

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 rection ([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

and dividing by the total observation time for focal individual. Each male–female dyad was then treated as an independent point and a linear mixed-effects model was performed, with pregnancy sign status, male rank, female rank, female age and observer (C.P. or A.B.) as fixed effects, and male and female identities as random effects. We compared the least squares means across pregnancy sign status for analysis of each behaviour and adjusted them for the other fixed effects.

Female–female interactions. Female focal follows were analysed for agonistic interactions between the focal pregnant female and other female group members, distinguishing kin from nonkin. Maternal kinship was well established in the long-term data set at Gombe and was restricted to mothers, maternal sisters and daughters, as studies suggest that the benefits of kin selection drop off significantly beyond immediate kin (Hamilton, 1964) and DNA profiles were not available to determine paternal kin in this population. Analyses were performed in the same way as for male–female interactions, and each female–female dyad was treated as an independent point. We analysed kin and nonkin dyads separately using linear mixed-effects models, with pregnancy sign status, focal female rank, age and the interaction of female rank*age as fixed effects, and the identities of pregnant and interacting females as random effects; we again compared least squares means across pregnancy sign status and adjusted them for the other fixed effects.

Male Playback Experiments

Study population

We conducted female distress call playback experiments on 17 captive adult male olive baboons, *Papio anubis*, and olive–yellow hybrid baboons, *P. anubis* × *P. cynocephalus*, at the Southwest National Primate Research Center (SNPRC) in San Antonio, Texas, U.S.A. Each male was housed in a breeding enclosure measuring approximately 9 × 9 m with 10–15 females. Groups consisted primarily of olive baboons, although a small number of olive–yellow, olive–hamadryas and yellow–hamadryas hybrids were also present. Only the focal female and group male could be reliably recognized during data collection. All baboons were weaned by ~10 months of age and reared in communal crèches by an unrelated male and female. Upon sexual maturity (typically ~4 years of age in this facility), females were introduced into breeding enclosures that were unlikely to include close kin (SNPRC, personal communication), but even if kin were present, kin recognition in baboons seems to depend heavily on socialization (Alberts, 1999); thus, females in enclosures were unlikely to know whether they were housed with close relatives. Female rank is largely determined by the length of group tenure in captive cercopithecines (Tung et al., 2012), but the dominance relationships were not known for the females in this study.

Playback methodology

We collected female screams opportunistically from individuals throughout the facility using a Marantz PMD620 hand-held digital recorder and a Sennheiser ME66 shotgun microphone with a K6 power module. The identity, cage number and reproductive status of each caller were recorded. Focal males were then exposed to six different call types over the subsequent 3 months: (1) screams from pregnant females in their home cage (probability of paternity = 100%); (2) screams from pregnant females in a neighbouring cage (males can interact with these females through the wire mesh but likelihood of paternity = 0); (3) screams from pregnant females from enclosures far from the focal male and with whom he had had no opportunity to interact; (4) screams from cycling females in their home cage; (5) screams from cycling

females in a neighbouring cage; (6) screams from 'distant' cycling females. Cycling females had sexual swellings both when their calls were recorded and when their calls were played to males, and pregnant females exhibited pregnancy coloration during both call collection and playback to control for any potential differences deriving from changes in reproductive status. Sixteen of the 17 males were exposed to at least one of each call type, with some males hearing multiple samples of one or more call types, for a total of 199 playbacks. However, males only heard each individual female on a single occasion. Mean ± SE scream length was 4.74 ± 0.063 s ($N = 57$) and calls were introduced in a random order. To avoid habituation, no male experienced more than one call in a 72 h period, and several 'dummy' playbacks were conducted on each male, where equipment was set up but no call was played.

During the playback procedure, we connected a MacBook Pro laptop to a Sony RDPX200iP speaker and placed the speaker 3–5 m away from the focal male. We then mounted a JVC Everio digital camcorder on a tripod and placed it behind the speaker to record the subjects' reactions to the playback vocalization. The equipment was set up 10 min before each playback to allow individuals to acclimate. After the waiting period, the experimenter started the camcorder to record at least 20 s of male behaviour prior to the playback, during which time the experimenter remained out of view. The call was played, and the video recorded at least an additional 20 s. Calls were only played if the calling female was neither near the target male nor in his line of sight, and if no female from the home or neighbouring cage had given a distress call for a minimum of 10 min.

The length of time each male spent gazing at the speaker pre-versus post-call was noted, as well as any behaviours directed towards the speaker, including approaches (defined as any movement towards the camera) and appeasement (such as tongue protrusion or grunting) or agonistic behaviours. Neither of the two student judges who scored these behaviours was involved in the playback procedures or knew the subjects' identities or call types in each test. Net gaze length post-call was calculated by subtracting the length of male gaze towards the camera in the 20 s before the playback from the length of gaze in the 20 s after the playback was begun. For playbacks with disagreement between scorers (13% of calls), a third individual viewed the video to adjudicate the judges' interpretations.

We performed a logistic regression to determine whether males were more likely to respond to calls from pregnant or cycling females from their home cage or from a neighbouring cage. For calls to which males reacted, we then used linear mixed-effects models to compare the net time that males spent gazing at the speaker after each call type. We compared the least squares means across call types for each analysis using a Tukey–Kramer adjustment for multiple comparisons. We compared responses to calls from unknown cycling and pregnant females separately to assess whether males could differentiate between the calls of pregnant and cycling females.

Colour Manipulation Experiments

Painting methodology

We conducted colour manipulation experiments on 18 parous pregnant female olive baboons at the SNPRC. Each female was at least in her second trimester of pregnancy and therefore had been exhibiting pregnancy coloration for a minimum of 5 weeks. Each resided in the cage with the father of her fetus, and each was randomly assigned a painting treatment, either grey/purple or clear paint. The grey/purple paint was mixed to visually match photographs of the rump skin colour of a flat, cycling female, with the same paint mixture used on each test subject so that each

experienced the same colour change, while the clear paint was used as a control. Test females ($N = 9$) were anaesthetized and the paracallosal and sexual skin of each individual cleaned. A thin coat of nontoxic grey/purple paint (Createx™ Airbrush Colors: opaque purple, red, black and white; Createx Colors, East Granby, CT, U.S.A.) was applied over the entire rump area to obscure all visible pregnancy coloration. After ~15 min, a coat of the nontoxic clear glossy paint (Createx™ Airbrush Colors, gloss top coat) was applied. Test females were then transferred to a recovery area prior to reintroduction to their group. An identical procedure was completed for control females, using the same clear glossy paint without the colour application. The paint typically persisted for only 4–5 days (maximum ~14 days), thereby eliminating the need to re-anaesthetize the animals for paint removal. Each cage only included one painted female at a time, with at least a 2-week gap between the final observation of the first female and the first observation of the second.

Behavioural observations

Prior to the painting treatment, each test subject was observed for a total of 10 h over the course of 3 days (3.3 h/day). All interactions between the focal female and male and female conspecifics were recorded, including all aggressive (including threat and attack, displacement and avoidance) and affiliative (mutual greetings and grooming) behaviours, as well as any incidents of third-party support during an agonistic encounter. Greetings were defined as situations where the focal female or a conspecific approached and touched or grunted at the other and in which neither individual showed subordinate behaviours (e.g. subordinate vocalization, fear grin or avoidance). After the initial observations, females were painted and returned to their home cage the same morning and allowed to reacclimate to their group until the following day. Over the next 3 days, females were observed for an additional 10 h at similar times of day as the pre-painting observations. The percentage of paint coverage was noted, as paint deteriorated at different rates for different females.

Analysis

We compared all incidents of aggression and support between pre-painting and post-painting treatments for grey-painted females using a two-tailed Wilcoxon signed-ranks test. We also compared the amount of aggression and support received by clear-painted females pre- versus post-painting to test for any effects of the painting treatment.

We also compared the number of approaches by and towards the focal female, total negative interactions (aggression, displacement and avoidance), total number of positive interactions (mutual greetings and grooming events) and minutes spent grooming and being groomed. We conducted separate analyses for interactions between pregnant females with the group male and with other females. Observations on females with paint coverage below 65% were not used, and pre-painting observations were reduced at random so that pre- versus post-painting comparisons included the same number of observation hours. This procedure was necessary for six of the nine females (one female was observed 6.66 h before and after painting, four females were observed for 3.33 h before and after painting, and we excluded the data from one female because the female's paint wore away to a level of 55% before the first post-painting observation period). Paint wear was fairly uniform, typically beginning in the urogenital region and around the edges of the rump; the primary aspect of the rump remained coloured the longest, giving an overall impression of colour coverage despite wear.

All analyses were carried out in R version 3.1.1. All reported P values are two-sided, with $P < 0.05$ considered statistically significant.

Ethical note

Capture of females for application of colour did not differ significantly from routine movement of individuals for daily cleaning and is a familiar process to all animals at SNPRC. All females recovered from the anaesthetic without event and did not suffer any injuries as a result of the experimental protocol.

RESULTS

Observational Study

Aggression towards pregnant focal female baboons by female maternal kin was rare at Gombe (7 distinct instances in 96 focal hours), and levels did not differ before and after the appearance of the pregnancy sign ($t_{22,12} = -0.69$, $P = 0.50$; note: all tests performed on data from the observational study are summarized in [Supplementary Table S1](#)). However, pregnant focal females received significantly less aggression from nonkin females when they exhibited the pregnancy sign than when they exhibited the pre-pregnancy sign ($t_{48,8} = -2.585$, $P = 0.013$; [Fig. 1](#)). Avoidance rates of nonkin female conspecifics by focal females did not differ significantly ($t_{46,03} = -1.276$, $P = 0.21$), nor did grooming rates received ($t_{21,84} = 0.397$, $P = 0.70$) or given by ($t_{24,28} = -0.747$, $P = 0.46$) focal females, pre- versus post-pregnancy sign. Interaction rates between the focal female and other nonkin female group members also remained unchanged ($t_{105,08} = -0.781$, $P = 0.44$), and there was no effect of rank or age in any of the analyses.

Male rates of aggression towards pregnant Gombe females did not change after the appearance of pregnancy sign ($t_{53,72} = -0.268$, $P = 0.79$; [Fig. 2](#)). However, pregnant females avoided males less after the pregnancy sign appeared ($t_{59,92} = -2.634$, $P = 0.011$) and interacted with them less ($t_{188,53} = -2.089$, $P = 0.038$; [Fig. 3](#)), primarily because males initiated fewer interactions with the females once they exhibited the pregnancy sign ($t_{199,87} = -1.979$, $P = 0.049$). Pregnant females initiated interactions with males at similar rates before and after the appearance of pregnancy sign ($t_{194,35} = -1.294$, $P = 0.20$). The proportion of interactions involving avoidance behaviour did not differ significantly with pregnancy sign ($t_{58,4} = -0.524$, $P = 0.60$), suggesting that the decreased avoidance behaviour after the appearance of the pregnancy sign was a by-product of decreasing rates of interaction. Similarly, the proportion of interactions involving threats or attacks did not differ

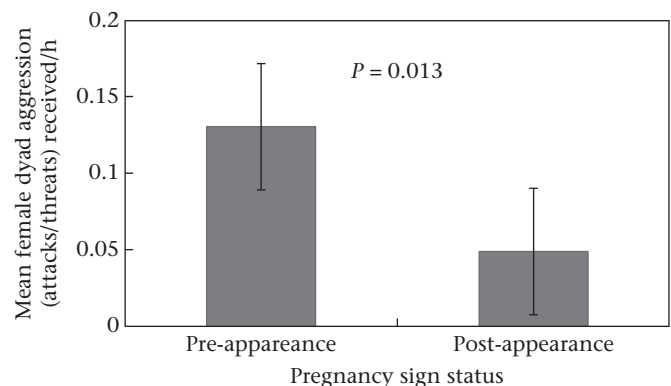


Figure 1. Least squares mean \pm SE rate of nonkin female aggression (attacks and threats/h) received by wild female baboons in the observational study before and after the appearance of the pregnancy sign, averaged across female–female dyads.

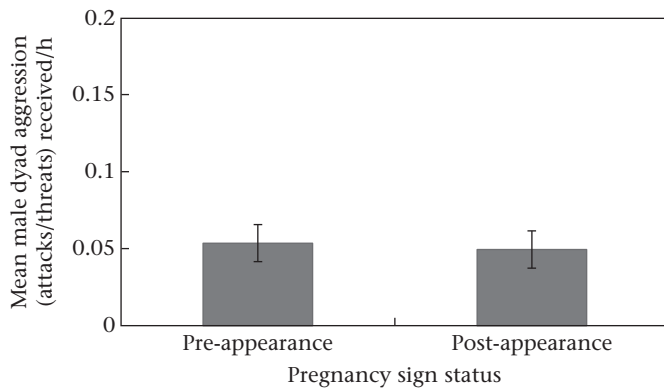


Figure 2. Least squares mean \pm SE rate of male aggression (attacks and threats/h) received by wild pregnant female baboons in the observational study before and after the appearance of the pregnancy sign, averaged across male–female dyads.

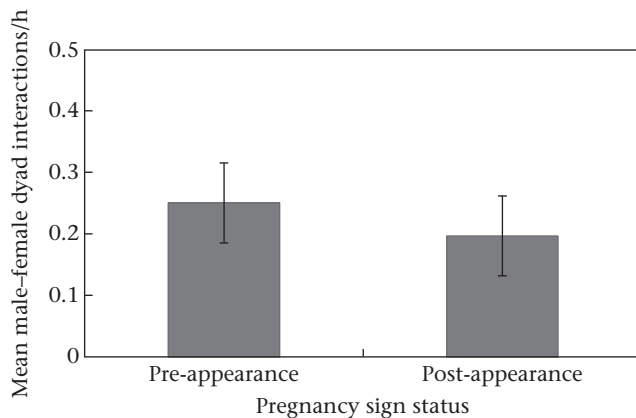


Figure 3. Least squares mean \pm SE rate of interactions/h between wild male baboons and pregnant females before and after the appearance of the female's pregnancy sign in the observational study, averaged across male–female dyads.

significantly with pregnancy status ($t_{55.65} = 0.078$, $P = 0.94$). Pregnant females groomed males and were groomed by males at similar rates regardless of pregnancy coloration (grooming of males: $t_{54.37} = 0.479$, $P = 0.63$; grooming of females: $t_{51.41} = -1.055$, $P = 0.30$). Neither male rank nor female rank affected the significance of these results.

Third-party support was rarely witnessed during focal follows, but of eight incidents, four occurred prior to the onset of pregnancy coloration, two occurred during the fourth week when the pregnancy sign was developing, and two occurred during the first 3 weeks after the appearance of the pregnancy sign. Seven cases involved matrilineal kin; in the eighth case, an adult male supported a female that exhibited the pregnancy sign.

Male Playback Experiments

Males at SNPRC gazed longer at the speaker in response to broadcasts of screams from known pregnant females than they did in response to screams from known cycling females ($t_{45.35} = -2.64$, $P = 0.011$; Fig. 4). In particular, males gazed at calls from pregnant females from their home cage longer than they did calls from cycling females either from their home cage ($t_{40.03} = -2.77$, $P = 0.040$) or from a neighbouring cage ($t_{42.71} = -2.86$, $P = 0.032$; Fig. 4). Males did not appear to differentiate between calls from their home cage and neighbouring cages ($t_{44.81} = 1.281$, $P = 0.21$; Fig. 4), nor between calls from pregnant females from their home

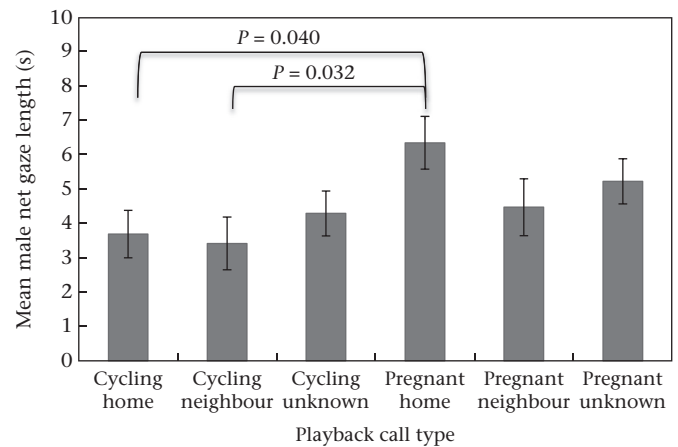


Figure 4. Mean \pm SE net gaze length of captive male baboons in response to broadcasts of distress calls from (1) cycling females from the home cage, (2) cycling females from a neighbouring cage, (3) cycling females from a distant cage that were unknown to the male, (4) pregnant females from the home cage, (5) pregnant females from a neighbouring cage and (6) pregnant females from a distant cage that were unknown to the male.

cage and from a neighbouring cage ($t_{40.25} = 1.77$, $P = 0.30$; Fig. 4). Males did not differentiate between the calls of unknown pregnant and cycling females ($t_{21.82} = -1.23$, $P = 0.23$), nor were they more likely to react to any one call type ($\chi^2_3 = 1.8$, $P = 0.61$). Note that males only approached the speaker five times in response to 154 call playbacks and they never directed threat gestures towards the speaker.

Colour Manipulation Experiment

Pregnant captive females received significantly less aggression from other females when the females' pregnancy sign was obscured with grey paint (Wilcoxon signed-ranks test: $W = 21$, $N = 8$, $P = 0.031$; Fig. 5). There was no significant change in the amount of aggression received by females in the clear-painted control group ($W = 18.5$, $N = 9$, $P = 0.49$; Fig. 5). Pregnant females received similar amounts of aggression from the group male before and after the pregnancy sign was painted with grey ($W = 0$, $N = 8$, $P = 1.00$) or clear ($W = 9$, $N = 9$, $P = 0.77$) paint (Fig. 6).

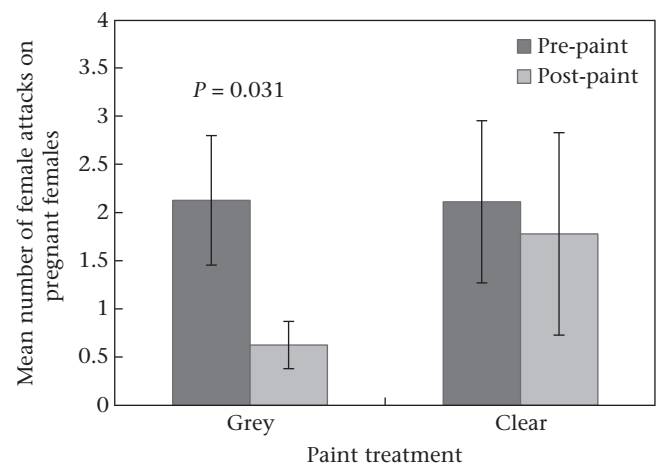


Figure 5. Mean \pm SE number of attacks by captive female baboons towards pregnant females before and after females' pregnancy signs were painted with grey ($N = 8$) or clear ($N = 9$) paint.

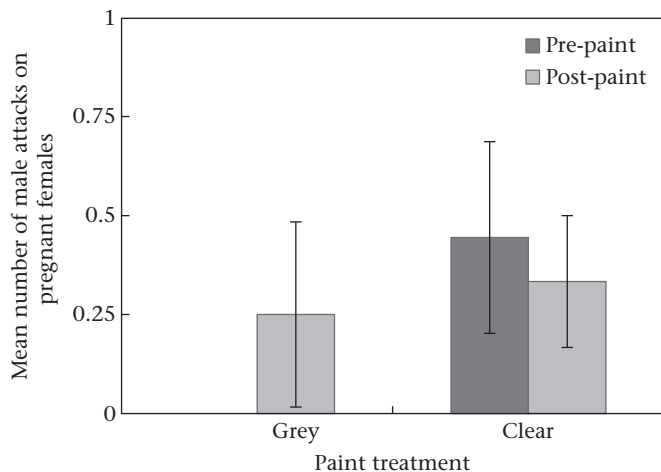


Figure 6. Mean \pm SE number of attacks by captive male baboons towards pregnant females before and after females' pregnancy signs were painted with grey ($N = 8$) or clear ($N = 9$) paint.

Males supported pregnant females in agonistic encounters with other females a total of six times, and each incident occurred while females had pregnancy coloration (five incidents prior to painting, one incident after being treated with clear paint). One pregnant female was supported twice by another female: once while exhibiting pregnancy coloration and once after the coloration had been obscured.

The total amount of time a pregnant female was groomed by other females did not differ pre- versus post-painting with grey ($W = 8$, $N = 8$, $P = 0.20$) or clear ($W = 12$, $N = 9$, $P = 0.24$) paint, nor did pregnant females in either paint treatment groom other females at different rates (grey: $W = 12.5$, $N = 8$, $P = 0.48$; clear: $W = 16.5$, $N = 9$, $P = 0.89$). Pregnant females were not approached by other females at different rates in either paint treatment (grey: $W = 6$, $N = 8$, $P = 0.79$; clear: $W = 23.5$, $N = 9$, $P = 0.95$), nor did they approach those females at different rates (grey: $W = 16.5$, $N = 8$, $P = 0.89$; clear: $W = 35$, $N = 9$, $P = 0.16$). Pregnant females also did not change their levels of aggression towards other females in grey ($W = 10$, $N = 8$, $P = 0.58$) or clear ($W = 25.5$, $N = 9$, $P = 0.06$) treatments. There was no significant difference in the rates of male interactions with pregnant females pre- versus post-painting, including approaches towards pregnant females (grey: $W = 11$, $N = 8$, $P = 0.36$; clear: $W = 31.5$, $N = 9$, $P = 0.31$), approaches by pregnant females (grey: $W = 27$, $N = 8$, $P = 0.23$; clear: $W = 34.5$, $N = 9$, $P = 0.17$), grooming of pregnant females (grey: $W = 0$, $N = 8$, $P = 1$; clear: $W = 3$, $N = 9$, $P = 0.35$), or grooming by pregnant females (grey: $W = 3$, $N = 8$, $P = 0.37$; clear: $W = 10$, $N = 9$, $P = 0.10$).

DISCUSSION

The pregnancy signal elicited female aggression in captivity, where individuals were completely surrounded by nonkin. However, pregnant females received less aggression from other females after the appearance of the pregnancy sign at Gombe, where families were available to support pregnant kin. These results are consistent with the hypothesis that the pregnancy sign not only reduces aggression, but that it elicits protective responses from family members, thereby inhibiting attacks from members of rival matriline. The bright coloration of the pregnancy signal may make a pregnant female easier to identify and locate, and may communicate a warning to nonkin that family members are willing to intercede on her behalf.

If the risk of intercession by family members reduces aggression directed at pregnant females, rates of agonistic support should have increased after the appearance of pregnancy coloration, but we only rarely observed third-party support. However, these intercessions may not be necessary if the signal successfully deters harassers through an elevated risk of retaliation. Thus, it is notable that females' pregnancy coloration increased the amount of aggression they received in captivity, and thus, in the absence of protective kin. Also, warning coloration across species deters interaction because it communicates a cost to receivers (Mappes, Marples, & Endler, 2005) through the use of colours that contrast well with the surrounding environment (Arenas, Troscianko, & Stevens, 2014).

The nature of captivity probably influenced the rate of aggression at SNPRC. In this setting, competitors are not only in constant proximity to their aggressors, but they have no means to escape repeated attacks. Thus, rates of aggression among captive baboons are probably higher than those in the wild. Our results suggest that pregnancy coloration makes captive individuals a target for unrelated females, and, as such, these females may be especially vulnerable to repeated attacks. However, these elevated rates of aggression in captivity do not fully explain the contrasting patterns between the captive and wild populations. Although females at Gombe may be able to avoid aggressors more easily, we should still expect to see increases in aggression with the appearance of pregnancy coloration, since rates of aggression towards pregnant females at SNPRC were higher prior to paint treatment than when pregnancy coloration was obscured. Yet, the opposite pattern emerged, suggesting the existence of an agonism-reduction mechanism in populations with intact kinship ties.

It is also possible that the Gombe females either changed their behaviour as their pregnancies progressed, or underwent physiological changes that were obvious to other female group members but not to human observers. Mammals experience behavioural and hormonal changes throughout pregnancy (Bazer & Spencer, 2011; Kinsley & Amory-Meyer, 2011; Marchant-Forde & Marchant-Forde, 2004) and conspecifics may be sensitive to these changes. As in the captive population, however, the number and nature of most interactions with other females did not alter pre- versus post-appearance of the pregnancy sign, suggesting that the changes in aggression probably stemmed from the pregnant female's change in reproductive status per se. However, it is uncertain whether the free-ranging females at Gombe were responding to the colour of the pregnancy signal, or some other cue, such as olfaction.

Males at Gombe initiated fewer interactions with pregnant females after the onset of the females' bright pregnancy coloration, perhaps because these females were now clearly unavailable as potential reproductive partners. These males, too, may have reacted to other cues besides the colour of the pregnancy sign, and further investigation is merited. Alternatively, aposematic coloration is a common deterrent across the animal kingdom (Ruxton, Sherratt, & Speed, 2004) and pregnant females may be using a similar tactic to warn males of the danger of a heightened familial response to male harassment (Gerald et al., 2009). Note that only recent immigrants in group-living mammals truly gain from harassing pregnant females to the point of miscarriage (Lukas & Huchard, 2014), and only 3 out of 20 pregnant Gombe females were exposed to such males during their first 7 weeks of pregnancy.

Males do, however, stand to benefit from protecting mothers that carry their unborn offspring. Although adult males only rarely supported pregnant females (one observation in the wild population versus six in captivity), all seven cases occurred when females exhibited pregnancy coloration (sign test: $P = 0.016$). In addition, captive males spent significantly longer gazing in the direction of distress calls from pregnant females than they did in response to

distress calls from cycling females. Curiously, these males paid similar attention to the distress calls of females carrying their offspring, of which they had high paternity certainty (being the only male in the group), and distress calls from neighbouring females, with which they could interact through a barrier but of whom their paternity certainty was quite low. Although selection is likely to favour males in polygamous species to correctly assess their probability of paternity (Neff, 2003; Westneat & Sherman, 1993), males may use a rule of thumb, assuming some probability of paternity if they were present at the time of conception. Male baboons have been shown to increase care towards offspring for whom they have high paternity estimates, based upon mating effort with the mother (Moscovice et al., 2010) and, although males with low estimates are unlikely to invest heavily, there may be selection on males to assume some probability of paternity based on residency patterns to avoid injuring or killing their own offspring. In many infanticidal rodent species, males limit infanticidal behaviour towards females with whom they have mated, regardless of actual paternity (Gubernick, Schneider, & Jeannotte, 1994; vom Saal & Howard, 1982). Thus, male baboons may show care towards any female that becomes pregnant during their residency. Also, in the captive setting, despite a chain-link barrier, males may have engaged in some limited mating contact with neighbouring females during their conceptive cycle, causing a modest possibility of paternity. Attention, though, is not direct support, and it is likely that paternity certainty plays a substantial role in male willingness to actively intercede on behalf of a pregnant female (M. Smith, 1977; Moscovice et al., 2010; Trivers, 1972). The lone example of male support in the wild baboons was by the top-ranking male in the group. Since rank is highly correlated with paternity in baboons (Bulger, 1993; Cowlshaw & Dunbar, 1991; but see also Alberts, Watts, & Altmann, 2003), this male was a likely the father. Further investigation will be necessary to elucidate the role of paternity certainty in these male–female interactions.

Although pregnancy status, and specifically pregnancy coloration, apparently alters the behaviour of both male and female group members, further exploration is required to determine the importance of male protection and kin protection towards pregnant females. In particular, a focus on family structure, with comparisons of aggression towards pregnant females with and without numerous close female kin may clarify the role of familial support on inhibiting aggression. Furthermore, the existence of pregnancy signals in baboons and analogous signals in lizards (Cooper & Greenberg, 1992; Hager, 2001) and fish (Deaton, 2008; Farr & Travis, 1986) suggests that similar mechanisms may exist throughout the animal kingdom and may even extend beyond visual cues, opening new avenues for understanding the challenges faced by pregnant/gravid females.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2015.07.026>.

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