

Evidence from rhesus macaques suggests that male coloration plays a role in female primate mate choice

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Male animals of many species use conspicuous coloration to attract mates. Among mammals, primates possess the most brilliant secondary sexual coloration. However, whether colour plays a part in primate female mate choice remains unknown. Adult male rhesus macaques undergo a hormonally regulated increased reddening of facial and anogenital skin during their mating season. We experimentally investigated whether red male facial coloration is preferred by simultaneously presenting female rhesus macaques ($n = 6$) with computer-manipulated pale and red versions of 24 different male faces. The duration and direction of gaze were measured to discern visual preferences. Females exhibited preferences for the red versions of male faces. It is proposed that male coloration might provide a cue to male quality.

Keywords: secondary sexual coloration; mate choice; primates; *Macaca mulatta*

1. INTRODUCTION

Brilliant displays of secondary sexual coloration occur throughout the animal kingdom, although among mammals these displays are limited to the primates, who are unique among placental mammals in possessing trichromatic colour vision (Jacobs 1993). The functions of primate secondary sexual coloration, however, are largely unknown. Adult males of many Old World monkey species have particularly vivid displays, usually involving the skin of the face and anogenital regions referred to as 'sexual skins' (Dixson 1998). Various authors have proposed that these displays function in male–male competition and dominance ranking (e.g. Vandenberg 1965; Henzi 1985; Gerald 2001). Associations of status and intensity of coloration have been reported in at least three primate species (vervet monkeys, *Cercopithecus aethiops* (Gartlan & Brain 1968); gelada baboons, *Theropithecus gelada*

(Dunbar 1984); and mandrills, *Mandrillus sphinx* (Setchell & Dixson 2001)), although experimental evidence supporting this link has only recently been demonstrated (vervets, *C. a. sabaeus* (Gerald 2001)). Another function might involve female mate choice, as studies with insects, fishes, reptiles and birds have reported males using conspicuous coloration to attract mates (see Andersson (1994) for a review). However, whether colour plays a role in female mate choice in non-human primates remains unreported.

Rhesus macaques (*Macaca mulatta*) possess conspicuous secondary sexual coloration, with adults of both sexes undergoing an increased reddening of facial and anogenital skin (including the areas surrounding the scrotum, perineum, circumanal region, and paracallosal fields in males) during the mating season (Baulu 1976). Changes in coloration result from an increase in epidermal blood flow (Rhodes *et al.* 1997). Among males, testosterone levels induce reddening indirectly via aromatization to oestrogen and the degree of coloration is highly variable among individuals (Rhodes *et al.* 1997). In many male vertebrates, testosterone is linked to lowered immunocompetence, and a male's ability to display costly testosterone-dependent traits might act as an 'honest' indicator of health and genetic quality (Folstad & Karter 1992). Female preferences for highly developed testosterone-dependent traits have been reported among a variety of species (red junglefowl, *Gallus gallus* (Zuk *et al.* 1990); Gambel's quail, *Callipepla gambelii* (Hagelin & Ligon 2001); and African lion, *Panthera leo* (West & Packer 2002)), consistent with the indicator-mechanism hypothesis. Therefore, it is possible that hormonally regulated colour changes could provide a cue to male rhesus quality and function in female mate choice as well.

It was the aim of this study to explore whether male coloration might mediate attractiveness to females among rhesus macaques. To evaluate this hypothesis, we experimentally assessed whether females exhibited visual preferences for red male facial coloration in a captive setting.

2. METHODS

(a) Study animals

Study animals were six adult female rhesus macaques assumed to be experiencing ovulatory cycles based on visual inspection. Animals were housed together in an all-female group at the Hillcrest Colony, University of Oxford.

(b) Stimuli

A digital video camera was used to capture images of adult males from the free-ranging population of rhesus macaques on Cayo Santiago, Puerto Rico. Images were taken across the year to obtain pictures of differences in coloration during and outside the mating season. Only full-face images with neutral expressions were used and backgrounds were standardized.

To manipulate coloration, two composite faces were constructed by blending (i.e. creating computerized amalgamations), each made of 15 images. The 'red' composite consisted of images taken during the mating season and the 'pale' composite of images taken outside the mating season. Multiple faces were used to form composites to control for individual differences in coloration and differences in ambient lighting. To construct composites, the mean RGB (red, green, blue) colour values at each pixel were calculated for the sample. The pixel RGB means of the two composites were then applied to 24 different male faces, producing a red and a pale version of each face (figure 1). See Rowland & Perrett (1995) for detailed methodology.

(c) Procedure and equipment

During testing, females individually entered a 45 cm × 61 cm × 56 cm testing chamber attached to their enclosure. The front of the chamber was constructed of Plexiglas, allowing a clear view of the stimuli. Views of the home cage and the experimenter were blocked.



Figure 1. Example of stimuli (same face colour-transformed to construct red and pale versions).

The timing and display of stimuli were controlled by computer and images appeared on two computer colour-calibrated monitors situated 20 cm apart, 50 cm from the testing chamber. Over each testing session, animals were each presented with 24 pairs of images. In each trial, red and pale versions of the same face (image size of 531×511 pixels) appeared in 24-bit colour simultaneously on the two monitors. Each pair of stimuli was displayed for 10 s, with an inter-trial duration of 2 s. The order of stimuli was randomized between subjects and left–right presentation of red and pale stimuli was counterbalanced within subjects.

A digital video camera was placed between the monitors to record behaviour for later analysis. Study animals' gaze direction and duration were recorded, as well as any postural or facial expressions (i.e. hindquarter presentation, lipsmacking, grimaces, etc.). Order and left–right presentation of stimuli were unknown to the experimenter recording these data. Trials where external noise caused distraction, eye gaze was obscured, and where animals were orientated away from the monitors were excluded (mean of 17.50 trials included per animal, s.d. = 3.15).

For assessing intra-observer reliability of visual fixation time, sessions from two individuals were randomly selected and reanalysed. Original and reanalysed scores were compared in trial-by-trial correlations, yielding reliability coefficients of 0.94 and 0.87.

3. RESULTS

A two-tailed repeated measures *t*-test was performed comparing gaze duration for red (mean/trial = 2.41 s, s.d. = 0.43) and pale faces (mean/trial = 1.67 s, s.d. = 0.16). Overall, females spent significantly more time looking at the red faces than pale faces ($t_5 = 4.82$, $p = 0.005$). The viewing time of red faces was higher among five out of the six individuals, with the remaining animal having similar viewing times for both stimuli sets. Stimuli-directed behaviour consisted entirely of lipsmacking and hindquarter presentation. These were not analysed as occurrences were infrequent and highly variable among individuals.

4. DISCUSSION

Red sexual skins occur among a variety of male primates (e.g. mandrills, gelada baboons, and Japanese macaques, *M. fuscata*: see Gerald (2003) for a review). Darwin (1876) was the first to postulate that male primate coloration functioned in attracting females. The results from this study suggest that male coloration might indeed mediate male attractiveness in rhesus macaques, as females demonstrated clear visual preferences for red male faces over pale versions.

Male skin coloration could provide a reliable short-term cue to quality among rhesus macaques. In free-ranging animals, facial coloration is highly variable, ranging from surrounding only the outer canthal (eye) region to encompassing the entire face, and may be flecked to solid in appearance. Males can also vary in degree of coloration

from one year to the next (C. Waitt, personal observation). As skin colour is regulated by testosterone, which is reported to have immunosuppressive effects (Folstad & Karter 1992), only males in good condition may be able endure the costs of colourful displays. By preferentially mating with males possessing highly developed displays, females might gain indirect benefits by providing offspring with heritable resistance to pathogens (Folstad & Karter 1992), or direct benefits by reducing pathogen transmission to themselves from infected males (Loehle 1997). Females exhibit a high degree of choice when selecting mates, and do not appear to choose males based on dominance rank (Manson 1994a) or on established affiliative relationships (Manson 1994b). Our results may help to explain these findings, suggesting that females may instead use physical features as a basis of mate selection. Pathogen avoidance might be particularly relevant as rhesus macaques have a promiscuous mating system, and promiscuous species may incur greater rates of sexually transmitted disease (STD) infection (Nunn *et al.* 2000). Naturally occurring STDs are present in wild primate populations (e.g. simian immunodeficiency virus (Phillips-Conroy *et al.* 1994); and B virus (Orcutt *et al.* 1976)) and it is interesting to note that many of the species in which males possess red sex skins have promiscuous mating systems (Dixson 1998).

Alternatively, it could be suggested that females' visual preference for red faces does not reflect sexual interest, but rather is an artefact of the experimental procedure, tapping into preferences for unusual or novel stimuli. Although visual preference measures are widely used in both human infants and non-human primates, it is difficult unequivocally to establish their underlying significance. However, there is evidence that viewing time does relate to stimuli attractiveness and biological relevance, rather than simply to novelty. Human infants prefer gazing at faces rated as attractive over those rated as unattractive by adults (Langlois *et al.* 1987). Additionally, among adult humans, viewing duration and degree of sexual attraction do correlate when viewing images of the opposite sex (Quinsey *et al.* 1996). Various studies examining species discrimination among macaques report that individuals prefer viewing images of their own versus novel macaque species (e.g. Fujita 1987; Demaria & Thierry 1988). Such preferences have greater biological relevance, and are in line with mating preferences, as naturally occurring hybrids are rare among sympatric macaque species (Bernstein & Gordon 1980). Some study animals displayed limited sexual interest in the stimuli, indicated by occurrences of lipsmacking and hindquarter presentation. Although these behaviours can occur in other contexts, both function as sexual invitation (Dixson 1998) and, in the absence of submissive and fearful reactions, could be so interpreted.

Although this study is preliminary, it provides the first experimental evidence, to our knowledge, that male coloration may influence male attractiveness to females among non-human primates. Despite the technique's artificiality, it offers the benefits of allowing repeated presentation of identical stimuli to different individuals and manipulation of colour independently of other cues that might influence female preferences. Stimuli manipulations were based on actual colour changes that occurred in real animals,

providing greater ecological validity to the results. However, whether visual preferences are indicative of sexual preferences is open to debate, and the link between male coloration, health status and female mating preferences requires further study. Male coloration, none the less, would appear to provide a suitable dynamic mechanism for females to assess male condition in rhesus macaques.

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