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Females Pay Attention to Female Secondary Sexual Color: An Experimental Study in *Macaca mulatta*

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Researchers have long considered the color of female sexual skin to play a role in attracting or inciting competition among males, or both; however, females may also use color in intrasexual communication. To assess this possibility, we examined whether variation in same-sex sexual skin color is salient to female rhesus macaques (*Macaca mulatta*). We exposed adult females to computerized images of conspecific female faces and hindquarters manipulated for color (red vs. non-red), within the natural range of color variation. Females visually attended more to both reddened faces and hindquarters over the non-red counterparts. We conclude that female color might be biologically meaningful to other females.

KEY WORDS: *Macaca mulatta*; primate; secondary sexual color; sex skin.

INTRODUCTION

Secondary sexual coloration of the face and/or anogenital region occurs in many diverse species of primates (Dixson, 1998; Gerald, 2003).

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There has been considerable discussion regarding the function of secondary sexual coloration and swellings in female primates, and how color might enhance attractiveness to, or incite competition among males (Bielert *et al.*, 1989; Dixon, 1998; Domb and Pagel, 2001; Hrdy and Whitten, 1987; Nunn, 1999; Stallmann and Froehlich, 2000; Zinner *et al.*, 2004). Although evidence from avian species, e.g., pinyon jays (*Gymnorhinus cyanocephalus*; Johnson, 1988); Gulanan cock-of-the-rock birds (*Rupicola rupicola*; Trail, 1990) suggests that color is involved in female intrasexual competition there has been no report re whether female color is important in intrasexual interactions in primates.

Rhesus macaque (*Macaca mulatta*) males and females experience reddening of the face and hindquarters coinciding with times of heightened mating activity (Baulu, 1976). As a necessary step to address whether the colored areas play a role in intrasexual communication, we tested whether differences in female face and hindquarter colors are salient to female rhesus macaques. Experiments consisted of exposing adult females to color-manipulated digital images of other females. The method allowed us to isolate female attention to coloration, uncoupled from other potentially color-related cues, including behavior.

METHODS

Subjects

The subjects were 9 adult female rhesus macaques, singly housed at the Caribbean Primate Research Center, Sabana Seca Field Station (SSFS), Puerto Rico, age 3.75–14.25 yr (mean = 6.32, SE = 1.23). A separate research protocol unrelated to the present study required individuals to live in single housing, and at the end of which, all were to be placed in social housing. Subjects were naïve to experimental procedures involving pictorial stimuli. Testing took place at the SSFS between October and early November 2004, during the annual peak in mating activity. No female was pregnant, and we presumed they were cycling normally, but we did not know the stage of the menstrual cycle.

Stimuli

We used a digital video camera (Sony DCR-PC100E) to capture images of 24 individual female rhesus macaques at SSFS, unfamiliar to the experimental subjects. We took facial images while individuals exhibited neutral expressions, with mouths closed and faces and eyes pointed

regarding the function of secondary sexual coloration among males (Bielert *et al.*, 2001; Hrdy and Whitten, 1987; Nunn, 2001; Pinner *et al.*, 2004). Although evidence from *Gymnorhinus cyanocephalus* and *Rupicola rupicola* (Trail, 1967) suggests that color is important in intrasexual in-

teractions, males and females experience red coloration coinciding with times of heightened social activity. A necessary step to address whether the color is important in communication, we tested whether red and blue colors are salient to female rhesus macaques by exposing adult females to color-matched faces. The method allowed us to test color perception uncoupled from other potentially

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Rhesus macaques, singly housed at Sabana Seca Field Station (SSFS), were used (mean age = 6.32, SE = 1.23). A separate study required individuals to live in pairs. In this study, all were to be placed in social groups. All procedures involving pictorial stimuli were conducted between October and early November. All individuals were sexually active. No female was pregnant during the study, but we did not know

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(Sony DCR-PC100E) to capture images of rhesus macaques at SSFS, unfamiliar to the subjects. Images were taken while individuals exhibited social activity. Faces and eyes pointed

directly at the camera. As the images showed direct gaze, subjects may not have perceived them as neutral because prolonged eye contact is associated with aggressive intent (Hinde and Rowell, 1962). However, macaques also use different facial attributes to interpret intent, e.g., mouth configuration and brow position (Perrett and Mistlin, 1990). Eye contact also occurs in other communicative contexts, e.g., appeasement gestures (van Hooff, 1967). Controlling for eye gaze direction was essential because it can influence looking behavior (Sato and Nakamura 2001). We took hindquarter images directly from behind while the individuals stood with tails erect, exposing the entire anogenital and surrounding regions of sexual skin. We frame grabbed images from digital video and downloaded them onto a computer (Sony Vaio V505 series) as 640 × 480 pixel images in jpeg format. We calibrated all images in Adobe Photoshop Elements 2.0 via RGB (Gerald *et al.*, 2001).

To manipulate coloration, we adapted computer graphics techniques used to alter human facial color (Rowland and Perrett, 1995). Waite *et al.* (2003, 2006) used the techniques successfully in 2 previous studies examining conspecific response to altered secondary sexual coloration among rhesus macaques. We constructed 2 composite faces—red and non-red—via computerized amalgamations of 8 of the reddest and 8 of the least red images. We used multiple images to control for individual differences in coloration and differences in ambient lighting. To make composites, we calculated the mean RGB color values at each pixel for the color sample and converted the measures into hue and saturation values. We then applied hue and saturation values and combined them with the individual brightness component of each pixel of 8 individual female stimulus faces, from the 8 individuals of intermediate color range, not used in the composites, producing a red and a non-red version of each face. We followed the same procedure to transform hindquarter coloration. All color manipulations were within the natural range of variation, but as the techniques combine the applied hue and saturation with the existing values, there was a small degree of variation between stimuli of the same color category. We standardized backgrounds across images by cropping and placing faces and hindquarters against the same color-calibrated background image taken on Cayo Santiago. We thus created a natural contrast to the stimuli, as is recommended when using artificial visual stimuli to investigate the significance of color in animal communication (Fleishman and Endler, 2000).

Procedure and Equipment

Caretakers moved females to the testing area adjacent to their living quarters. We habituated individuals to the testing area for 1–3 h before

