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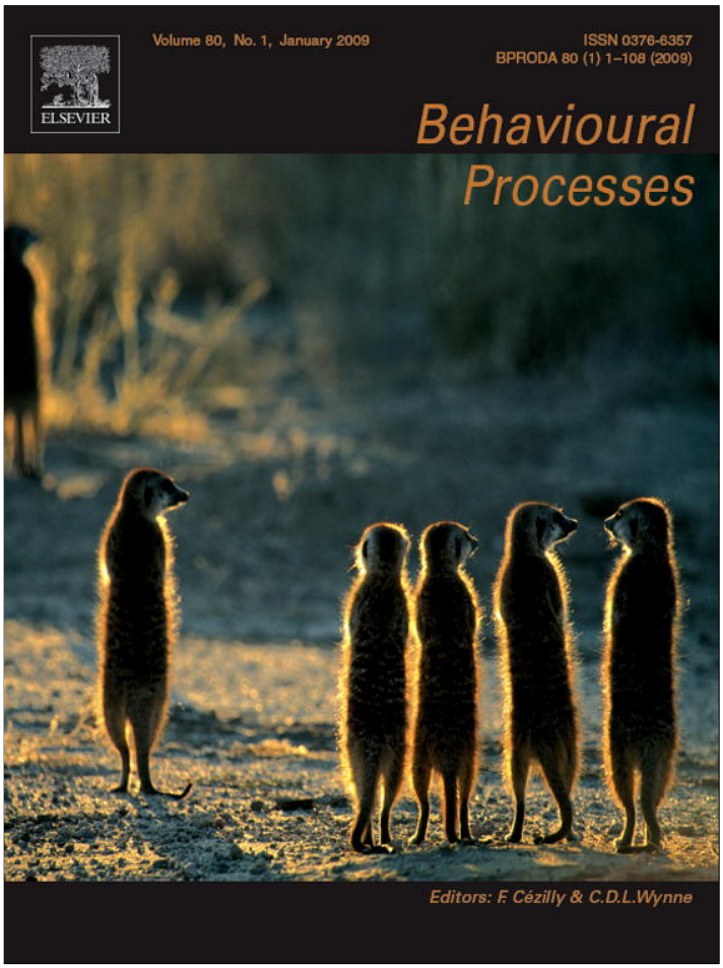

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Pregnancy coloration in macaques may act as a warning signal to reduce antagonism by conspecifics

Melissa S. Gerald[a,b,c,*], Corri Waitt[a,d], Anthony C. Little[e]

[a] Cayo Santiago, Caribbean Primate Research Center, PO Box 906, Punta Santiago, PR 00741, USA
[b] University of Puerto Rico, Department of Medicine, Medical Sciences Campus, San Juan, PR 00936-5067, USA
[c] Laboratory for Primate Morphology & Genetics, c/o Department of Anatomy & Neurobiology, University of Puerto Rico Medical School, PO Box 365067, San Juan, PR 00936-5067, USA
[d] Department of Zoology, University of Oxford, John Krebs Field Station, Wytham, Oxford, UK
[e] Department of Psychology, University of Stirling, Stirling FK9 4LA, UK

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ABSTRACT

Instances of bright, hormonally induced coloration among females during gestation have been reported in a few reptile and primate genera. Gravid coloration in lizards has been linked to female aggression but the influence of color changes associated with pregnancy has not yet been experimentally pursued for primates. As a first step to determine whether the crimson to magenta hues common to pregnancy coloration in rhesus macaques (*Macaca mulatta*) contains information, to which conspecifics of either sex attend, we evaluated whether male and female rhesus macaques discriminate between pregnant and non-pregnant female faces. To these ends, we presented 19 adult rhesus macaques with color-manipulated digital images of female faces where pregnancy coloration was present or absent, and measured visual attention and behavioral reactions. Males were significantly more attentive to female faces with pregnancy coloration over those without pregnancy coloration. Both sexes engaged in higher levels of appeasement behavior toward stimulus with pregnancy coloration, and males showing signs of anxiety did so exclusively when exposed to faces with pregnancy coloration. Our results suggest that pregnancy coloration might be an attention grabbing stimulus to males and a warning stimulus to both male and female rhesus macaques. The findings provide a comparative perspective on the use of color in intra-specific communication, and suggest similarity in female similarity in signalling properties in distantly related taxa.

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Research into the evolution and signalling functions of secondary sexual coloration has traditionally focused largely on males. More recent studies, however, have reported the diversity of ways in which female displays of conspicuous coloration are involved in intra-specific communication. For example, female secondary sexual coloration might be related to competition over resources (e.g. pinyon jays, *Gymnorhinus cyanocephalus*: Johnson, 1988; Eclectus parrots, *Eclectus roratus*: Heinsohn et al., 2005); or to mate attraction (e.g. two-spotted gobies, *Gobiusculus flavescens*: Amundsen and Forsgren, 2001; blue-footed booby, *Sula nebouxii*: Torres and Velando, 2005). Amongst a few genera, including some species of lizards and primates, females display bright coloration during gestation, distinct from that which is displayed during the peri-ovulatory period (Cooper and Greenberg, 1992; Hager, 2001; Gerald, 2003).

Divergent results stemming from studies of gravid coloration in lizards suggest that gravid coloration can convey different messages to conspecifics. Two main hypotheses available to account for the function of gravid coloration in lizards are the "aggressive avoidance" and "courtship rejection" hypotheses (Cooper, 1984; Cooper and Greenberg, 1992). Assuming that gravid females are aggressive, the aggressive avoidance hypothesis proposes that gravid coloration in female lizards somehow prevents or reduces the likelihood that males will return aggression toward them. Alternatively, the courtship rejection hypothesis advances that gravid coloration reliably signals that a female will reject courtship attempts by males, thereby reducing the probability that females (or males attending to the signal) will be vulnerable to the risk of predation during fruitless courtship attempts (Cooper and Crews, 1987; Cooper and Greenberg, 1992; Watkins, 1997).

While observational and experimental studies have investigated gravid coloration in lizards, little is known about pregnancy coloration in primates. Certainly there is a large difference

* Corresponding author at: Laboratory for Primate Morphology & Genetics, c/o Department of Anatomy & Neurobiology, University of Puerto Rico Medical School, PO Box 365067, San Juan, PR 00936-5067, USA. Tel.: +1 787 753 8656; fax: +1 787 753 8656.
E-mail address: melissa.gerald@gmail.com (M.S. Gerald).

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between lizards and primates. Nevertheless, previous research in lizards provides a useful framework to speculate about the function across divergent species. In primate species where females exhibit red coloration in the hormonally sensitive areas of the face and anogenital regions, reddening may be brighter or deeper during pregnancy than during ovulatory cycling (e.g. gray-cheeked magabey, *Lophocebus albigena*: Rowell and Chalmers, 1970; gelada baboon, *Theropithecus gelada*: Dunbar, 1977; guinea baboons, *Papio papio*: Gauthier, 1999; savannah baboons, *Papio cynocephalus*: Altmann, 1973). Despite this documentation for pregnancy coloration, no experimental studies to date have examined the potential communicative function of primate pregnancy coloration.

In the present study, we attempt to assess whether male and female rhesus macaques (*Macaca mulatta*) modulate their attention and behavioral responses toward digitised images of females exhibiting pregnancy versus non-pregnancy coloration. Rhesus macaques are seasonal breeders, restricting mating activity to approximately 6 months of the year on Cayo Santiago (e.g. Rawlins and Kessler, 1985). Female rhesus macaques experience reddening of the sexual skin during the mating season. During the last trimester of their 5 1/2 month gestation, up until the timing of parturition, coloration distinct from that expressed during the mating season appears. Facial coloration takes on crimson to magenta hues covering the ocular and nasal regions, giving a mask-like appearance across the face (Rowell, 1972). We proposed that the finding that males or females discriminated between images of pregnant and non-pregnant females would suggest that pregnancy coloration is functional to rhesus macaques. While our experimental paradigm could not directly permit us to evaluate whether either hypotheses for gravid coloration applied to primates, we predicted that animals would perceive pregnancy coloration stimuli as threatening, as both hypotheses in lizards predict female aggression toward conspecifics. However, we propose that if effects are seen equally in both sexes, then the aggression avoidance hypothesis would possibly be most plausible. For the present study, we consider the courtship rejection hypothesis in a broad sense in that this hypothesis suggests the signal serves only as a warning to males and moderates male behavior rather than serving as a general signal to all conspecifics. As such, if effects are limited to male observers then the courtship rejection hypothesis would be more plausible.

1. Materials and methods

For our experimental design, we used digitised images of rhesus macaques. Two-dimensional media are used widely in ethological research and offer certain benefits over utilising real animals as stimuli. These benefits include the ability: (1) to present identical stimuli repeatedly to a number of individuals and (2) to control, to a high degree, stimulus presentation, and (3) to manipulate physically target stimuli independently of other traits (e.g. olfactory or auditory cues, or coercive or dominance cues: reviewed in D'Eath, 1998). Findings show that two-dimensional images provoke meaningful autonomic, neurophysiological, and appropriate behavioral responses in non-human primates (reviewed in Anderson, 1998; Pascalis et al., 2001; Vick, 2001).

1.1. Subjects

Study animals were nine adult female (age range = 4.25–17.7 years, mean = 10.00 years, S.D. = 4.57) and 10 adult male (age range = 4.25–23.83 years, mean = 13.33, S.D. = 5.97) rhesus macaques. All subjects were housed in single cages at the Caribbean Primate Research Center, Sabana Seca Field Station (SSFS). Single housing was temporarily required for animals according to an unrelated separate research protocol, after which the animals were to be placed in group housing. Although free-ranging rhesus experience distinct birth seasons, animals at SSFS give birth all year round, though experiencing birth peaks. Testing took place between the months of March and August 2006, which overlapped with the timing of these peak births.

1.2. Stimuli

A digital video camera (Sony DCR-PC100E) was used to capture images of adult female rhesus macaques who were from SSFS, but unfamiliar to subjects, and who were either pregnant and exhibited pregnancy facial coloration or who were not pregnant and lacked red facial coloration (i.e., non-cycling, non-pregnant females). Facial images were taken of animals with mouths closed and faces and eyes pointed directly at the camera. Images were 'frame grabbed' from digital video footage and were then colour calibrated in Adobe Photoshop Elements 2.0 using the RGB techniques established by Gerald et al. (2001). Multiple images of different individuals were used to form composites to control for inter-individual color differences.

To manipulate coloration, we adapted Rowland and Perrett's (1995) computer graphics techniques that are used to alter human facial coloration. Five previous studies have successfully employed these techniques in examining conspecific response to altered primate coloration (Waitt et al., 2003, 2006, 2007; Gerald et al., 2006, 2007). Two composite faces, one exhibiting pregnancy and the other lacking pregnancy coloration, were created by generating computerised blends of images of five pregnant females in the latter stages of gestation (taken between 44 and 2 days prior to parturition, mean = 21.20 days, S.D. = 19.21 days, according to retrospective data from colony records) and five non-pregnant females.

To construct composites, the mean RGB color values for each pixel in the image were calculated for the sample and then transformed into hue and saturation values. Hue and saturation values were then applied and combined with the individual brightness component of each pixel of 12 female stimulus faces (consisting of different females than those included in the composites), producing a pregnancy and a non-pregnancy colored version of each stimulus face (for details see Rowland and Perrett, 1995). We attempted to create a natural contrast to the stimuli as Fleishman and Endler (2000) have suggested when investigating color in animal communication. Each image was standardised by cropping and pasting faces against the same color calibrated naturalistic background, which consisted of natural vegetation from the island of Cayo Santiago, which is home to a population of free-ranging rhesus macaques.

1.3. Stimuli and procedure

During the experiment, each individual was presented with a total of 12 images of different female faces, with six of these facial images exhibiting pregnancy coloration and six images without it. Animals were tested within their home cages, where they had ad libitum access to food and water. Timing and display of stimuli were controlled by computer, and images appeared on a 15-in. LCD color monitor, situated 60 cm from the testing cage. A Spyder™ colorimeter and OptiCAL software (Pantone ColorVision) were utilised to color calibrate the monitor. Views of the experimenter were blocked. Behavior was monitored remotely and recorded for later analysis via a digital camera, placed in a central location directly above the monitor.

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A trial began when the subject's eyes were oriented toward the monitor. During a trial, a single approximately life-sized image appeared in 24-bit color for 5 s. The number of trials was kept to a minimum as repeated exposure to pictorial images can lead to inattention (e.g. Nahm et al., 1997), which can decrease the magnitude of behavioral responses. Order of stimuli was randomised, and presentation of pregnant or non-pregnant stimuli was counterbalanced in that animals viewed only a pregnant or non-pregnant version of each face (i.e., a version of a face lacking pregnancy coloration would be seen with pregnancy coloration by the following subject). Order of stimuli was unknown to the experimenter recording these data. Trials were excluded if eye gaze was obscured (i.e., animals were orientated with their backs to the monitors or had their eyes closed for the entire trial). Subjects were tested only once and testing sessions lasted between 2 min 12 s and 10 min 59 s (mean = 4 min 59 s, S.E. = 39 s). Variation in testing time resulted from individual differences in the time it took for animals to return their attention to the computer screen. All individuals attended to a minimum of 10 trials and the mean number of trials included per animal was 11.47 (S.E. = .14).

1.4. Behavioral observations

The Observer software (Noldus, Version 3.0) programme was configured to permit the recording of the study animals' visual gaze duration and behavioral reactions to stimuli during frame-by-frame analyses, on a continuous basis. In terms of behavioral reactions, we anticipated that animals would react toward stimuli with pregnancy coloration, in ways which indicated that they perceived this coloration as threatening. As such we recorded and measured the duration of behavioral 'states' (Altmann, 1974), including (1) eye gaze, which is interpreted to be a measure of the extent to which an individual perceives a threat from a stimulus (Humphrey and Keeble, 1974; Nahm et al., 1997; Sato and Nakamura, 2001); (2) lipsmacking, which is used in varying contexts, including aggression avoidance and appeasement (van Hooff, 1967), in male courtship displays (Partan, 2002); and (3) self-directed behavior (scratching, self-grooming), an indicator of anxiety in primates (e.g. Maestripieri, 2005; Maestripieri et al., 1992). We recorded and measured the frequency of instantaneous, or so-called 'event' behaviors (Altmann, 1974) including retreats and approaches toward the monitor.

To assess intra-observer reliability, an entire testing session from two subjects was randomly selected, and re-analysed. Scores for gaze duration were compared in trial-by-trial correlations, yielding reliability coefficients of 0.947 and 0.959, respectively (Martin and Bateson, 1993).

1.5. Analysis

Mean gaze durations for faces with and without pregnancy coloration, total number of instances for event behaviors and total duration for state behaviors were compared. Statistical analyses of gaze duration and behavioral measures in relation to color were evaluated via repeated measures analysis of variance (ANOVA). Stimulus type (pregnancy versus non-pregnancy coloration) served as a within-subjects factor while sex served as the between-subjects factors. We used two-tailed tests to test main effects of sex as we made no specific predictions regarding sex specific effects. However, as we predicted that animals would show avoidance and appeasement behaviors toward pregnant faces, we used one-tailed tests to evaluate this possibility. All statistical analyses were conducted with SPSS 12.0.

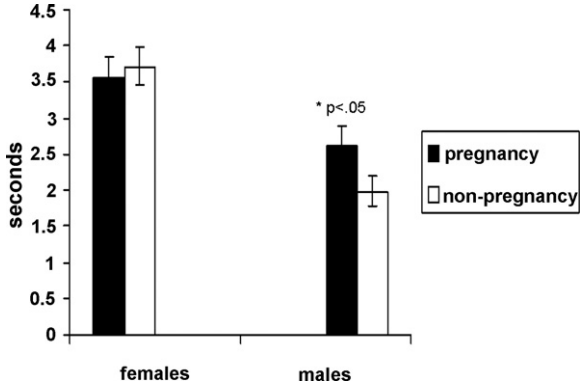

Fig. 1. Means and S.E. for gaze duration per trial for female and male subjects in response to female faces with pregnancy vs. non-pregnancy coloration.

2. Results

There was no significant main effect of coloration on gaze duration (one-tailed: $F_{1,17} = 1.976$, $P = 0.089$); however, there was a statistically significant interaction between coloration and subject sex on gaze duration (two-tailed: $F_{1,17} = 4.771$, $P = 0.043$). Means and standard errors are given in Fig. 1. Post hoc two-tailed paired t-tests (Bonferroni adjusted probability of 0.05/2 = 0.025) revealed that males gazed significantly longer at female faces displaying pregnancy coloration versus at those without ($t_9 = -2.767$, $P = 0.022$), but female gaze duration did not differ significantly between these stimuli ($t_8 = 0.506$, $P = 0.627$).

Both males and females showed behavioral reactions to stimuli, but not all animals did. Although these results cannot provide conclusive evidence, given the reduced sample size representative of the animals who did show behavioral responses, we consider how responsive animals behaved and to what stimuli.

For those animals who displayed behavioral reactions, 15 of the 19 study animals (9/10 males, 6/9 females) engaged in lipsmacking behavior. For these individuals, there was a significant main effect of color, with animals displaying significantly higher levels of lipsmacking to stimuli showing pregnancy coloration (one-tailed: $F_{1,13} = 5.421$, $P = 0.018$; Fig. 2). Eight males and three females retreated from stimuli, with both sexes retreating more from female faces displaying pregnancy versus non-pregnancy color, although this result was not statistically significant (one-tailed: $F_{1,9} = 2.708$, $P = 0.064$). Similarly, six males and three females approached non-pregnant stimuli more frequently, but differences in approach rates were not statistically different (one-tailed: $F_{1,7} = 3.316$, $P = 0.055$). No females engaged in self-directed behavior, whereas half of the

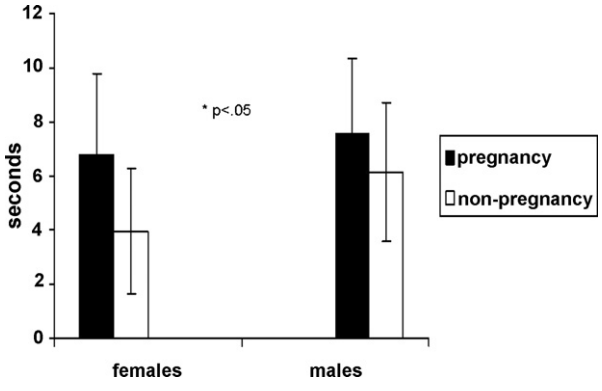

Fig. 2. Means and S.E. for total lipsmacking duration per trial for female and male subjects in response to female faces with pregnancy vs. non-pregnancy coloration.

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males did; with self-directed behavior occurring exclusively when the five males were exposed to faces with pregnancy coloration (one-tailed: $t_4 = -2.947$, $P = 0.021$).

3. Discussion

The present study sought to examine the influence of pregnancy coloration in the faces of rhesus macaques by comparing visual attention and behavioral reactions of males and females to color-manipulated digital images of females with and without pregnancy coloration. While our experiments are artificial, bearing little resemblance to the social life which exists for rhesus macaques, the behavioral responses of males and females in our experiments can offer clues into what pregnancy coloration might convey to conspecifics. Our results therefore allow us to evaluate, provisionally, previous explanations of the signaling value of pregnancy coloration, contrasting the aggressive avoidance versus courtship rejection hypothesis.

In terms of gaze duration, only males paid significantly more attention to females with pregnancy coloration versus females without it. Given that macaques are reported to selectively attend to threatening stimuli (Humphrey and Keeble, 1974; Nahm et al., 1997; Sato and Nakamura, 2001), our findings suggest that males may perceive female pregnancy coloration as threatening. Rates of lipsmacking were higher when both males and females viewed pregnant stimuli, suggesting that lipsmacking reflected appeasement, over behavior related to courtship. Additionally, males engaged in greater levels of self-directed behavior when presented with female stimuli displaying pregnancy coloration. Behavioral data lend further support for the idea that pregnancy coloration is a warning stimulus to both male and female rhesus macaques.

The stronger reactions of males to stimuli may suggest that males are the targets of these signals or that they suffer increased aggression from pregnant females. Alternatively, this may be a side-effect of the testing paradigm since male rhesus macaques display higher levels of stress-related behavior when shown pictures of unfamiliar cycling females than do females (Waitt and Gerald, unpublished data). We note that, given that males did not discriminate between images of cycling females with reddened faces of cycling females relative to pale controls in previous experiments (Waitt, 2005; Waitt et al., 2006), this suggests that pregnant facial coloration is particularly salient to males. Furthermore, this suggests that the signal content of pregnancy coloration differs from that of the red coloration common to cycling females.

Returning to the dominant hypotheses for gravid coloration in lizards, we speculate about the various functions of pregnancy coloration, while we acknowledge that results from our study do not permit us to draw firm conclusions. Producing pregnancy colors late in pregnancy, when females are at an energetic low, might confer extra protection against attack from conspecifics. Pregnant females can benefit from the display as it could reduce the number of antagonistic encounters they enter, if other macaques avoid them more, as suggested by our results. Both males and females could benefit from receiving such a signal, to avoid incurring potential costs associated with female aggression, which may be more likely during pregnancy.

Alternatively, females may display conspicuous pregnancy coloration to convey reliably that females will aggressively reject copulation attempts by males (reviewed in Cooper and Greenberg, 1992). Signalling females then benefit by avoiding unnecessary costs of predation related to male sexual advances. Males benefit in similar ways, and also benefit by avoiding the incurrence of energetic costs associated with wasted mating efforts. While rhesus macaque females engage in post-conception sex during the first half of pregnancy (e.g. Conaway and Koford, 1964; Kauffman, 1965), sexual activity ceases in the second half of pregnancy, when pregnancy coloration appears (Bielert et al., 1976). It is not clear whether mating cessation results from females aggressively rebuffing copulation attempts or whether male sexual interest has decreased. All the same, these observations are consistent with the hypothesis that females could use pregnancy coloration to prevent courtship attempts, or negative consequences associated with male behavior, as we so broadly proposed. However, the demonstration of effects in both males and females favours the aggression avoidance hypothesis.

The finding that primates appear to converge with lizards with respect to attending to pregnancy coloration provides an important contribution toward understanding female secondary sexual coloration from a comparative perspective. For future investigations, it might be useful to conduct long-term studies to check if indeed females increase their aggression rates when pregnant. Furthermore, longitudinal studies which track changes in female coloration across their reproductive cycle may also shed additional light on the specific role of primate pregnancy coloration, and why females in some species might delay exhibiting pregnancy coloration until late in gestation. More studies are also needed to determine how our findings may generalise across the Primate order to improve our understanding of secondary sexual coloration.

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