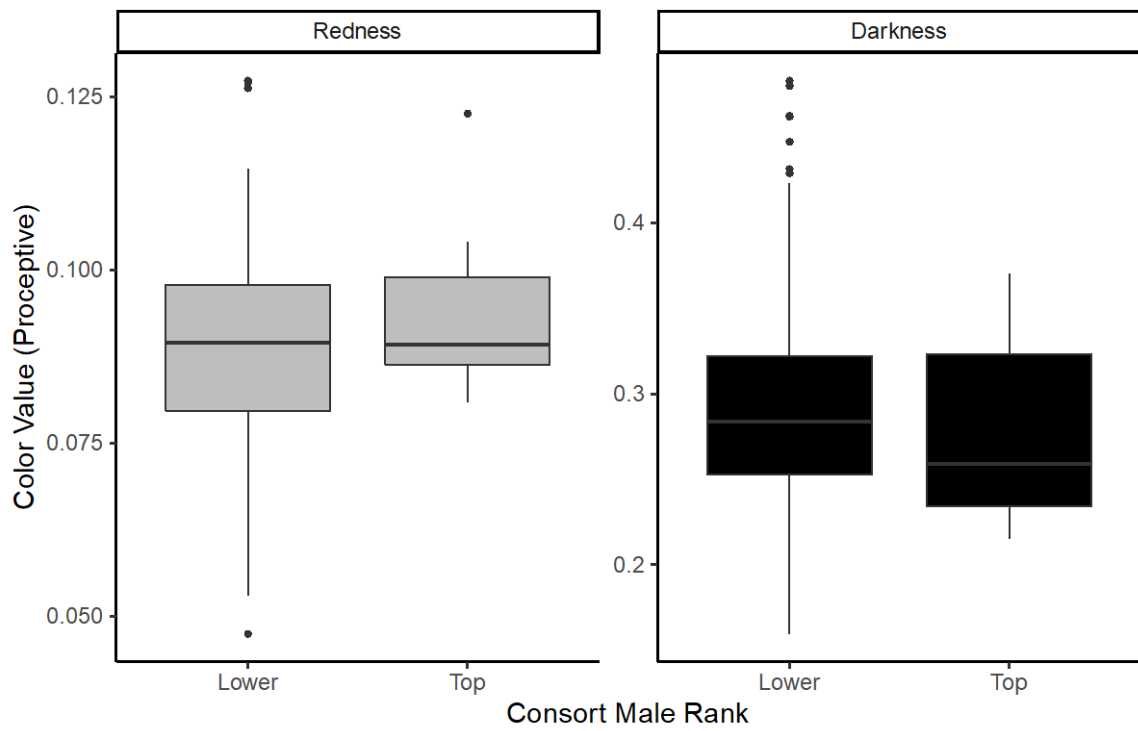
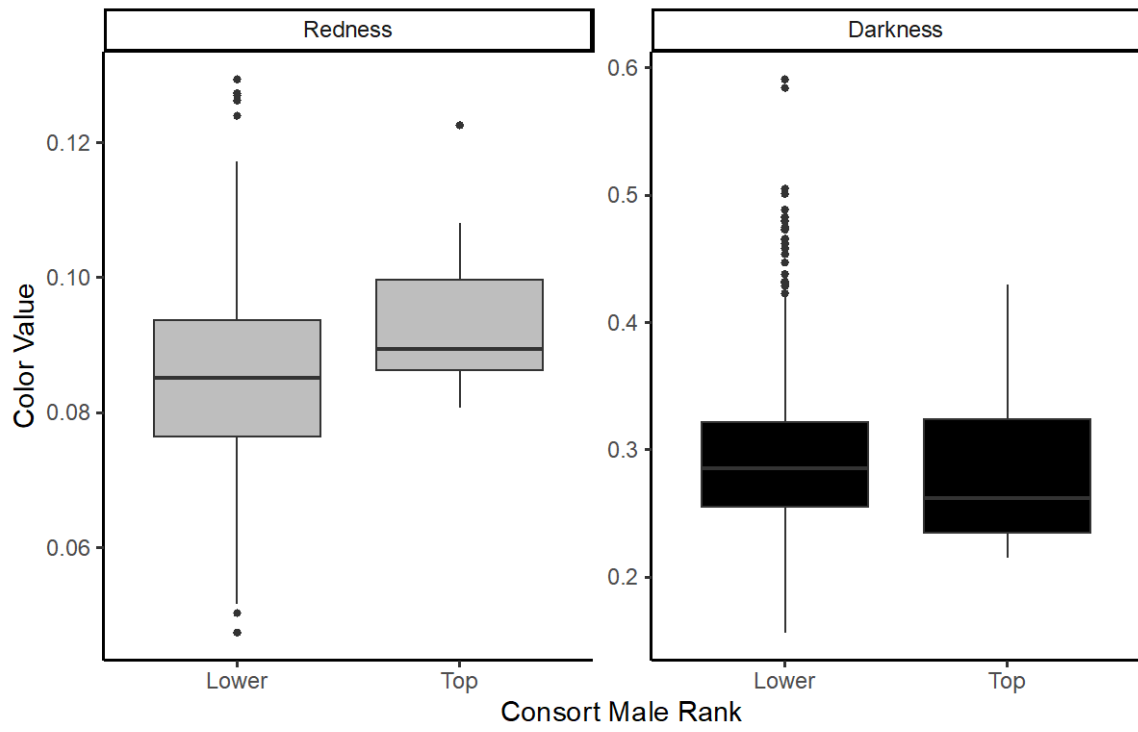
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862 **Figure 1.**



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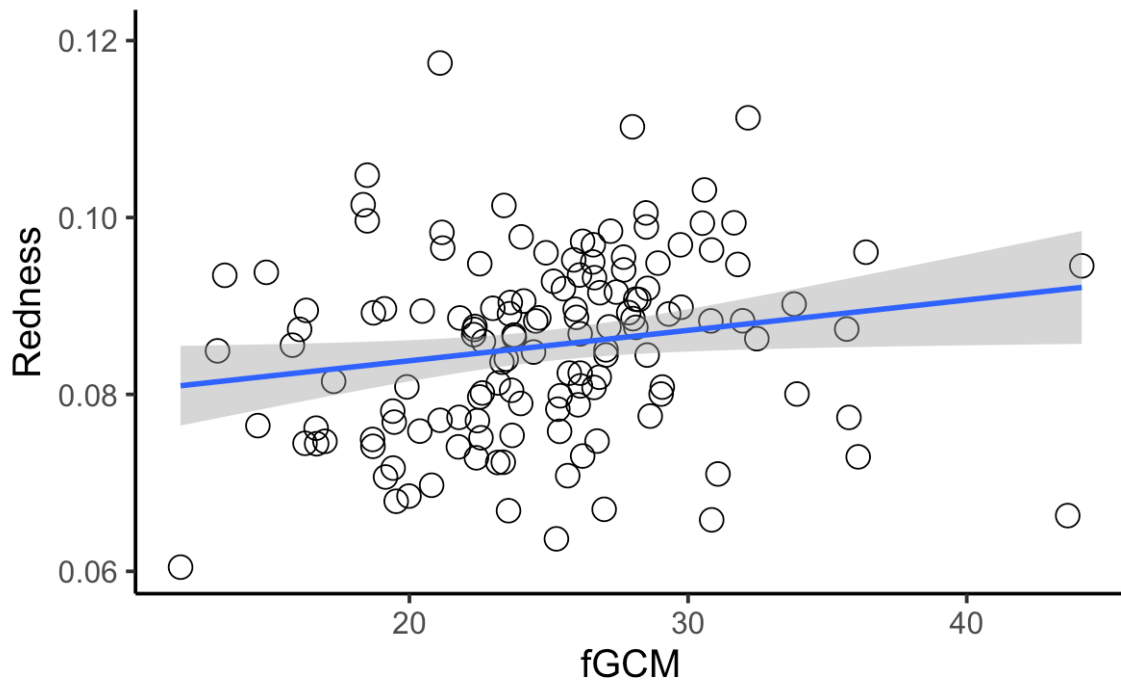
866 **Figure 2.**



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868 **Figure 3.**

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