

Field Notes: A Journal of Collegiate Anthropology

Volume 1

Article 10

2009

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Recommended Citation

Danzy, J and Gutierrez, V (2009) "Female Rhesus Macaques (*Macaca mulatta*) Sexual Skin Color Variability," *Field Notes: A Journal of Collegiate Anthropology*. Vol. 1 , Article 10.
Available at: <https://dc.uwm.edu/fieldnotes/vol1/iss1/10>

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Female Rhesus Macaques (*Macaca mulatta*) Sexual Skin Color Variability

J. Danzy and V. Gutierrez

Abstract

Many primate species use colorful signals to communicate sexual receptivity, rank, pregnancy, health, and developmental maturity. Reproductive coloration may not be limited to signaling sexual receptivity or pregnancy, but may also communicate aspects of female quality. Our preliminary study examined the relationships between female sexual skin coloration, mating status, and female traits, including age and dominance rank. The study took place at the Cayo Santiago (CS) facility in Puerto Rico; data were collected May through August of 2006. We examined two questions: 1) Is sexual skin coloration related to mating status?; and 2) Are inter- and intra-individual color differences related to female traits?

Facial coloration was not significantly related to mating status; genital saturation was significantly higher among mating females and among high-ranking females. Age was negatively correlated with both genital hue and genital saturation range; older females had more restricted coloration and younger females had more variable color. These preliminary results suggest that female coloration may reliably indicate aspects of female quality or condition to conspecifics, including potential mates.

Introduction

Darwin (1871:293) observed that “with the Rhesus monkey (*M. rhesus*) the female has a large surface of naked skin round the tail, of a brilliant carmine red, which periodically becomes..., even more vivid, and her face is also pale red” suggesting that sexual selection and mate choice played an important role in the evolution of the vivid coloration patterns

observed in some primates. Among non-human primates, coloration functions to signal sexual receptivity (Bielert et al. 1989; Domb and Pagel 2001; Engelhardt et al. 2004), to signal social relationships (Bercovitch 1996; Gerald 2001; Struhsaker 1967), to signal rank and facilitate mate choice (Cooper and Hosey 2003; Setchell and Dixson 2001; Setchell and Wickings 2004), to enforce evolutionary relationships (Kingdon 1988), and to entice mothers to care for their young (Ross and Regan 2000; Treves 1997).

Among non-human primates, examples of secondary sexual characteristics include ornamentation, acoustic sound, enlarged canines, body size, and sexual skin coloration (see Gerald 2003). Sexually selected characteristics are driven by two components of sexual selection: male competition for access to females, and female mate choice (Trivers 1972). Although attention has traditionally focused on female choice of male coloration (see reviews in Andersson 1994; Dixson 1998), males may be able to use color as a signal of female characteristics as well. For some species, recent research has indicated that female ornaments are used by males to assess female quality (Amundsen et al. 1997; Amundsen 2000; Berglund and Rosenqvist 1993; Jones and Hunter 1993; LeBas et al. 2003; Moller et al. 1995; Velando et al. 2001).

Rhesus macaques live in multimale-multifemale groups; during the mating season, males compete for access to females because many females are sexually receptive simultaneously. Therefore, rhesus males in particular need a way of assessing female sexual receptivity and quality due to the costs associated with competition, such as mate guarding, and resource acquisition. Resident males that have had significant tenure time with the females may use different cues than extra-group males who temporarily enter a group during the mating season. Studies have demonstrated that differences in vaginal chemosignals (Cerdeña-Molina et al. 2006), sexual swelling size (Bielert and Girolami 1986; Domb and Pagel 2001), sexual skin color (Bielert et al. 1989; Waitt et al. 2006), and behavior (Engelhardt et al. 2005) stimulate male interest in

and preference for particular females. Rhesus females do not exhibit the large, conspicuous sexual swellings (Darwin 1871; Pocock 1925; Pagel 1994) and unidentified, alternative cues (Ostner et al. 2006) common to many other catarrhines; instead, rhesus macaque females have colorful sexual skin that reddens during the mating season, meaning that color, in this species, may be an important cue in terms of reproduction.

Many secondary sexual characteristics are dependent on hormonal control (see reviews in Andersson 1994; Dixson 1998). In rhesus macaque females, the reddening of sexual skin is caused by sex hormones and increased vascularization (Collings 1926); inter- and intra-female sexual skin coloration is extremely variable during the mating season (Carpenter 1942; personal observation). Within this reproductive context, changes in sexual skin coloration may serve to inform selective males about female qualities. Gerald et al. (2004) found that female coloration was linked with age and body composition, suggesting that female color signals aspects of female quality among rhesus macaques. Other studies have found that inter-individual coloration did not predict body condition or life history traits, but was instead related to intra-individual changes in physiology such as menstrual cycle phase, parity and age (Higham et al. 2008; Setchell et al. 2006a).

Our study evaluates the communicative role of female sexual skin coloration in a reproductive context. We examined the relationship between female coloration and life history traits to assess what, if any, information color may convey to conspecifics and potential mates during the mating season. Our study examined two main questions: 1) Is sexual skin coloration related to mating status?; and 2) Are inter- and intra-individual color differences related to female traits?

Methods

Cayo Santiago, a 15.2 ha (38 acre) island located off the eastern coast of Puerto Rico, is home to approximately 950

rhesus monkeys (for site details see Altmann 1962; Carpenter 1942; Rawlins and Kessler 1986). Research was conducted on Cayo Santiago from May through August of 2006, to span most of the *M. mulatta* mating season. As part of a larger study examining links between female coloration, behavior, hormones, and life history (Danzy 2007), data were collected from Group S, which was composed of 76 members, including 16 multiparous females. The subjects of this study were ten randomly selected multiparous females; those analyses which examine mating vs. non-mating females exclude one subject because mating behavior was not observed.

Female age was obtained from the Cayo Santiago census database, which has detailed life history information on each subject from the time of birth. Rank was determined by matriline and birth age (using the census database), in addition to ad-libitum dyadic agonistic interactions. Mating status (mating or non-mating) was noted ad-libitum for every study subject; females were considered to be mating only if observed with a copulatory plug or receiving a true mount. Digital photographs of sexual skin were identified as being associated with a mating or non-mating female.

Sexual skin coloration was measured following the protocol by Gerald et al. (2001). Daily photographs were taken opportunistically. Coloration was objectively quantified (Gerald et al. 2001) using digital image software; three components of color were measured using Adobe Photoshop 6.0: hue, saturation, and brightness (HSB). Hue refers to what we generally term as color; saturation refers to the relative purity of color; and brightness refers to the relative lightness of color.

Color data were examined in two ways. First, we analyzed our results using the absolute measurements of color that were generated by Adobe Photoshop in order to group the data by category, or determine an average score per subject. For each subject, we also calculated color range (maximum-minimum) for each facial and genital color component (HSB). Examining color range allowed us to determine if intra-

individual variability was related to female traits. Two types of color data are reported: 1) average color, in order to compare variation across females and control for repeated measures; and 2) color range, to quantify the level of color variability within a female.

We performed statistical analyses using a statistical software package, SPSS 16.0. To examine the relationship between measures of facial and genital coloration (hue, saturation, and brightness) and mating status (mating vs. non-mating), we used paired t-tests. We also used Pearson's correlation tests to analyze the relationships between color, color range, and female traits. All tests were two-tailed, unless otherwise noted.

Results

We separated female color data into two categories, mating and non-mating to determine if sexual skin coloration was associated with mating status. We found no significant relationship between facial coloration and mating status (hue: $t=1.61$, $df=8$, $p=0.15$; saturation: $t=-0.59$, $df=8$, $p=0.57$; and brightness: $t=0.54$, $df=8$, $p=0.61$). Genital saturation was significantly higher in mating females than in non-mating females ($t=2.61$, $df=8$, $p=0.03$); genital hue ($t=-0.17$, $df=8$, $p=0.87$) and brightness ($t=0.00$, $df=8$, $p=1.00$) were unrelated to mating status. To further examine the relationship between genital saturation and mating status, we examined the relationship of mating genital saturation with age and dominance rank. On days when females were mating, genital saturation was correlated with rank ($r=0.67$, $n=9$; $p=0.05$); high-ranking females had significantly higher genital saturation values than low-ranking females.

We also examined the relationships between coloration, age, and rank to determine if color, in general, predicts female age or dominance rank. Using average color scores for each female, we found no relationship between age and facial ($n=10$;

hue: $r=-0.22$, $p=0.55$; saturation: $r=0.33$, $p=0.35$; brightness: $r=-0.05$, $p=0.90$) or genital ($n=10$; hue: $r=-0.22$, $p=0.54$; saturation: $r=0.50$, $p=0.14$; brightness: $r=-0.26$, $p=0.47$) coloration. We also found no significant relationships between rank and average facial ($n=10$; hue: $r=0.54$, $p=0.11$; saturation: $r=0.32$, $p=0.37$; brightness: $r=-0.27$, $p=0.45$) or genital ($n=10$; hue: $r=-0.08$, $p=0.96$; saturation: $r=-0.57$, $p=0.08$; brightness: $r=-0.10$, $p=0.78$) coloration.

To examine if the amount of intra-individual variation was correlated with age or rank, we quantified color range using the maximum and minimum score for each color component. Age was negatively correlated with both the range of genital hue (see Fig. 1; $r=-0.64$, $n=10$, $p=0.05$) and genital saturation (see Fig. 2; $r=-0.69$, $n=10$, $p=0.03$), but independent of range of genital brightness range ($r=-0.45$, $n=10$, $p=0.19$). In effect, younger females had more variable genital hue and saturation than older females, who had much more restricted color values. We did not find a relationship between rank and facial ($n=1$; hue: $r=-0.19$, $p=0.61$; saturation: $r=0.19$, $p=0.59$; brightness: $r=-0.08$, $p=0.83$) or genital ($n=10$; hue: $r=0.12$, $p=0.75$; saturation: $r=0.43$, $p=0.21$; brightness: $r=0.52$, $p=0.13$) color range.

Discussion

Several studies suggest that coloration is important in reproductive and non-reproductive contexts; rhesus males and females are attentive to individual coloration differences (Gerald 2001, 2003, 2006; Gerald and Waitt 2005; Gerald et al. 2007; Setchell 2005; Setchell et al. 2006a; Waitt et al. 2003) though it is unclear if and what information is conveyed by sexual skin color among rhesus macaques. Our study examined the relationships between female sexual skin coloration, mating status, and female traits to determine if observed color variation communicates aspects of female condition or quality to potential mates. Our study specifically examined two main questions: 1) Is sexual skin coloration related to mating status?;

and 2) Are inter- and intra-individual color differences related to female traits?

While some females tended to have higher coloration values on mating days when compared to non-mating days, genital saturation was the only component of coloration significantly higher among mating females than non-mating females. We further examined mating color to determine if genital saturation was related to female age or dominance rank. On days when females were mating, genital saturation was positively related to rank; high-ranking females had significantly higher genital saturation values than low-ranking females.

We used average color scores for each female to examine if inter-individual differences in overall color were related to age or dominance status. We found that average coloration did not predict age or rank. Although the average scores were not significantly different across females, we noticed that some females showed more intra-individual color variation than others. Using color range as a measure of intra-individual color variability, we also examined potential links between color range and female traits (dominance rank and age). We did not find a significant relationship between rank and facial or genital color range. Instead, our results indicate age is significantly related to components of genital color range. We found that older females have much more constrained genital hue and saturation, while younger females have more variable genital hue and saturation; although their average color scores are similar across females, the level of intra-individual variation is significantly different across females. We suggest that the pattern of limited color variability among older females may be related to age related hormonal changes. Our data suggest that female genital color variability is linked with age, while facial coloration is not; these results seem to suggest previous research indicating that facial and

genital color may have different signal content (Gerald et al. 2003).

Older females tend to have very defined genital color, less variable than that of younger females; this may suggest that physiological mechanisms associated with senescence contribute to color production. Intra-individual variations in color may be an indication of hormonal fluctuations that may be age-related in females; perhaps the effects of estrogen on sexual skin coloration change with age.

Our study demonstrates that female coloration may play a communicative role in rhesus monkeys. We suggest that female sexual skin coloration may be a signal that communicates past and/or present female condition, meaning that components of sexual skin color of female rhesus may be particularly important for reproductive communication. The patterns that we observed may be different among free-ranging populations (Setchell 2006b). Our study did not examine if males readily gain information from color and use it to discern between mates. At this stage, it is only possible to say that there is a connection between aspects of color and female traits that may allow males to discriminate between females.

Males most likely use a suite of characteristics about a female to determine her reproductive status, and to determine which females to focus their attentions on when several females are in estrus. It isn't clear if males are cognizant of differences in female traits such as age or dominance rank, or if males bias their reproductive efforts based on differences in female quality. Demonstrating a relationship between female coloration and female traits is an important first step in determining if female coloration plays a role in male mate choice in this species. Additional observations of male reproductive strategies and mate choice would give us a better understanding of which qualities (if any) males prefer in their mates. Understanding the physiological basis of coloration, as well as the life history correlates of coloration is fundamental to future exploration of the communicative role that coloration

may play in mate choice and the evolution and maintenance of trichromatic vision in catarrhine primates.

Acknowledgements. We extend our deepest thanks to Dr. M. Gerald, without whom this project would not have been possible. Thank you to Drs. M. McCrossin, B. Benefit, W. Trevathan, T. Wright, and R. Steiner at New Mexico State University (NMSU) for review of various parts of this project; to B. Cramer, M. Banegas, and A. Lujan for assistance with data collection in the field. Thank you to the entire Cayo Santiago staff for their daily dedication to the well being of all subjects and researchers, and to fellow Cayo Santiago researchers for their support and friendship; special thanks to J. Ayala and A. Accamando. Thanks to Trinity (36D) and Iris (I56), who kept us entertained and made everyday more enjoyable; and to Esther (82H) who vanished soon after the completion of this study.

Cayo Santiago is supported by Grant Number CM-5-P40RR003640-13 from the National Center for Research Resources (NCR), a component of the National Institutes of Health (NIH). The contents of this thesis are solely the responsibility of the author and do not necessarily represent the official views of NCR or NIH. Funding for this project was provided by the NMSU Sociology-Anthropology Graduate Student Organization, the NMSU College of Arts & Sciences, and the Associated Students of NMSU. This research was approved by the Institutional Animal Care and Use Committees (IACUC) of the University of Puerto Rico and NMSU.

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