



Does pregnancy coloration reduce female conspecific aggression in the presence of maternal kin?



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Colour signals arise in a variety of sexual contexts, including advertising reproductive status. Despite potentially attracting negative attention from unrelated competitors, bright pregnancy coloration may communicate gestation to kin and potential fathers, thereby garnering aid during agonistic encounters and reducing the overall amount of aggression received by pregnant females. To establish whether this 'pregnancy sign' influences rates of aggression in the presence versus absence of maternal kin, we conducted behavioural observations of wild olive baboons, *Papio anubis*, in Gombe National Park, Tanzania, in groups composed of maternal kin and nonkin, and of captive baboons at the Southwest National Primate Research Center (SNPRC, San Antonio, TX, U.S.A.), in group enclosures that were unlikely to include close kin. At SNPRC, we also experimentally obscured the coloration of the pregnancy sign, and we performed playback experiments to measure male responses to the distress calls of pregnant females. Free-ranging female baboons experienced significantly less aggression from nonkin females after the onset of the pregnancy sign compared to the pre-pregnancy sign. In contrast, captive pregnant females whose pregnancy coloration was obscured with paint experienced significantly lower aggression rates from female conspecifics compared to pre-painting. Male aggression towards females did not differ in the presence versus absence of the pregnancy sign in either the wild or the captive population, although captive fathers paid significantly more attention to distress calls of pregnant cage-mates than they did to those of cycling cage-mates, suggesting a willingness to aid mothers that were carrying their unborn offspring.

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Conspicuous coloration serves as a reproductive signal in numerous species of fish (Andersson, 1994), birds (Baker & Parker, 1979), reptiles (Cooper & Greenberg, 1992) and mammals (Caro, 2005; Clutton-Brock & McAuliffe, 2009). Such visual signals can be easily localized, rapidly transmitted (Bradbury & Vehrencamp, 2011; Rosenthal & Ryan, 2000) and sensitive to underlying hormonal profiles (Bagnara & Hadley, 1973). In particular, some females use colour changes, such as bright plumage (Amundsen, 2000), skin colour (Dubuc et al., 2009; Weiss, 2006) or swellings (Higham, Heistermann, Ross, Semple, & MacLarnon, 2008), to signal sexual receptivity, and colour displays by both sexes are known to attract mates (Andersson, 1994). However, in only a few cases do females use colour to communicate other aspects of reproductive status, such as gestation (e.g. some nonhuman primates: Altmann, 1973; Dunbar, 1977; Gerald, Waite, & Little, 2009;

Loy, 1974; Rowell & Chalmers, 1970; Setchell, Wickings, & Knapp, 2006) or gravidity (e.g. some live-bearing fish: Deaton, 2008; Farr & Travis, 1986; lizards: Cooper & Greenberg 1992).

Investigations into gravid signals in lizards suggest that females may use colour to signal the likelihood of aggressively responding to a male's approach or courtship (Cooper & Greenberg, 1992; Watkins, 1997). Specifically, female lizards in the genus *Holbrookia* exhibit a bright 'nuptial coloration' only at the onset of the breeding season, but once they become gravid, this coloration darkens and deters males from attempting further copulations (Hager, 2001). Yet, few studies have examined the role of pregnancy coloration, often referred to as the 'pregnancy sign' (Altmann, 1973), found in many primates, including gelada baboons, *Theropithecus gelada* (Dunbar, 1977), yellow baboons, *Papio cynocephalus* (Altmann, 1973), rhesus macaques, *Macaca mulatta* (Gerald et al., 2009), patas monkeys, *Erythrocebus patas* (Loy, 1974), grey-cheeked mangabeys, *Cercocebus albigena* (Rowell & Chalmers, 1970), and mandrills, *Mandrillus sphinx* (Setchell et al., 2006). This bright red or magenta coloration typically manifests on exposed skin of the posterior in baboons and on the face in macaques, patas monkeys and mandrills. In rhesus macaques, the pregnancy sign may

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function as a 'warning' to conspecifics: [Gerald et al. \(2009\)](#) found that males showed more visual attention, and both males and females showed more appeasement behaviours, to photographs of pregnant females' faces than they did to faces of nonpregnant females, although the nature of this warning is poorly understood.

Advertising gestational status may confer considerable risks from competing females and, in species with pronounced sexual dimorphism in body size, from incoming males. Agonistic encounters can provoke acute stress, thereby causing decreased uterine blood flow and fetal hypoxemia in pregnant animals ([Morishima, Yeh, & James, 1979](#); [Shnider et al., 1979](#)) and even lead to miscarriage ([Clark, Banwatt, & Chaouat, 1993](#); [Field & Diego, 2008](#)). In social mammals, fetuses represent future competition for nonrelated group members and thus pregnant females may suffer from aggression by members of other matrilineal ([Silk, Samuels, & Rodman, 1981](#)). Similarly, males with a low probability of paternity may attack gestating females to induce miscarriage, thereby causing the females to resume cycling ([Agoramoorthy, Mohnot, Somer, & Srivastava, 1988](#); [Berger, 1983](#); [Mori & Dunbar, 1985](#); [Pereira, 1983](#); [Roberts, Lu, Bergman, & Beehner, 2012](#); [Storey & Snow, 1990](#); [van Schaik & Dunbar, 1990](#)). Given these potential costs, the persistence of the pregnancy sign implies some over-riding evolutionary benefit.

In female philopatric species, females persistently associate with close kin. Genetic relatives can benefit by enhancing each other's reproductive success ([Hamilton, 1964](#)), including interventions that prevent stress or injury during pregnancy. Likewise, some vertebrate fathers defend their juvenile offspring, both from predators ([Gross & Shine, 1981](#); [Gubernick & Klopfer, 1981](#); [Montgomerie & Weatherhead, 1988](#)) and aggressive conspecifics ([Buchan, Alberts, Silk, & Altmann, 2003](#); [Ferreira, Izar, & Lee, 2006](#); [Grinnell, Packer, & Pusey, 1995](#); [Itzkowitz & Nyby, 1982](#); [Palombit, 2000](#); [Watts, 1997](#)). Juveniles often remain in close proximity to their mothers, thus males that respond to maternal distress calls protect their own genetic interests ([Palombit, Seyfarth, & Cheney, 1997](#)). Fathers earn similar benefits from defending gestating females and are expected to intercede during conflicts with other group members ([Kleiman & Malcolm, 1981](#); [Palombit et al., 1997](#); [van Schaik & Kappeler, 1997](#)). Pregnancy coloration may be one mechanism by which females overtly advertise their reproductive status in order to garner such support from their mates as well as their maternal kin, thereby reducing the amount of aggression they receive during gestation.

Olive baboons are a highly gregarious primate species in which multiple females and males live in each group. Female baboons remain in their natal troop their entire lives ([Packer, 1979](#)) and exhibit a deep reddening of the paracallosal skin approximately 3 weeks after conception ([Altmann, 1973](#)). To test the 'aggression reduction' hypothesis, we collected observational data on wild baboons to establish whether pregnant females experience reduced aggression after the appearance of pregnancy coloration and whether they receive greater support from mating partners and close maternal kin. We then experimentally obscured the pregnancy sign of captive female baboons and compared rates of aggression towards these females pre- versus post-colour alteration. Finally, we conducted playback experiments to test whether fathers are more attentive to the screams of pregnant females than they are to the screams of cycling females.

METHODS

Observational Study

Study area and population

All behavioural observations on wild baboons were collected at Gombe National Park, Tanzania. Gombe is located on the eastern

shore of Lake Tanganyika and is characterized by steep valleys descending from a rift escarpment to the east ([van Lawick-Goodall, 1968](#)). Baboons at Gombe have been observed since 1967, with continuous demographic data dating from 1972. All study animals are individually recognized by natural markings. We collected data during two distinct time periods when the mean \pm SE group size was 22.0 ± 1.6 adults. Group composition ranged from 4 to 11 adult males (mean \pm SE = 6.9 ± 0.9) and 12 to 19 adult females (mean \pm SE = 15.1 ± 1.2).

Focal follows

Focal follows were conducted by two observers on separate occasions. First, focal follows were conducted by C.P. on 23 adult male baboons during May–November 1972 and June 1974–May 1975. Each focal follow lasted 2.5 h, and a mean \pm SE of 57.6 ± 6.5 h was collected for each male. These observations included detailed data on behaviour during all interactions between the focal male and every other troop member, including 14 pregnant females. The second set of focal follows was conducted by A.B. on six pregnant females during May–December 2012. Each follow lasted 1.5 h, and each female was followed a mean \pm SE of 18.5 ± 0.3 h during the first 7 weeks of her pregnancy. These follows included all interactions with conspecifics, including any aggressive encounters with males or females and any incidences of agonistic support, which was defined as any aggressive interaction involving the pregnant female in which a third party directed aggression towards the pregnant female's opponent.

Analysis of focal data

In the Gombe females, pregnancy coloration has a characteristic deep magenta hue that is distinct from the lighter pink of the sexual swelling and typically appears after the third week of pregnancy. Initial coloring was defined as any hint of red on the perineal skin after the onset of detumescence of the sexual swelling. Focal females at Gombe showed the first signs of pregnancy coloration a mean \pm SE of 21.7 ± 1.3 days ($N = 6$ females) days after initial detumescence. Based on this mean and the low variance in the appearance of pregnancy coloration, the first 3 weeks of gestation were considered the 'pre-pregnancy sign'. However, if any female began to exhibit pregnancy coloration prior to the end of this 3-week period, we excluded these data from the pre-pregnancy sign data analysis. Pregnancy coloration typically requires several days to become conspicuous, with overt coloration occurring on day 28.8 ± 1.0 post-detumescence for all focal females, by which time the pregnancy is no longer in question to an experienced observer. Thus, weeks 5–7 of gestation were defined as the 'pregnancy-sign' period. Although females maintain bright coloration until parturition, we chose to compare two time spans in the early stages of pregnancy to limit any potential effects of other physical changes through later stages of gestation. Focal females were followed an average \pm SE of 7.75 ± 0.25 h during the pre-pregnancy sign and 8.25 ± 0.34 h during post-appearance of the pregnancy sign.

Male–female interactions. For both male and female focal follows at Gombe, we tallied all incidences of male aggression (combining physical attacks with visual/vocal threats) towards pregnant females in their pre- and post-pregnancy sign periods. We also tallied female avoidance of males (defined as a female moving in the opposite direction of a male that approached to within 5 m), minutes spent grooming and being groomed, incidents of support and number of social interactions initiated by males and females, respectively. Because of the rarity of events, we calculated interaction rates for each male–female dyad during each reproductive phase by summing the total number of interactions of each type

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