CONSPECIFIC AGGRESSION AS A REPRODUCTIVE CONSTRAINT AND THE
VALUE OF KIN IN OLIVE BABOONS, *PAPIO ANUBIS*

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ABSTRACT

Agonism can also have profound reproductive consequences when fetuses and infants are targeted during aggressive interactions. In group-living mammals, inducing miscarriage in pregnant individuals may benefit males and females alike if the death of the infant returns the mother to estrous and removes a future competitor. Abortion in response to the arrival of a new male—termed the "Bruce effect"—has been widely documented, but evidence from wild populations is rare, and, though aggression between unrelated females in social groups is common, the consequences of these encounters for pregnant females and the strategies they may employ to ameliorate these costs remain poorly understood. In several non-human primates, aggression between adult males often involves the utilization of infants as agonistic "buffers", further endangering the reproductive output of mothers. This dissertation explores the relationship between conspecific aggression and the survival of infants and fetuses in captive and wild olive baboons, *Papio anubis*, and investigates the role maternal kin and fathers may have in protecting these vulnerable group members. Long-term data collected on wild baboons in Gombe National Park, Tanzania provide a lens through which to explore overall trends in reproductive output and family relationships, while focal follows give fine-scale understanding of rates of behavior. I also conducted color manipulation and playback experiments on captive baboons to assess how females may use color and vocal signals to recruit help from potential fathers and maternal kin. Chapter 1 reveals that bright colors signaling pregnancy may deter attackers, but that kin may play an important role in the efficacy of this signal. Chapter 2 assesses the role of maternal kin and potentially infanticidal males, and finds little evidence kin support is vital for avoiding miscarriage. However, the risk of fetal loss rises for pregnant females exposed to new immigrants that ascend rank quickly. Chapter 3 investigates the impact of male use of infants during agonistic encounters and suggests that, though this infant carrying behavior may have roots in paternal protection, new immigrant males can exploit this signal to the mortal detriment of the infants involved. Together, these chapters identify several reproductive costs for mothers at the hands of aggressive group members and highlight the possible pervasiveness of evolutionarily selected signals of pregnancy, male-induced abortion, and the use of "living tools" to signal aggressive intent.

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INTRODUCTION

The ubiquity of intraspecies aggression belies a strong selective pressure for animals to maximize their access to resources and mates to the detriment of those around them. Individuals that can outcompete conspecifics typically enjoy higher reproductive output and, in turn, pass on the traits that make them more successful. Aggression is one tool animals use to meet this goal. Males physically battle one another for access to sexual partners (Maynard Smith and Brown 1986; Andersson 1994; Hagelin 2002; Clutton-Brock 2007), females harass other females over the best feeding sites (Thouless 1990; Barton and Whiten 1993; Stockley and Bro-Jorgensen 2011; Pusey and Schroepfer-Walker 2013), and both sexes defend territories from potential interlopers (e.g. Stamps and Krishnan 1997; Garcia and Arroyo 2002; Desjardins *et al.* 2008). These behaviors often come at some risk to all parties involved (Maynard Smith and Harper 1988; Duckworth 2006), but those that fight and win reap important benefits.

Receiving aggression can be costly, resulting in injury and even death (Smuts and Smuts 1993; Chilvers *et al.* 2005; MacCormick *et al.* 2012). In mammals, pregnant and lactating females pay particularly high costs if their offspring are directly involved in the aggressive encounter. Infanticide can be an adaptive strategy of both males and females and has been catalogued across mammalian taxa (reviewed in Hrdy 1979; Sherman 1981; Hausfauter and Hrdy 1984; Wolff and Cicerello 1989; Agrell *et al.* 1998; Ebensperger 1998; Stockley and Bro-Jorgensen 2011). Because female competition is typically driven by a need for specific resources, females harass and kill the infants of competitors in order to reduce competition for them and their offspring (Le Boeuf and Briggs 1977; Sherman 1981; Silk *et al.* 1981; Balfour 1983; Brody and Melcher 1985; Lloyd and Rasa 1989; Tuomi *et al.* 1997; Ylonen *et al.* 1997; Kunkele 1992; Muller 2007; Townsend *et al.* 2007). Infanticidal males, on the other hand, often have relatively short opportunities to monopolize access to reproductive females and, as a consequence, will kill the dependent offspring of potential partners in order to accelerate a return to estrous (Mallory and Brooks 1978; Hrdy 1979; Packer and Pusey 1984; Mannella and Moltz 1988; Ryder and Massena 1988; Pereira and Weiss 1991; Pusey and Packer 1994;

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Pluhacek and Bartos 2000; Palombit 2003; Pluhacek and Bartos 2005; Korpela *et al.* 2010). Similar pressures guide male and female aggression toward pregnant individuals, with the ultimate goal of inducing miscarriage (Berger 1983; Pereira 1983; Mori and Dunbar 1985; Agoramoorthy *et al.* 1988; Storey and Snow 1990; van Schaik and Dunbar 1990; Roberts *et al.* 2012; Beehner and Lu 2013), though documentation of such examples are rare.

　　These threats to female reproductive success, in turn, select for behaviors to help mothers mitigate the costs of conspecific aggression. For some species this entails forming tight bonds with family members that might intercede during agonistic encounters. Long-lived female philopatric mammals successfully defend territories, obtain resources, and repel predators and infanticial males by living alongside mothers, sisters, and daughters (Hamilton 1964; Eberhard 1975; Pusey and Packer 1994; Creel and Creel 1995; Silk 2002; Wahaj *et al.* 2004; Archie *et al.* 2011). In social groups with multiple matrilines, these females also can support one another against other aggressive non-kin (Silk 2002). In baboons, lactating females build close relationships with resident males. Though the function of these "friendships" appears to differ somewhat between species, male friends will defend the offspring of their female associates from both non-lethal harassment and the murderous advances of infanticidal males (Smuts 1985; Palombit *et al.* 1997; Lemasson *et al.* 2008; Nguyen *et al.* 2009; Palombit 2009; Moscovice *et al.* 2010). Whether or not pregnant females—which are subjected to similar dangers as their lactating counterparts—benefit from such strategies, and the nature of how they utilize them, though, has been largely unexplored.

　　In several species of group-living primates, male interactions with infants extend beyond the infanticidal tendencies of new immigrants, though they may be just as negative. In some macaques and baboons, males carry infants in the presence of other males as a means to diminish aggression. The ritualization of agonism is widespread in animals, functioning to reduce the need for outright battle. Visual displays allow individuals to assess competitors and their aggressive intent prior to escalation, and these primate males appear to use infants as a signal of intent, with the ultimate response of de-escalation (Itani 1959; Kummer 1967; Ransom and Ransom 1971; Deag and Crook 1971;

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Packer 1980; Busse and Hamilton 1981; Busse and Gordon 1984; Dunbar 1984; Paul *et al.* 1996). Though prior work suggests carrying males are typically fathers acting protectively (Busse and Hamilton 1981; Busse and Gordon 1984), the promiscuous mating system of these primates creates opportunities for non-fathers to use this display dishonestly, possibly to the detriment of the infant.

In this dissertation, I explore the myriad ways that aggression within social groups affects the birth and survival of its most vulnerable members—i.e. fetuses and infants—and the specific strategies pregnant mothers may employ to minimize these costs. Specifically, I focus on aggression directed towards pregnant female olive baboons (*Papio anubis*), their risk of miscarriage, and factors that influence this risk. I also address male infant carrying and investigate its function as an agonistic display and the repercussions this has for the carried infants themselves.

I address these questions using focal observations of wild olive baboons conducted by both Craig Packer (1972 – 1975) and myself (2012) as well as long-term demographic data collected at Gombe National Park, Tanzania since 1968. Focal observations provide detailed information on rates of aggression as well as the specific identities of all individuals involved in a given interaction, while the long-term data set allows analysis of patterns of infant survival and miscarriage over the course of almost 30 years in a relatively long-lived species. I also conducted color manipulation and playback experiments on captive baboons at the Southwest National Primate Research Center in San Antonio, Texas, conducted in 2013 to address questions of the role of pregnancy signaling and kin in male and female aggression toward pregnant female baboons.

I explore the role of conspecific aggression and kin and their effects on reproduction in the following three chapters:

Chapter 1: *Does pregnancy coloration reduce aggression in the presence of maternal kin?*

Several social primate species exhibit distinct coloration at the outset of pregnancy and I test the hypothesis that this signal reduces the amount of

aggression pregnant females receive by garnering support from resident males and/or maternal kin during agonistic encounters. I use both focal follows on wild pregnant females and color manipulation and playback experiments on captive females and males, respectively, and assess levels of aggression/support when females exhibit pregnancy coloration vs. when they do not.

These results illustrate a probable adaptive function of pregnancy coloration as a signal and hint at the importance kin may play in the effectiveness of this signal. They also demonstrate that fathers, in addition to supporting their infants, may invest in their unborn offspring as well, with a willingness to intercede on behalf of the fetus's mother.

Chapter 2: *Patterns of miscarriage in a social mammal: evidence of a Bruce effect in wild olive baboons*

Using long-term demographic data on male immigration events, pregnant female wounding, miscarriage, and rank, I evaluate the role new immigrant males may play in the likelihood of female abortion and how the wounds obtained during aggressive encounters provide a mechanism by which miscarriage is caused.

Though fetal abortion in response to a new male has been documented in the laboratory setting, examples in the wild are rare. This chapter provides evidence of miscarriage in response to superior males that rise quickly in rank upon arriving in a new group and shows that females wounded during pregnancy are at a higher risk of miscarriage.

Chapter 3: *Possible co-option of an honest signal: male care vs. exploitation of infants in olive baboons*

Viewing male carrying of infants during agonistic encounters as a display meant to communicate aggressive intent is a new lens through which to consider these interactions. I use this framework to address predictions that infants are primarily carried by fathers wishing to communicate a protective intent and that,

given promiscuity in mothers, non-fathers will be able to co-opt this signal during agonistic encounters. To test these predictions I utilize observations of infant carrying culled from the long-term data set as well as focal follows conducted by Craig Packer between 1972 and 1975.

Although possible fathers are more likely to carry infants than other males, a finding corroborated by other studies, the data give no indication that this carrying behavior increases rates of survival in carried infants. However, infants carried by non-fathers suffer higher hazards of death, providing evidence that this protective signal can be used dishonestly by un-related males to the detriment of the infant involved.

CHAPTER 1

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

Conspicuous coloration serves as a reproductive signal in numerous species of fish (Andersson 1994), birds (Baker and Parker 1979), reptiles (Cooper and Greenberg 1992), and mammals (Caro 2005; Clutton-Brock and McAuliffe 2009). Such visual signals can be easily localized, rapidly transmitted (Bradbury and Vehrencamp 2011; Rosenthal and Ryan 2000), and sensitive to underlying hormonal profiles (Bagnara and Hadley 1973). In particular, some females utilize color changes, such as bright plumage (Amundsen 2000), skin color (Weiss 2006; Dubuc *et al.* 2009), or swellings (Higham *et al.* 2008), to signal sexual receptivity, and color displays by both sexes are known to attract mates (Andersson 1994). However, in only a few cases do females employ color to communicate other aspects of reproductive status such as gestation (e.g., some non-human primates (Rowell and Chalmers 1970; Altmann 1973; Loy 1974; Dunbar 1977; Setchell *et al.* 2006; Gerald *et al.* 2009)) or gravidity (e.g. some live-bearing fish (Farr and Travis 1986; Deaton 2008) and lizards (Cooper and Greenburg 1992)).

Investigations into gravid signals in lizards suggest that females may use color to signal the likelihood of aggressively responding to a male approach or courtship (Cooper and 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 gravid, this coloration darkens and deters males from attempting further copulations (Hager 2001). Yet, few studies have addressed the pregnancy coloration—often referred to as the "pregnancy sign" (Altmann 1973)—found in many primates, including gelada baboons (Dunbar 1977), savanna baboons (Altmann 1973), rhesus macaques (Gerald *et al.* 2009), patas monkeys (Loy 1974), gray-cheeked mangabeys

(Rowell and Chalmers 1970), and mandrills (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. Work with rhesus macaques suggests that the pregnancy sign may function as a "warning" to conspecifics, as males paid more visual attention and both males and females demonstrated higher amounts of appeasement behaviors to photographs of pregnant faces than to non-pregnant faces, though the nature of this warning is poorly understood (Gerald *et al.* 2009).

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 *et al.* 1979; Shnider *et al.* 1979) and even lead to miscarriage (Clark *et al.* 1993; Field and Diego 2008). In social mammals, fetuses represent future competition for non-related group members and thus pregnant females may suffer from aggression by members of other matrilines (Silk *et al.* 1981). Similarly, males with a low probability of paternity may attack gestating females to induce miscarriage, thereby causing the females to resume cycling (Berger 1983; Pereira 1983; Mori and Dunbar 1985; Agooromorthy *et al.* 1988; Storey and Snow 1990; van Schaik and Dunbar 1990; Roberts *et al.* 2012). 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 and Shine 1981; Gubernick and Klopfer 1981; Montgomerie and Weatherhead 1988) and aggressive conspecifics (Itzkowitz and Nyby 1982; Grinnell *et al.* 1995; Watts 1997; Palombit 2000; Buchan *et al.* 2003; Ferreira *et al.* 2006). Juveniles often remain in close proximity to their mothers, thus males that respond to maternal distress calls protect their own genetic interests (Palombit *et al.* 1997). Fathers earn similar benefits from defending gestating females and are expected to intercede during conflicts with other

group members (Kleiman and Malcolm 1981; Palombit *et al.* 1997; van Schaik and 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 three weeks after conception (Altmann 1973). To test the "aggression-reduction" hypothesis, we collected observational data on wild baboons to establish whether pregnant females experienced reduced aggression after the appearance of pregnancy coloration and received 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 toward these females pre- vs. post-color alteration. Finally, we conducted playback experiments to test whether fathers were more attentive to the screams of pregnant females than of cycling females.

Methods

Observational Study

Study area and population

All behavioral 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. Data were collected during two distinct time periods when group size averaged 22.0 (+/- 1.6 SE) adults. Group composition ranged from 4 - 11 adult males (mean: 6.9 +/- 0.9 SE) and 12 – 19 adult females (mean: 15.1 +/- 1.2 SE).

Focal follows

        Focal follows were conducted by two separate observers. First, focal follows were conducted by CP on 23 adult male baboons between May and November, 1972 and June 1974 – May 1975. Each focal follow lasted 2.5 hours and an average of 57.6 hours (+/- 6.5 SE) was collected for each male. These observations included detailed data on behavior 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 AB on six pregnant females between May and December, 2012. Each follow lasted 1.5 hours, and each female was followed an average of 18.5 hours (+/- 0.3 SE) during the first 7 weeks of her pregnancy. These follows included all interactions with conspecifics, including any aggressive encounters with either males or females and any incidences of agonistic support, which was defined as any aggressive interaction involving the pregnant female when a third party directed aggression toward her 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 21.7 (+/- 1.3 SE, n=6 females) days after initial detumescence. Based on this mean and low variance in the appearance of pregnancy coloration, the first three weeks of gestation were considered "pre-pregnancy sign". However, if any female began to exhibit pregnancy coloration prior to the end of this three-week period, these data were excluded 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 SE) post-detumescence for all focal females by which time the pregnancy was no longer in question to an experienced observer. Thus weeks 5-7 of gestation were defined as the "pregnancy-sign" period. Though 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 of 7.75 hours (+/- 0.25 SE) pre-pregnancy sign and 8.25 hours (+/- 0.34 SE) 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) toward pregnant females in their pre-pregnancy sign and 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 meters), 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, interaction rates were calculated 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 with pregnancy-sign status, male rank, female rank, female age, and observer (CP or AB) as fixed effects and male and female identities as random effects. The least-squares means were compared across pregnancy sign status for analysis of each behavior and adjusted for the other fixed effects.

Female-female interactions

Female focal follows were analyzed for agonistic interactions between the focal pregnant female and other female group members, distinguishing kin from non-kin. 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 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. Kin and non-kin dyads were analyzed separately using linear mixed effects models with pregnancy sign status, focal female rank and age, and interacting

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female rank and age as fixed effects and the identities of pregnant and interacting females as random effects; least squares means were again compared across pregnancy sign status and adjusted for the other fixed effects.

<u>Male Playback Experiments</u>
Study Population

Female distress-call playback experiments were conducted on 17 captive adult male olive (*Papio anubis*) and olive-yellow hybrid (*Papio anubis/Papio cynocephalus*) baboons at the Southwest National Primate Research Center (SNPRC) in San Antonio, Texas. Each male was housed in a breeding enclosure measuring approximately 30 ft. x 30 ft. with 10-15 females. Groups consisted primarily of olive baboons, though 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 mos of age and reared in communal crèches by an unrelated male and female. Upon sexual maturity (typically ~4 yrs of age in this facility), females were introduced into breeding enclosures which 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 if they were housed with close relatives. Female rank is largely determined by the length of group tenure in captive Cercopithecines (Tung 2012), but the dominance relationships were not known for the females in this study.

Playback Methodology

Female screams were collected opportunistically from individuals throughout the facility using a Marantz PMD620 handheld 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 three months: screams from 1) pregnant females in their home cage (probability of paternity = 100%); 2) pregnant females in a

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neighboring cage (males can interact with these females through the wire mesh but likelihood of paternity = 0); 3) pregnant females from enclosures far from the focal male with whom he has had no opportunity to interact); 4) cycling females in their home cage; 5) cycling females in a neighboring cage; 6) "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. 16 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 scream length was 4.74 +/- 0.063 SE seconds (n=57) and calls were introduced in a random order. To avoid habituation, no male experienced more than one call in a 72-hour period, and several "dummy" playbacks were conducted on each male, where equipment was set up but no call played.

During the playback procedure, a Sony RDPX200iP speaker connected to a MacBook Pro laptop was set up at a distance of 3-5 meters from the focal male. A JVC Everio digital camcorder mounted on a tripod was placed behind the speaker to record reactions to the playback vocalization. The equipment was set up 10 minutes before each playback to allow individuals to acclimate. After the waiting period, the camcorder was started to record at least 20 seconds of male behavior 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 seconds. 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 neighboring cage had given a distress call for a minimum of 10 minutes.

The length of time each male spent gazing at the speaker pre- vs. post-call was noted, as well as any behaviors directed toward the speaker, including approaches (defined as any movement toward the camera), and appeasement (such as tongue protrusion or grunting) or agonistic behaviors. Neither of the two student judges who scored these behaviors was involved in the playback procedures or knew the identities and call types in each test. Net gaze length post-call was calculated by subtracting the

length of male gaze toward the camera in the 20 seconds before the playback from the length of gaze in the 20 seconds 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.

A logistic regression was performed to determine if males were more likely to respond to calls from pregnant or cycling females from the home or the neighboring cage. For calls to which males reacted, linear mixed effects models were then used to compare the net time males spent gazing at the speaker after each call type. The least squares means were compared across call types for each of these analyses using a Tukey-Kramer adjustment for multiple-comparisons. Calls from unknown cycling and pregnant females were compared separately to assess if males could differentiate between the calls of pregnant and cycling females.

Color Manipulation Experiments

Painting methodology

Color manipulation experiments were conducted on 18 parous pregnant female olive baboons at the Southwest National Primate Research Center. Each female was at least in her second trimester of pregnancy and therefore had been exhibiting pregnancy coloration for a minimum of five 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 color of a flat, cycling female, with the same paint mixture used on each test subject so that each experienced the same color change, while the clear paint was used as a control. Test females (n=9) were anesthetized and the paracallosal and sexual skin of each individual cleaned. A thin coat of non-toxic grey/purple paint (Createx™ Airbrush Colors, opaque purple, red, black, and white) was applied over the entire rump area to obscure all visible pregnancy coloration. After ~15 minutes, a coat of the non-toxic 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

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the color application. The paint typically persisted for only 4-5 days (maximum ~14 days) thereby eliminating the need to re-anesthetize the animals for paint removal. Each cage only included one painted female at a time, with at least a two-week gap between the final observation of the first female and the first observation of the second.

Behavioral Observations

Prior to the painting treatment, each test subject was observed for a total of ten hours over the course of three days (3 hours and 20 minutes per 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) behaviors, as well as any incidents of third-party support during an agonistic encounter. Greetings were defined as any behavior in which either the focal female or her conspecific approached and either touched or grunted at the other and in which neither individual exhibited a subordinate behavior (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 re-acclimate to their group until the following day. Over the next three days, females were observed for an additional ten hours at similar times of day as the pre-painting observations. The percent of paint coverage was noted, as paint deteriorated at different rates for different females.

Analysis

All incidents of aggression and support were compared between pre-painting and post-painting treatments for gray-painted females using a 2-tailed Wilcoxon signed rank test. The amount of aggression and support received by clear-painted females pre- vs. post-painting were also compared as a means to test for any effects of the painting treatment.

Number of approaches by and toward 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 were also compared. Separate analyses were conducted for pregnant female interactions with

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the group male and other females. Observations on females with paint coverage below 65% were not used and pre-painting observations were reduced at random so that pre- vs. post-painting comparisons included the same number of observation hours. This procedure was necessary for 6 of the 9 females, with 1 female observed 6 hrs, 40 minutes, before and after painting, 4 females for 3 hrs, 20 minutes, before and after, and 1 female's data was not used at all as her 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 colored longest, giving an overall impression of color coverage despite wear.

Ethical Note: Capture for females for application of color 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 anesthetic without event and did not suffer any injuries as a result of the experimental protocol.

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.

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 or after the appearance of the pregnancy sign ($t(22.12) = -0.69$, $p = 0.50$; All results of least square means of linear mixed effects models summaraized in Table 1). However, pregnant focal females received significantly less aggression from non-kin females while exhibiting pregnancy coloration than pre-pregnancy sign ($t(48.8) = -2.585$, $p = 0.013$ Fig. 1). Avoidance rates by focal females of non-kin female conspecifics did not differ significantly ($t(46.03) = -1.276$, $p = 0.21$), nor did grooming rates on ($t(21.84) = 0.397$, $p = 0.70$) or by ($t(24.28) = -0.747$, $p = 0.46$) focal females, pre- vs. post-pregnancy sign. Interaction rates between the focal female and other non-kin 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 toward pregnant Gombe females did not change after the appearance of pregnancy coloration (t(53.72) = -0.268, p = 0.79; Fig. 2). However, pregnant females avoided males less after the coloration appeared (t(59.92) = -2.634, p = 0.011). Females with the pregnancy sign also interacted less with males (t(188.53) = -2.089, p = 0.038; Fig. 3), with males initiating fewer of these interactions than with the same females pre-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 coloration (t(194.35) = -1.294, p = 0.20). The proportion of interactions involving avoidance behavior did not differ significantly with pregnancy sign (t(58.4) = -0.524, p = 0.60), suggesting the decreased avoidance behavior 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 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 nor female rank affected the significance of these results.

Third-party support was rarely witnessed during focal follows, but of 8 incidents, 4 occurred prior to the onset of pregnancy coloration, 2 during the 4th week when the pregnancy sign was developing, and 2 during the first three weeks after the appearance of the pregnancy sign. Seven cases involved matrilineal kin; in the eighth case, an adult male supported a female with the pregnancy sign.

Male Playback Experiments

Males at SNPRC gazed longer at the speaker when played screams from known pregnant females than screams from known cycling females (t(45.35) = -2.64, p = 0.011; Fig. 4). In particular, males gazed longer at calls from pregnant females from their home cage than those from either cycling females from their home (t(40.03) = -2.77, p = 0.040) or neighboring cages (t(42.71) = -2.86, p = 0.032; Fig 4). Males did not appear to

differentiate between calls from the home cage and neighboring cages ($t(44.81) = 1.281$, $p = 0.21$; Fig. 4), nor calls from pregnant females from the home cage vs. a neighboring 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 ($X^2(3) = 1.8$ $p = 0.61$). Note that males only approached the speaker 5 times in response to 154 calls and that males never directed threat gestures toward the speaker.

Color Manipulation Experiment

Pregnant captive females received significantly less aggression from other females when the pregnancy sign was obscured with gray paint ($W(7) = 21$, $p = 0.031$, Fig. 5). There was no significant change in the amount of aggression received by females in the clear-painted control group ($W(8) = 18.5$, $p = 0.49$, Fig. 5). Pregnant females received similar amounts of aggression from the group male pre- vs. post-painting in both gray ($W(7) = 0$, $p = 1.00$) and clear paint groups ($W(8) = 9$, $p = 0.77$); Fig. 6.

Males supported pregnant females in agonistic encounters with other females a total of six times and each incident occurred while females had pregnancy coloration (5 incidents prior to painting and 1 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- vs. post-painting with gray ($W(7) = 8$, $p = 0.20$) or clear paint ($W(8) = 12$, $p = 0.24$), nor did pregnant females groom other females at different rates with gray ($W(7) = 12.5$, $p = 0.48$) or clear ($W(8) = 16.5$, $p = 0.89$) treatments. Pregnant females were not approached by other females at different levels in gray ($W(7) = 6$, $p = 0.79$) or clear treatments ($W(8) = 23.5$, $p = 0.95$), nor did they approach those females at different levels (gray: $W(7) = 16.5$, $p = 0.89$; clear: $W(8) = 35$, $p = 0.16$). Pregnant females also did not change their levels of aggression toward other females in gray ($W(7) = 10$, $p = 0.58$) or clear treatments ($W(8) = 25.5$, $p = 0.06$). There was no significant difference in the rates of male interactions with pregnant females pre- vs. post-painting, including

approaches toward pregnant females (gray: $W(7) = 11$, $p = 0.36$; clear: $W(8) = 31.5$, $p = 0.31$), approaches by pregnant females (gray: $W(7) = 27$; $p = 0.23$; clear: $W(8) = 34.5$, $p = 0.17$), grooming on pregnant females (gray: $W(7) = 0$; $p = 1$; clear: $W(8) = 3$, $p = 0.35$), or grooming by pregnant females (gray: $W(7) = 3$; $p = 0.37$; clear: $W(8) = 10$, $p = 0.10$).

Discussion

The pregnancy signal elicited female aggression in captivity, where individuals were completely surrounded by non-kin. 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 matrilines. The bright coloration may make a female easier to identify and locate, and communicate a warning to non-kin 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 coloration increased the amount of aggression received in captivity, where pregnant females did not live among protective kin. Also, warning coloration across species deters interaction because it communicates a cost to receivers (Mappes *et al.* 2005) through the use of colors that contrast well with the surrounding environment (Arenas *et al*. 2014),

Likely, the nature of captivity 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, the rates of aggression among captive baboons are likely 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

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captive and wild populations. Though 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 toward 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 could have changed their behavior as their pregnancies progressed or undergone physiological changes that were obvious to other female group members but not to human observers. Mammals experience behavioral and hormonal changes throughout pregnancy (R.M. Marchant-Forde and J.M. Marchant Forde 2004; Bazer and Spencer 2011; Kinsley and Armory-Meyer 2011) 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- vs. post-appearance of the pregnancy sign, suggesting that the changes in aggression likely stemmed from the pregnant female's changing reproductive status *per se*. However, it is uncertain whether the wild females relied on the visual color signal or responded to some other cue, such as olfaction.

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

Males do, however, stand to benefit from protecting mothers carrying their unborn offspring. Although adult males only rarely supported pregnant females — one

observation in the wild population vs. 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 of 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 those from neighboring females, with which they could interact through a barrier but of whom their paternity certainty was quite low. Though selection is likely to favor males in polygamous species to correctly assess their probability of paternity (Westneat and Sherman 1993; Neff 2003), 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 toward offspring for whom they have high paternity estimates based upon mating effort with the mother (Moscovice *et al.* 2010) and, though 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 behavior toward females with whom they have mated, regardless of actual paternity (vom Saal and Howard 1982; Gubernick *et al*. 1994). Thus, male baboons may show care toward any female that became pregnant during their residency. Also, despite a chain-link barrier, males may have engaged is some limited mating contact with neighboring 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 (Trivers 1972; Maynard Smith 1977; Moscovice *et al.* 2010). 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 (Cowlishaw and Dunbar 1991; Bulger 1993; but see also Alberts *et al.* 2003), this male was a likely father. Further investigation will be necessary to elucidate the role of paternity certainty in these male-female interactions.

Though pregnancy status and, specifically, coloration apparently alter the behavior of both male and female group members, further exploration is required to

determine the importance of male and kin protection to pregnant females. In particular, a focus on family structure, with comparisons of aggression toward pregnant females with and without numerous close female kin may clarify the role of familial support on inhibiting aggression. Further, the existence of pregnancy signals in baboons and analogous signals in lizards (Cooper and Greenburg 1992; Hager 2001) and fish (Farr and Travis 1986; Deaton 2008) 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.

Tables and Figures

Table 1-1: Linear mixed effect model results.

Least squares means results for focal data collected during the observational study of free-ranging olive baboons at Gombe National Park, Tanzania.

	Mean (SE) during pre-pregnancy sign (weeks 1-3)	Mean (SE) during pregnancy sign (weeks 5-7)	Effect estimate (SE) *	p-value*
Male-female interactions				
Male-female aggression rate (incidents/hr)	0.536 (0.041)	0.049 (0.012)	-0.0042 (0.016)	0.79
Female avoidance rate of males (avoids/hr)	0.113 (0.018)	0.052 (0.018)	-0.061 (0.023)	**0.01**
Grooming rate on male (min/hr)	0.334 (0.113)	0.406 (0.113)	0.072 (0.150)	0.63
Grooming rate on female (min/hr)	0.148 (0.042)	0.089 (0.042)	-0.058 (0.055)	0.30
Interaction rate (interactions/hr)	0.254 (0.065)	0.197 (0.065)	-0.057 (0.028)	**0.04**
Proportion of interactions initiated by male	0.376 (0.078)	0.281 (0.078)	-0.096 (0.048)	0.05
Proportion of interactions initiated by female	0.344 (0.074)	0.279 (0.074)	-0.065 (0.045)	0.20
Female-female interactions				
Aggression rate toward pregnant female by kin (incidents/hr)	0.075(0.056)	0.045 (0.061)	-0.030 (0.044)	0.50
Aggression rate toward pregnant female by non-kin (incidents/hr)	0.130 (0.041)	0.0488 (0.041)	-0.0815 (0.032)	**0.01**
Pregnant female avoidance rate of non-kin (avoids/hr)	0.119 (0.021)	0.081 (0.022)	-0.038 (0.030)	0.21
Grooming rate on pregnant female by non-kin (min/hr)	0.107 (0.086)	0.146 (0.086)	0.0389 (0.098)	0.70
Grooming rates by pregnant female on non-kin (min/hr)	0.370 (0.139)	0.257 (0.139)	-0.112 (0.150)	0.46
Interaction rate with non-kin (interactions/hr)	0.466 (0.104)	0.420 (0.104)	-0.046 (0.591)	0.44

* Effect estimate and p-value from a linear mixed model with pre-pregnancy sign vs. pregnancy sign as the primary test of interest, including adjustment for observer, female rank, and rank of the individual with which the interaction occurred, and including random effects for each baboon to account for multiple observations per dyad.

Figure 1-1: Non-kin female aggression toward pregnant females pre- vs. post-appearance of pregnancy coloration.

Least squares mean rates of wild non-kin female aggression (attacks/threats per hour +/- SE) received by wild female baboons in the observational study before and after the appearance of pregnancy coloration, averaged across female-female dyads ($t(45.8) = -2.585$, $p = 0.013$).
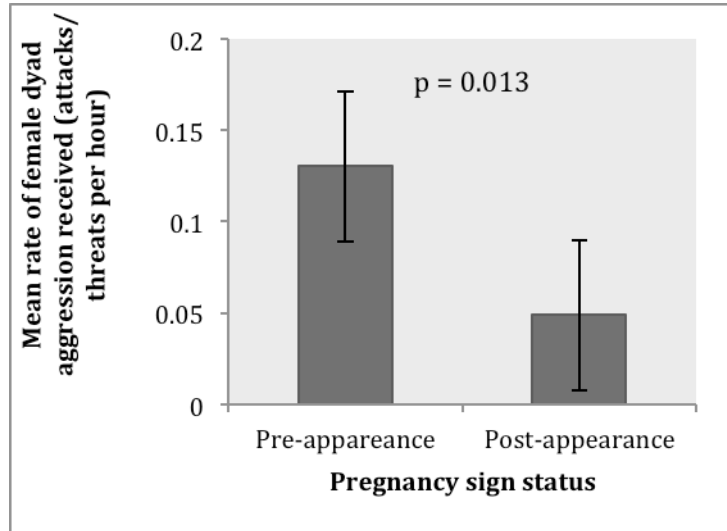

Figure 1-2: Male aggression toward pregnant females pre- vs. post-appearance of pregnancy coloration.

Least squares mean rates of wild male aggression (attacks/threats per hour +/- SE) received by wild pregnant female baboons in the observational study before and after the appearance of pregnancy coloration, averaged across male-female dyads ($t(53.72) = -0.268$, $p = 0.79$).
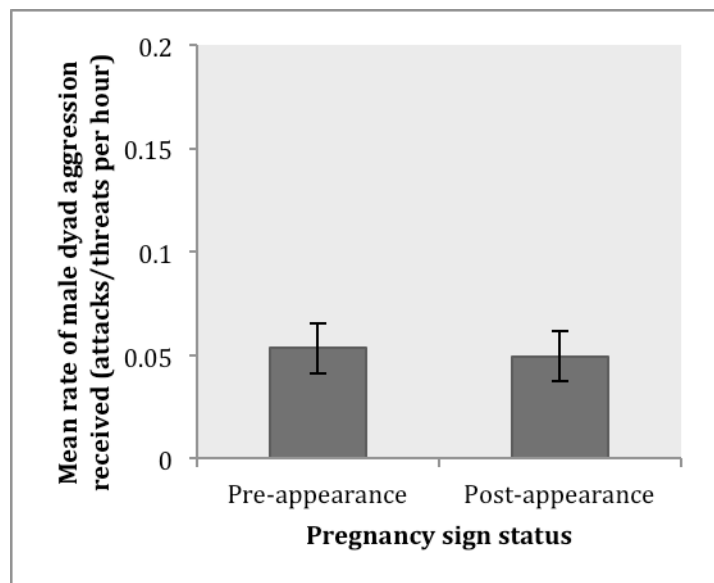
Figure 1-3: Male interaction with pregnant females pre- vs. post-appearance of pregnancy coloration.

Least squares mean rates of interaction per hour(+/- SE) between wild males and pregnant females pre- vs. post-appearance of the pregnancy sign in the observational study, averaged across male-female dyad (t(188.53) = -2.089, p = 0.0380). Males initiated significantly fewer interactions post-sign (t(199.87) = -1.979, p = 0.049), while there was no difference in rate of initiation by pregnant females (t(194.35) = -1.294, p = 0.20).
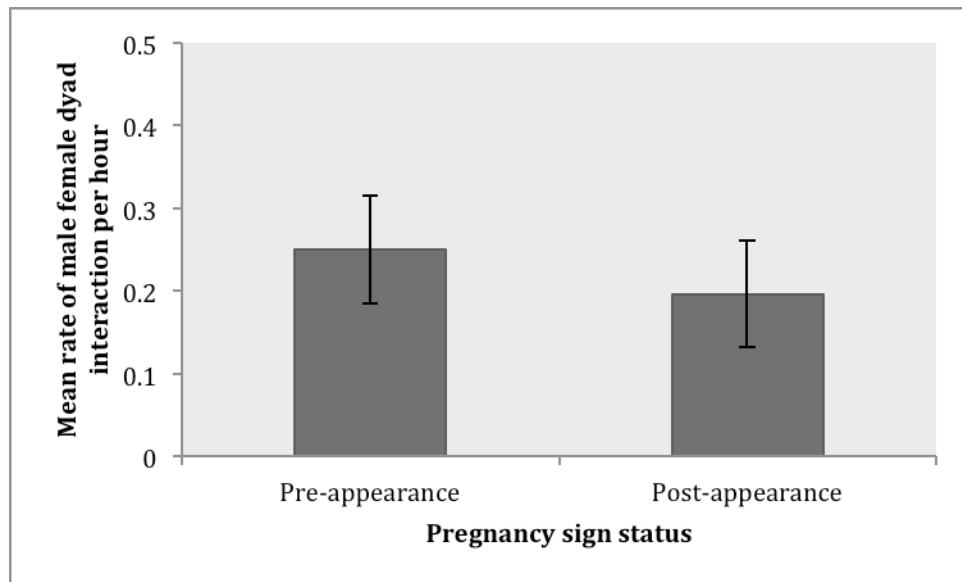
Figure 1-4: Male gaze length toward known and unknown pregnant and cycling females.

Mean captive male net gaze length (in seconds +/- SE) at distress calls from six female types: 1) cycling females from the home cage; 2) cycling females from a neighboring 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 neighboring cage; 6) pregnant females from a distant cage that were unknown to the male. Males gazed significantly longer at the calls of pregnant females from their home cage vs. calls from cycling females from their home (t(40.03) = -2.77, p = 0.040) or neighboring (t(42.71) = -2.86, p = 0.032) cages.

Figure 1-5: Attacks by females on pregnant females pre- vs. post-painting.
Mean number of captive female attacks (+/- SE) on pregnant females pre- vs. post-painting of pregnancy coloration with gray (n=8) (W(7) = 21, p = 0.031) or clear (n=9) (W(8) = 18.5, p = 0.49) paint. Of the females treated with gray paint, 7 of the 8 showed a decline in received aggression, while 1 of the 8 experienced similar levels of aggression.

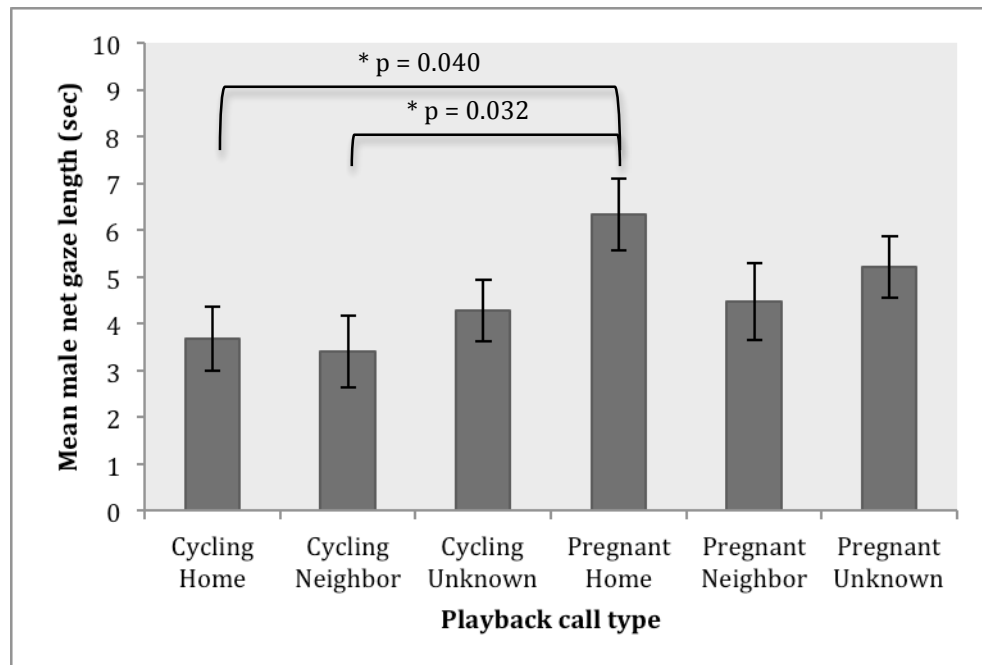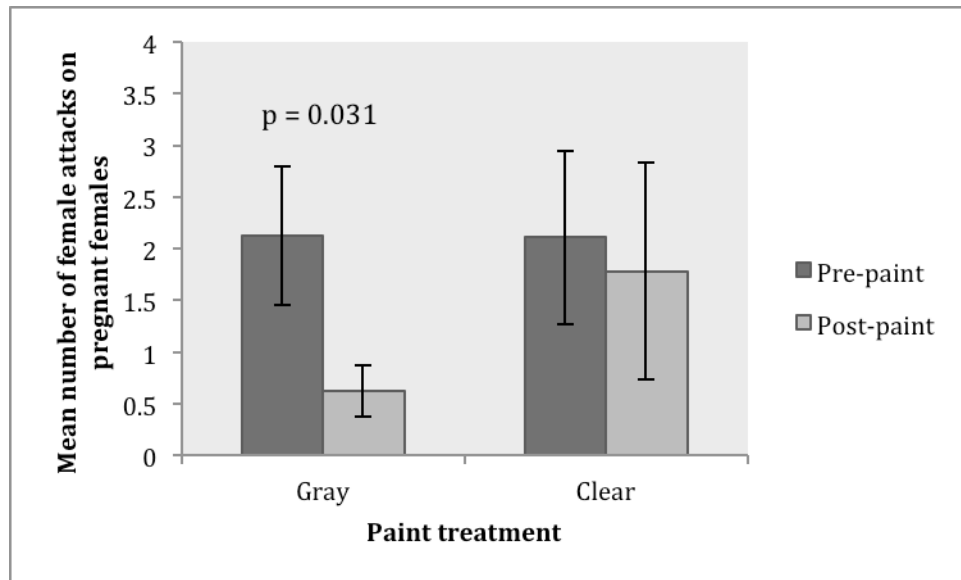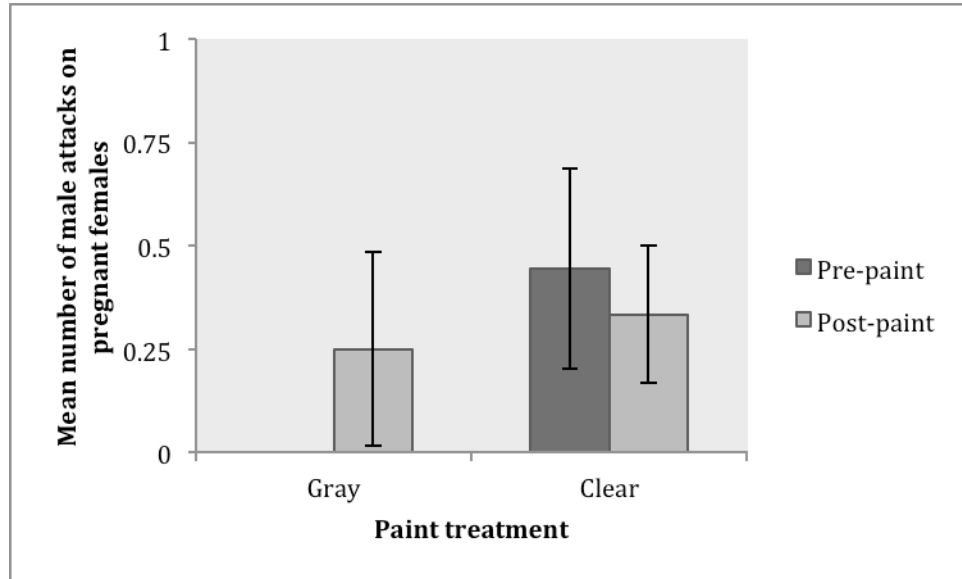**Figure 1-6: Attacks by males on pregnant females pre- vs. post-painting.**

Mean number of captive male attacks (+/- SE) on pregnant females pre- vs. post-painting of pregnancy coloration with gray (n=8) (W(7) = 0, p = 1.00) or clear (n=9) paint (W(8) = 9, p = 0.77).

CHAPTER 2

Patterns of miscarriage in a social mammal: evidence of a Bruce effect in wild olive baboons

Fetal abnormalities (Wilmut *et al.* 1986), disease (Lynch *et al.* 2011; Godfroid *et al.* 2010), nutrition (Strum and Western 1982; Cheney *et al.* 1988; Gibbens *et al.* 2010), age (Packer *et al.* 1998), and environmental changes (Dunbar and Sharman 1983; Wasser and Barash 1983; Bronson 1985; Loudon and Racey 1987; Beehner *et al.* 2006) can all influence the likelihood of conception, fetal development, and successful parturition, but in group-living mammals, social stress can also be a key factor in reproductive success (Wasser and Barash 1983; Pratt and Lisk 1989; Goymann *et al.* 2001; Young *et al.* 2006; Arck *et al.* 2007). Proximally, acute stress in mammals raises blood pressure while lowering uterine blood flow, thereby causing hypoxemia in the developing fetus (Morishima *et al.* 1979; Shnider *et al.* 1979), which may result in fetal abortion (Clark *et al.* 1993; Field and Diego 2008). In species where established social ranks and relationships ordinarily diminish social uncertainty, the prolonged stress accompanying group instability can have profound effects on embryo implantation and the likelihood of fetuses being carried to term (Cheney *et al.* 2004; Sapolsky 2005; Engh *et al.* 2006).

Yet certain individuals may benefit by inflicting miscarriage on conspecifics. When a male first enters a new group, pregnant and lactating females are devoting all their reproductive efforts toward nurturing offspring that are not his own. A typical male may only be able to gain reproductive opportunities for a few months or years, especially in species where access to fertile females is influenced by rank (Le Boeuf 1974; Clutton-Brock 1988; Cowlishaw and Dunbar 1991; Hirotani 1994) or direct male-male competition (Packer and Pusey 1982; Sommer and Rajporuhit 1989; Snyder-Mackler *et*

al. 2012). Pregnant and lactating females quickly resume cycling after the loss of a fetus or infant (Altman *et al.* 1977; Hrdy 1979; Packer and Pusey 1984; Palombit 2003; Beehner and Bergman 2008; Roberts *et al.* 2012; Lukas and Huchard 2014), granting infanticidal males accelerated access to fertile partners (Hrdy 1979; Van Schaik and Janson 2000; Palombit 2012; Lukas and Huchard 2014).

Known as the "Bruce effect", miscarriage in response to the arrival of a new male has been viewed as a strategy whereby pregnant females terminate investment in infants that would eventually be killed at birth (Bruce 1959; Becker and Hurst 2008; Beehner and Lu 2013). However, if infanticide is uncertain, a female that maintains her pregnancy may have a fitness advantage over aborting females. The incoming male would still benefit from inducing miscarriage, and, thus, fetal losses may instead result from harassment by the new male (Pereira 1983; Agoramoorthy *et al.* 1988; Beehner and Lu 2013) rather than any innate response by the female. Examples of either mechanism of fetal loss in response to incoming males in the wild are rare (but see Roberts *et al.* 2012), but male-induced miscarriages should be more likely in social groups with multiple males, including the fetuses' fathers.

High-ranking female matrilines gain priority of access to resources in competition with other matrilines (Vehrencamp 1983; Frank 1986; Silk 1993; Kahlenberg *et al.* 2008), and the infants of rival females represent future competition for food. Female toque and bonnet macaques selectively harass unrelated juvenile females (Dittus 1979; Silk *et al.* 1981), and, in the absence of female kin, female baboons with conspicuous pregnancy coloration receive significantly more aggression from other females compared to females whose coloration has been experimentally obscured (Bailey *et al.* 2015). Because agonistic behavior increases stress levels (Bronson and Eleftheriou 1964; Manogue *et al.* 1975; Creel 2001), abortion rates may be elevated among low-ranking females.

Given that stress-induced miscarriage may benefit both immigrant males and rival females, selection may have favored counterstrategies by pregnant females. In chacma baboons, females limit infanticide by forming friendships with males (usually fathers or "likely fathers") that protect their infants from immigrants (Palombit *et al.* 1997;

Palombit 2000; Weingrill 2000; Palombit 2009). Female kin also have a vested interest in the offspring of related females, and females have been observed to incur personal risk in the defense of close family (Hamilton 1964; Maynard Smith 1965; Dunford 1977; Silk 2002), as well as inhibit female aggression towards pregnant family members (Bailey *et al.* 2015).

In this study, we utilize long-term data collected on wild olive baboons at Gombe National Park in Tanzania, to test whether miscarriage rates vary in response to the arrival of new immigrants and to the presence and number of female kin. As only those incoming males that quickly attain high rank are likely to benefit from infanticide, we contrast the miscarriage rates following the arrival of "fast-rising" males vs. all other immigrants. Prior work at Gombe suggests high-ranking females are more likely to miscarry than their lower-ranking counterparts (Packer *et al*. 1995), and thus we aim to establish if this difference is an overall cost of dominance or is driven by social factors relating to the arrival of these new males. In addition, as noted above, changing environments and available nutrition can have profound impacts on fetal survival, so we control for the effects of significant decreases in rainfall at Gombe by isolating data before and after this change. We also analyze wounding data to determine if injured females experience an increased hazard of miscarriage.

Methods

Study Area and Population

Gombe National Park is approximately 52 km^2 and is located on the eastern shore of Lake Tanganyika in Tanzania. Characterized by small streams and steep valleys that descend from a rift escarpment, Gombe lacks large wild predators (van Lawick-Goodall 1968) and is home to several primate species, including olive baboons, chimpanzees, and red colobus monkeys. Baboons at Gombe have been observed since 1967, with continuous demographic data collected since 1972. Data were collected on two distinct study groups, which subsequently split several times throughout the years, yielding a total of 9 troops with a mean size of 22.1 (+/- 0.3 SE) adults, including 7.0 (+/- 0.08 SE) adult

males and 14.2 (+/- 0.2 SE) adult females. These data include reproductive statuses of females, immigration and emigration events, births, and deaths.

Miscarriage Data

Birth and miscarriage data are available from 1972 to 2002. Pregnancy in females is identified by the appearance of bright red coloration on the paracollosal skin of the rump (Altman 1973). This color change is overt, appearing approximately 3 weeks after the sexual swelling begins to detumesce (Bailey *et al.* 2015), and persists until several days after parturition, providing a reliable indicator of reproductive status. Gestation typically lasts 180 days (Altmann *et al.* 1977; Higham 2006). Some pregnant females bleed when they miscarry and this sign as well as the complete loss of pregnancy coloration were used to estimate fetal age. The underlying miscarriage rate for Gombe baboons is 10.7%, though this is likely an underestimate because miscarriages that occur during the first three weeks of pregnancy cannot be detected using our methodology. Full-term still-borns were not considered to have been miscarried.

Miscarriage Analysis:

Exposure to immigrant males

Fetal age at first exposure to a new immigrant male was determined for all pregnancies (n = 732) of females with known rank. Pregnant females that were not exposed to new immigrant males before parturition (180 days) were classified as non-exposed. A Cox regression with a time-dependent covariate was used to calculate hazard of miscarriage to fetal age of 180 days, with exposure to immigrant male updated to "yes" at the age of a fetus's first exposure to a new immigrant. A second analysis classified pregnant females by exposure to a male that ascended to top rank within one year of immigration, with only those pregnancies classified as "exposed" at the fetal age of first exposure. A significant decrease in rainfall at Gombe beginning in 1993 (Fig. 1, Fig. 2) introduced a strong non-linearity in the miscarriage data, so the data set was also divided into pre- vs. post-1994 periods and each period was analyzed separately, though, these results were only reported if the outcomes differed between the two time periods.

Kin and Miscarriage

Pregnancies were analyzed to determine the number of kin members for each pregnant female at the point of conception. Kin were first separated by mother, maternal sister, maternal brother, daughter and son and then combined to provide an overall kinship profile. Without DNA profiles, the identities of non-maternal kin were unknown. Four years was used as the cutoff for defining the age above which kin could effectively assist the pregnant females. By 4 yrs of age, females have generally reached sexual maturity and adolescent males are larger than adult females.

Mean rates of miscarriage were calculated for females with 0, 1, 2, etc. number of kin but a distinctly non-linear relationship emerged, and females were categorized as having "few" (0-1) and "many" (≥2) close kin. The initial model included the fixed effects of age, kin category ("few" or "many"), presence of an immigrant male (defined as any male that arrived in the group after conception), number of group females, number of group males, percent of group females that were non-kin, female rank, and whether the pregnancy occurred before or after 1994, with female identity as a random effect. A probit regression was then performed comparing pregnancy outcomes (miscarriage vs. no miscarriage) for a smaller model fit using AIC selection.

Wounding Analysis

Wounds are defined as a visible injury anywhere on the animal's body. Though varying in severity, we treated all wounds identically. Fetal age at each wounding event was determined for all pregnancies; unwounded females were classified as having 0 wounds during pregnancy and number of wounds was updated at the fetal age of each wounding event. A Cox regression with a time-dependent covariate was then used to calculate the hazard of miscarriage before day 180 for wounded vs. non-wounded pregnant females, controlling across maternal rank.

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

Results

Pregnant females exposed to new immigrant males were no more likely to miscarry than unexposed pregnant females (HR = 1.29 (0.76 – 2.16, p = 0.34). However, prior to the drought in 1994, females exposed to "fast-rising" males suffered a higher hazard of miscarriage (HR = 6.17 (1.47 – 25.83), p = 0.013; Fig. 1), and this effect was disproportionately large for higher-ranking females (HR = 0.77 (0.64 – 0.94), p = 0.0095; Fig. 1). These effects disappeared after 1994 ((exposure: HR = 0.82 (0.15-4.30), p = 0.81; maternal rank and exposure: HR = 1.11 (0.93 – 1.31), p = 0.24)). However, after 1994, low-ranking females experienced a significant increase in the rate of miscarriage (z = -2.68, p = 0.007) bringing their rates closer to those of high-ranking females, which experienced no significant increase (z = -1.59, p = 0.11, Fig. 2).

In contrast, we found no effect of female family structure on miscarriage rates: pregnant females with 0-1 maternal kin were no more likely to miscarry than females with ≥2 family members (z = -1.40; p = 0.16).

Wounded females had an increased hazard of miscarriage, though this effect did not increase significantly with each additional wound (1 wound: HR = 2.39 (1.06 – 5.39), p = 0.036; 2 wounds: HR = 4.44 (0.96 – 20.59), p = 0.057; 3 wounds: HR = 7.01 (0.99 – 49.46), p =0.051; Fig. 3)

Discussion

Though infanticide is rare in olive baboons (Henzi and Barrett 2003; Palombit 2003; but see Collins *et al.* 1984), pregnant females exposed to "fast rising" incoming males are at increased risk of fetal loss. Immigrant males may destabilize their new troop (Sapolsky 1983), and those that rapidly rise to top rank may disrupt group dynamics most of all. Thus, females may miscarry in response to an exceptional increase in social instability. However, these new immigrant males may also target pregnant females. Incoming chacma baboons quickly achieve top rank, and infanticide is a leading cause of infant mortality (Busse and Hamilton 1981; Palombit *et al.* 2000). In contrast, male olive baboons typically ascend more gradually (Palombit 2003), often mating with many

females before reaching the top, making infanticide less beneficial. For "fast-rising" olive males that follow the chacma pattern, though, inducing miscarriage may mirror the Bruce effect observed in other taxa (rodents: Bruce 1959; Storey and Snow 1990; horses: Berger 1983; Bartos *et al.* 2011; lions: Bertram 1975; primates: Agoramoorthy *et al.* 1988; Colmenares and Gomendio 1988; Mori and Dunbar 1985; Pereira 1983; Roberts *et al.* 2012; van Schaik and Dunbar 1990).

The difference in hazard of miscarriage between high and low-ranking females prior to 1994 hints at a tendency of fast-rising immigrants to selectively harass dominant females. Though top-ranking females at Gombe suffer higher rates of miscarriage, their full-term infants have higher survival and their daughters begin cycling sooner than those of lower-ranking females (Packer *et al.* 1995). Thus fast-rising males that successfully induce high-ranking females to return to sexual receptivity would gain fitness advantages for their own offspring. This result may help explain the previously puzzling observation that high-ranking Gombe females suffered the highest miscarriage rates: high-ranking females are the most valuable targets for fast-rising immigrants, but by being a preferred target, high-ranking females lose some of the overall benefit of their status.

The disappearance of the immigrant-related miscarriage effect in 1994 may have resulted from long-term environmental changes triggered by a marked transition to a prolonged period of below-average precipitation. The overall miscarriage rate rose for low ranking females to levels that had only been measured in the high-ranking females over the prior decades, suggesting that the nutritional stress that accompanies drought (Newsome 1965; Strum and Western 1982; Cheney *et al.* 1988; Gibbens *et al.* 2010) may overshadow the effects of harassing males on pregnancy loss.

Large predators are absent at Gombe, thus all wounds are considered to have resulted from intraspecific aggression (MacCormick *et al* 2012). Injured pregnant females suffer a higher hazard of miscarriage, suggesting a mechanism by which fetal loss can be induced. Wounds increase physiological stress and can easily become infected, especially when an individual's immune system is compromised by elevated stress (Cohen *et al.* 2007; Sapolsky 2011).

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Despite indications that kin may help protect pregnant females, we found no evidence that family size affected miscarriage rates. However, baboons may be able to identify and maintain relationships with paternal kin (Alberts 1999), and, lacking DNA profiles, the family connections in our study population may be more extensive than we originally classified them. Alternatively, if the primary threat to pregnancies is the arrival of particularly aggressive new males, close kin may not be helpful, as females and juvenile and sub-adult male baboons are significantly smaller than adult males. Captive male baboons pay more attention to the screams of known pregnant females than their cycling counterparts (Bailey *et al.* 2015), and female chacma baboons form friendships with resident males to protect their vulnerable infants from infanticidal immigrants (Palombit *et al.* 1997; Palombit 2000; Weingrill 2000; Palombit 2009), a behavior that could have similar benefits for pregnant females. Further investigation into the relationships between pregnant females and resident males may elucidate mechanisms that mitigate the potential reproductive costs of conspecific aggression.

TABLES AND FIGURES

Figure 2-1: Gombe National Park rainfall between 1972 and 2001.

Mean yearly rainfall (in mm) at Gombe National Park, Tanzania between 1972 and 2001.
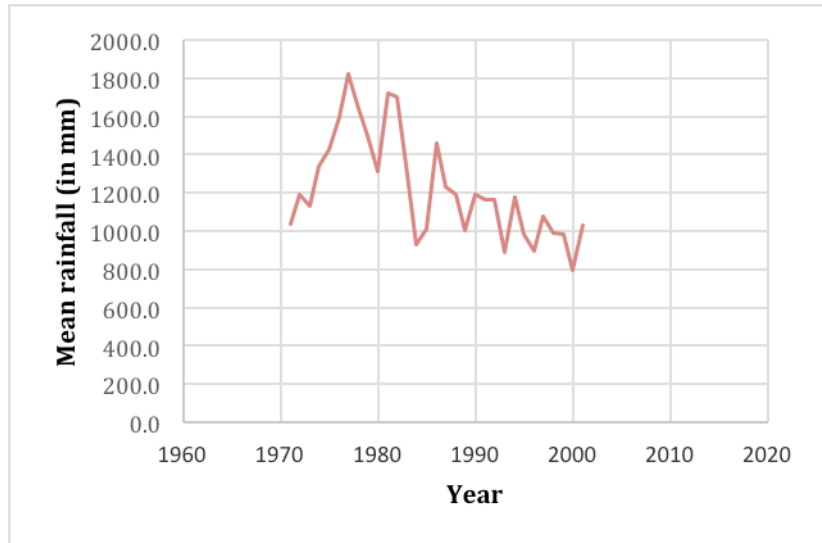
Figure 2-2: Rainfall pre- vs. post-1994.

Mean rainfall at Gombe National Park from 1972-1993 vs. 1994-2001 ($z = 3.01$, $p = 0.002$).
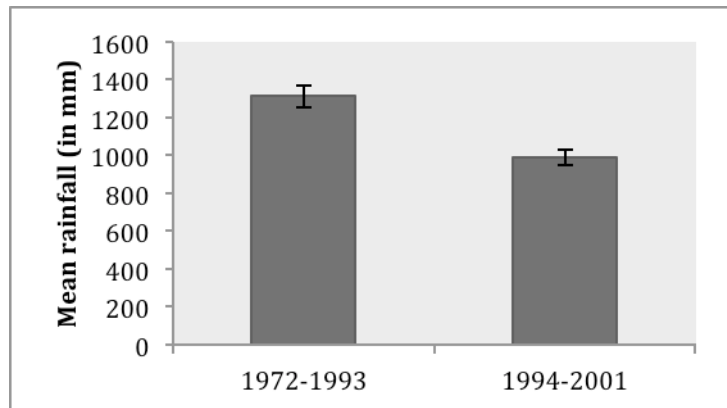
Figure 2-3: Comparison of parturition probability when exposed to "fast-rising" males for A) rank 1 and B) rank 5

The probability of a pregnant female carrying her fetus to parturition (180 days) for females exposed to a male that achieved top rank in the year following his immigration into the group vs. those females not exposed to such males. The effect of maternal rank on the probability of parturition for exposed females is illustrated using a) a female at the top of the dominance hierarchy (rank 1) and b) a female in the middle or bottom of the hierarchy, depending on group size (rank 5).
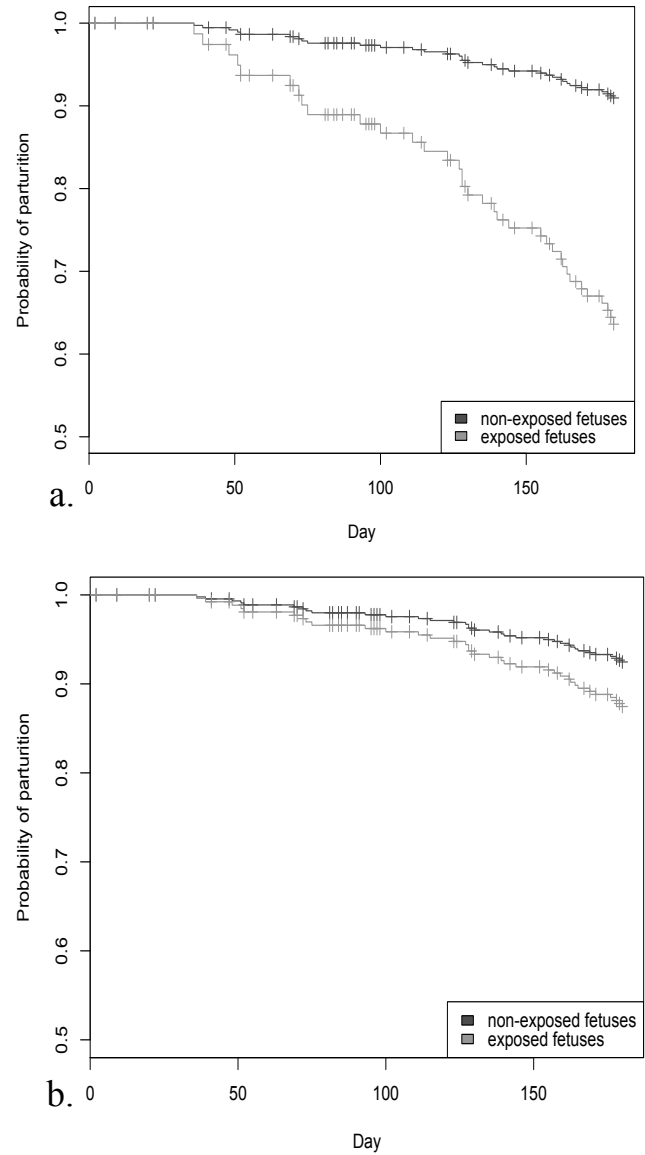
Figure 2-4: Comparison of miscarriages by rank pre- vs. post-1994.
The proportion of pregnancies that resulted in miscarriage between 1972 and
1993 vs. 1994 to 2001 for females in the top half of the hierarchy (high-ranking)
vs. those in the bottom half (low-ranking). High-ranking females had no
significant increase between the two time periods ($z = -1.59$, $p = 0.11$). Low-
ranking females experienced a significant increase in proportion of miscarriages
($z = -2.68$, $p = 0.007$)
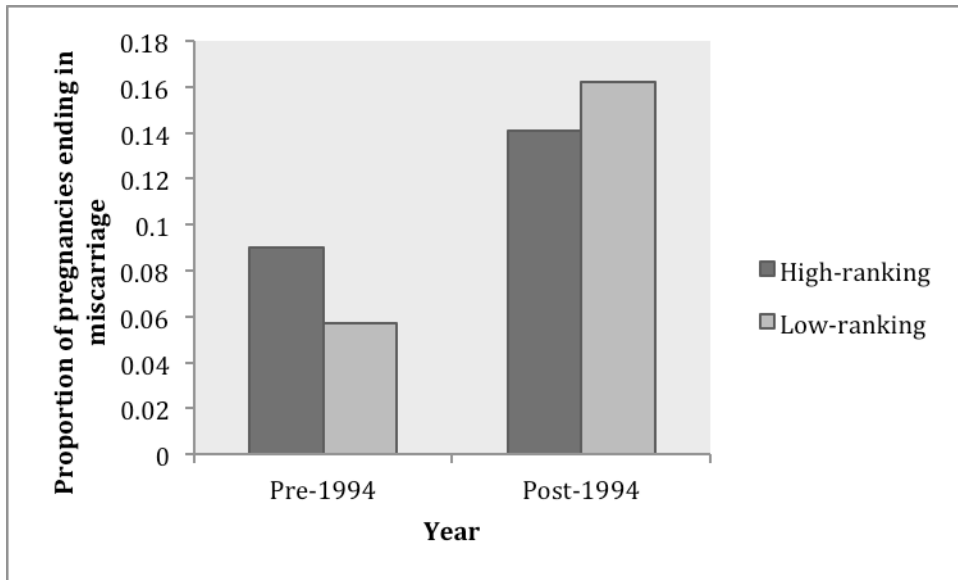
Figure 2-5: Influence of wounds on the probability of carrying a fetus to term
The probability of a pregnant female baboon carrying a fetus to term (as opposed to miscarrying) when she has 0, 1, 2, or 3 or more wounds (1 wound: HR = 2.39 (1.06 – 5.39), p = 0.036; 2 wounds: HR = 4.44 (0.96 – 20.59), p = 0.057; 3 wounds: HR = 7.01 (0.99 – 49.46), p =0.051).

CHAPTER 3

Possible co-option of an honest signal: male care vs. exploitation of infants in olive baboons

Animals often use visual signals to advertise their strength and willingness to fight conspecifics (Parker 1974; Andersson 1994). These displays allow individuals to assess each other before engaging in physica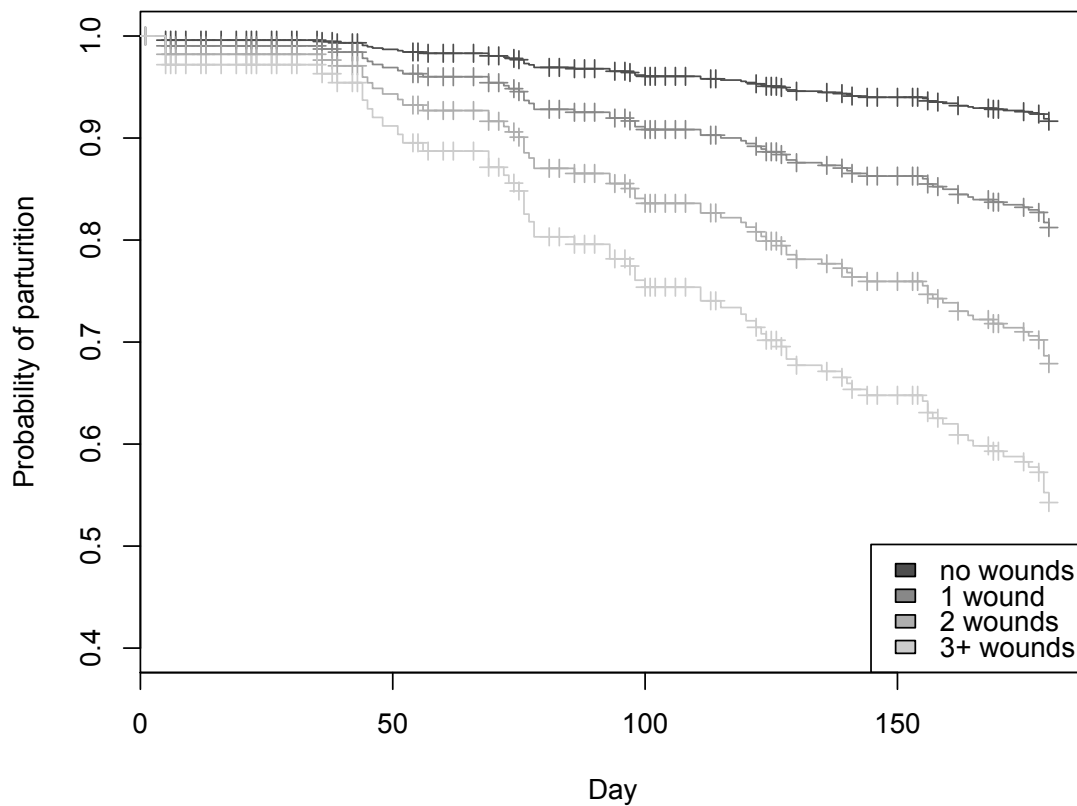l aggression, thereby decreasing risks of injury in contests with superior opponents (Maynard Smith and Price 1973; Maynard Smith and Parker 1976; Hammerstein 1981). Selection favors signals that accurately communicate fighting ability (Zahavi 1975; Maynard Smith and Harper 1988; Grafen 1990; Huntingford *et al.* 2000), but some displays apparently involve dishonest signaling. In fiddler crabs, male fighting success correlates strongly with claw size, and males assess the size of each other's claws before escalating. Males that have lost their major claw will regenerate replacements of similar size but inferior strength, yet successfully deter rivals via claw size alone (Backwell *et al.* 2000; Lailvaux *et al.* 2009). Similar examples of dishonest signaling occur in other crustacea (Steger and Caldwell 1983; Hughes 2000; Elwood *et al.* 2006; Wilson *et al.* 2007) but appear to be rare in other taxa (e.g. Candolin 2000 (sticklebacks); Bee *et al.* 2000 (green frogs)).

Male mammals are potentially emancipated from parental investment by the female reproductive system (Trivers 1972; Maynard Smith 1977; Clutton-Brock 1991). However, males in several mammalian species protect their offspring from predators and abusive conspecifics (Woodroffe and Vincent 1994; Gubernick and Teferi 2000). In several species of baboons and macaques, males grab infants during agonistic encounters with other resident males, potentially protecting the infant from possibly infanticidal newcomers and frequently de-escalating male-male aggression (Itani 1959; Kummer

1967; Ransom and Ransom 1971; Deag and Crook 1971; Packer 1980; Busse and Hamilton 1981; Busse and Gordon 1984; Dunbar 1984; Paul *et al.* 1996). Initial interpretations of this behavior suggested non-fathers carried infants as an agonistic buffer against biological fathers, relying on the risk of injury to the infant to allay aggression (Deag and Crook 1971). Packer (1980) suggested males carried infants both exploitatively and protectively, and Busse and Hamilton (1981) showed that fathers are the most likely to carry infants, suggesting instead that infant carrying is largely protective. Either way, the inhibitory response by the opponent implies that infant carrying is a signal that functions similarly to stereotyped displays performed during male-male encounters but where fathers communicate a willingness to fight as if protecting their genetic future.

Male baboons compete for high dominance rank, which strongly predicts reproductive success (Cowlishaw and Dunbar 1991; Bulger 1993; also see Alberts *et al.* 2003). New immigrants that rapidly ascend rank may commit infanticide to ensure access to more mating partners during their brief tenure at high rank (Palombit *et al.* 2000). Fathers of vulnerable offspring are expected to show various protective strategies against such newcomers (Palombit *et al.* 1997; Palombit *et al.* 2000; Lemasson *et al.* 2008), and a carrying male may be rescuing his offspring from a potential threat. However, female baboons often mate with multiple partners (Hrdy 1979; O'Connell and Cowlishaw 1994), so males that mated at least once with the infant's mother may also behave protectively (Buchan *et al.* 2003; Moscovice *et al.* 2010). Thus, any potential father may be communicating a willingness to escalate by carrying an infant. Paternity uncertainty, though, paves the way for dishonest signalers, such that males with no probability of paternity could possibly co-opt the signal of a protective father by carrying an infant during an aggressive encounter, effectively communicating a stereotyped willingness to escalate.

Here we investigate the nature of infant carrying and its possible function as a dishonest signal. If solely protective, infant carrying should mostly occur in the presence of newly immigrated, and hence potentially infanticidal, males, infants should only be carried by males with some estimate of paternity, and carried infants should enjoy a

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higher probability of survival than non-carried infants. However, dishonest signalers might often have a lower probability of paternity than their opponent, subject infants to increased mortality, and primarily carry an infant against higher-ranking opponents, regardless of that opponent's estimate of paternity.

Methods

Study Population and Data Collection

Eight troops of olive baboons (*Papio anubis*) in Gombe National Park, Tanzania were monitored between 1967 and 2012. Approximately 52 km^2, Gombe is located on the shores of Lake Tanganyika and consists of dense vegetation and steep valleys cut by streams that flow into the lake; a rocky beach runs the length of the park.

Demographic data on births, deaths, immigrations, emigrations, female reproductive state and consortships were collected on a near-daily basis by a staff of Tanzanian field assistants between 1967 and 2012. Behavioral data on male-infant relationships come from two sources. *Ad libitum* observations of infant carrying were recorded by the research assistants between 1984 and 2001, including the date of the interaction and the identities of the carrying male and infant but not the identity of the opponent. CP collected male-infant data during male focal follows between 1972 and 1975, identifying the carrying male, infant, and opponent.

Data Analysis

Determining Paternity:

In the absence of DNA tests, we assessed "likely" paternity from troop residence and consort behavior. Males form exclusive consortships with estrous females, and the male that monopolizes the female during the last 4 days of the follicular phase usually fathers the infant (Higham *et al.* 2008). However, males that have mated with females at earlier phases in the cycle often show affiliative behavior towards those infants (Moscovice *et al.* 2009; Moscovice *et al.* 2010; Nguyen *et al.* 2009), so every consort partner during a female's conceptive cycle was considered to be a "possible" father and categorized as a "consort male". Males resident at the time of conception but not observed consorting

were considered unlikely fathers, and categorized as either "natal males" (males born in that troop) or "resident males" (having originated from other troops). Finally, males that immigrated into the troop after the infant's conception were considered "immigrant males" and categorized as non-fathers.

Determining Dominance Rank:

Annual dominance ranks were determined by the outcomes of dyadic aggressive interactions between like-sexed individuals over the course of the year. Interactions were observed *ad libitum*, and an individual was said to have "won" if he or she: 1) chased/attacked/bit another individual that subsequently displayed a submissive behavior such as a retreat, scream, geck, or fear grin; 2) directed a threat behavior (e.g. eyebrow flash, ground-sweep, stiff-arm threat; Ransom 1971) toward another individual that responded submissively; or 3) displaced another individual. A displacement is defined as an interaction in which one individual approaches and occupies the spot previously occupied by a retreating individual. Interactions were tallied for all like-sexed dyads within each troop, and the individual with the most successful dominance interactions was ranked above the dyad partner. Individuals with unresolved dominance relationships were considered to hold the same rank.

Survival analysis:

Immigrant male analysis

The age at first exposure to a new immigrant male was determined for all infants (n = 682) of mothers with known rank. Infants that were not exposed to new immigrant males before their first birthday were classified as non-exposed. A Cox regression with a time-dependent covariate was used to calculate hazard of death to one year of age, with exposure to immigrant male at birth classified as "yes" or "no". For infants exposed after birth and before one year, all classifications were updated to yes at age of first exposure. A second analysis classified infants by exposure to a male that ascended to top rank within one year of immigration, with only those infants exposed to such males classified

as "exposed". Infants of higher-ranking mothers have lower mortality rates and thus all analyses were controlled across maternal rank (Packer *et al.* 1995).

Male carrying analysis

Data for which only the identity of the infant and the carrying male were known.

A Cox regression with a time-dependent covariate was used to calculate hazard of death before 1 year of age for infants of mothers of known rank, comparing carried and non-carried infants (n = 682). Infant status was assessed according to: a) the categorical identity of the carrying male (consort, resident, or immigrant) and b) the number of carries by each type of male. Counts were updated to 1, 2, 3, etc. at the age at which the behavior was observed. A second analysis restricted these data set to infants that had been carried at least once before their first birthday (n = 186), using a Cox regression to assess hazard of death according to age at first exposure to: 1) any immigrant male and 2) an immigrant male that subsequently achieved top rank.

Probit regressions were used to assess whether infants under 1 year of age were more likely to be carried: 1) by consort males vs. resident males and 2) when at least one immigrant male was present in the group vs. no immigrant males. Again, all analyses were controlled across maternal rank.

Data for which identities were known for both the male carrier and his opponent

Complete triadic identities were available from 151 carries observed between 1972 and 1975, allowing comparisons of the proportion of interactions involving carrying males and opponents of contrasting degrees of paternity (un)certainty. To determine if consort males acted more protectively than other carrying males, we restricted the analysis to cases involving infants for which we had consort data (n = 102). Two-sample z-statistics were used to compare respective proportions,

Results

Infants that were exposed to immigrants showed similar first-year mortality as infants that had not been exposed to immigrants (p = 0.60; Table 1; Fig. 1). Infant survival was also unaffected by exposure to immigrant males that achieved alpha status in the year following their entry (p = 0.24; Table 1). Infants carried by consort and resident males had similar hazards of death compared to un-carried infants (consort: p = 1.0, resident: p = 0.25; Table 1), but infants suffered a significantly higher risk of mortality if they were carried by males that had arrived after their conception (p = 0.018; Table 1). Among carried infants, the hazard of death was not significantly different for infants that were exposed to new immigrants vs. those that were unexposed (p = 0.17; Table 1) even when the new males quickly ascended to top rank (p = 0.09; Table 1).

Infants were much more likely to be carried by a consort male than by males that had not been seen consorting with the mother (z = 3.79, p <0.001; Fig. 2) but were no more likely to be carried when a new immigrant male was present in the group vs. when no new male was present (z = -1.44, p = 0.15). Among carries in which the identity of both males was known, consort males were just as likely as resident males to carry infants against new immigrants (z = 0.424, p = 0.67) and other consort males (z = -0.545, p = 0.59; Fig 3).

Discussion

Gombe infant olive baboons are not at increased risk upon the arrival of new immigrant males, even when those immigrants quickly ascend rank. Though common in chacma baboons, infanticide does not appear to be widespread in olive baboons (Henzi and Barrett 2003; Palombit 2003; but see Collins *et al.* 1984). The reproductive lifespan of a chacma male is very brief and largely restricted to his tenure as alpha male. In contrast, olive males show a variety of alternative reproductive strategies (e.g. coalition formation by subordinates (Bercovitch 1988), special relationships with females (Smuts 1985; Lemasson *et al.* 2008)). Thus although alpha olive males sire the majority of offspring conceived during their tenure, reproduction is far less skewed than in chacmas

(Palombit 2003). Also, whereas immigrant male chacmas typically attain alpha status shortly after entering a new troop, olive baboons usually only gain high rank after residing long enough to have mated with most of the females (Palombit 2003). This fundamental difference between the two species suggests that olive infants may require much less paternal protection against new immigrant males than their chacma counterparts.

Infants at Gombe were far more likely to be carried by their mothers' consort partners than by other males. Consort males were equally likely to carry infants against new immigrant males as against resident males, and infants were carried when new males were present in the troop as frequently as when no new males were present. Since the majority of carrying events involve a consort male carrying his potential offspring, this behavior is likely protective to some extent. However, a large proportion of these carries are against other resident males, many of which also have some estimate of paternity, and consort males and resident males both carry infants against immigrants at similar rates. It is also noteworthy that infants carried by possible fathers do not enjoy lower hazards of death compared to non-carried infants, suggesting that carrying does not confer substantial overall benefits to the infants.

In contrast, infants carried by new immigrant males suffered higher mortality than infants carried by consort and resident males. Thus, infant carrying by non-fathers likely functions as an agonistic buffer, signaling a willingness to escalate and thereby diminishing the opponent's aggression. In these situations, infants are carried into potentially dangerous altercations by non-fathers who co-opt the signal of a protective father. This possibility is supported by the tendency of new immigrants to carry infants primarily against higher-ranking opponents.

Overall, these results suggest that male motivation for carrying an infant may differ depending on his relationship to the infant and that non-fathers may wield infants as a dishonest signal of a willingness to protect that infant. Given that so many resident males carried infants to which they only had the slightest chance of kinship, there is likely a large "gray area" where males primarily "use" infants as signals rather than behave as protectors.

An alternative explanation for why infant carrying inhibits male aggression is that holding an infant communicates to the nearby father that his offspring is in danger and may thereby manipulate him into forming a coalition against the carrying male's opponent. In such a scenario, carrying provokes an honest risk to the opponent regardless of the relationship between the carrier and the infant. Further investigation is required to reveal the nuances of this complex behavior that involves both care and exploitation of vulnerable infants at the hands of the most powerful individuals in the social group.

TABLES AND FIGURES

Table 3-1: Cox regression results on infant hazard of death.
Hazard ratios (95% confidence interval) for infant exposure to immigrant males, including those that achieved top rank, infants carried by consort, resident, and immigrant males, and exposure to immigrant males, including those that achieved top rank, for carried infants only.
*Hazard ratio interpreted as exposed infant has 0.1 (10%) higher hazard of death than non-exposed infant.

Type of exposure	Hazard ratio (95% confidence interval)	p-value
Immigrant male	1.10 (0.77 - 1.56)	0.60
Immigrant male that achieved top rank	0.847 (0.64 - 1.11)	0.24
Carried by consort male	1.00 (0.84 - 1.20)	1.0
Carried by resident male	1.08 (0.95 - 1.23)	0.25
Carried by immigrant male	1.26 (1.04 - 1.53)	**0.018**
Carried infants only		
Immigrant male	2.7 (0.65 - 11.3)	0.17
Immigrant male that achieved top rank	3.50 (0.84 - 14.64)	0.09

Figure 3-1: Immigrant male exposure and the probability of infant survival.

Probability of infant survival to first birthday given exposure to new immigrant males (HR = 1.10 (0.77 – 1.56), p = 0.60).
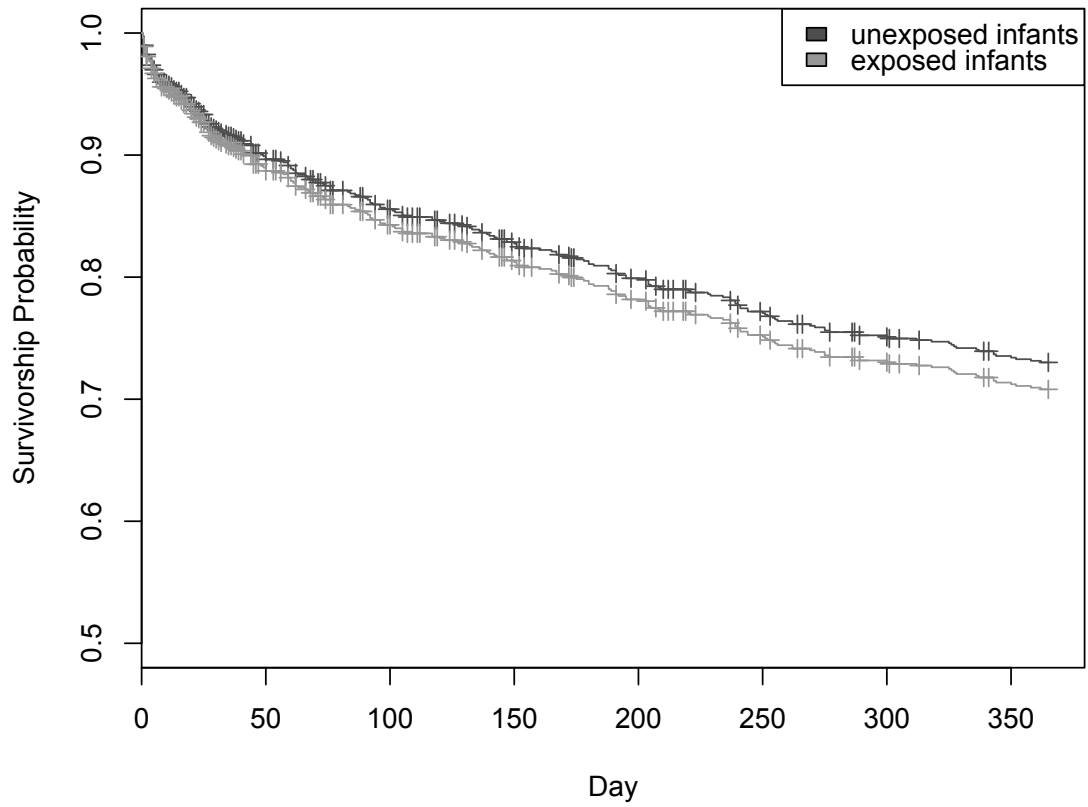
Figure 3-2: Comparison of infants carried by consort vs. non-consort males.
The proportion of infant-male dyads in which the infant was carried by a
male that had vs. had not been observed consorting with the carried
infant's mother (consort vs. non-consort). Infants were placed in dyads
with all current group males present that were also present at conception.
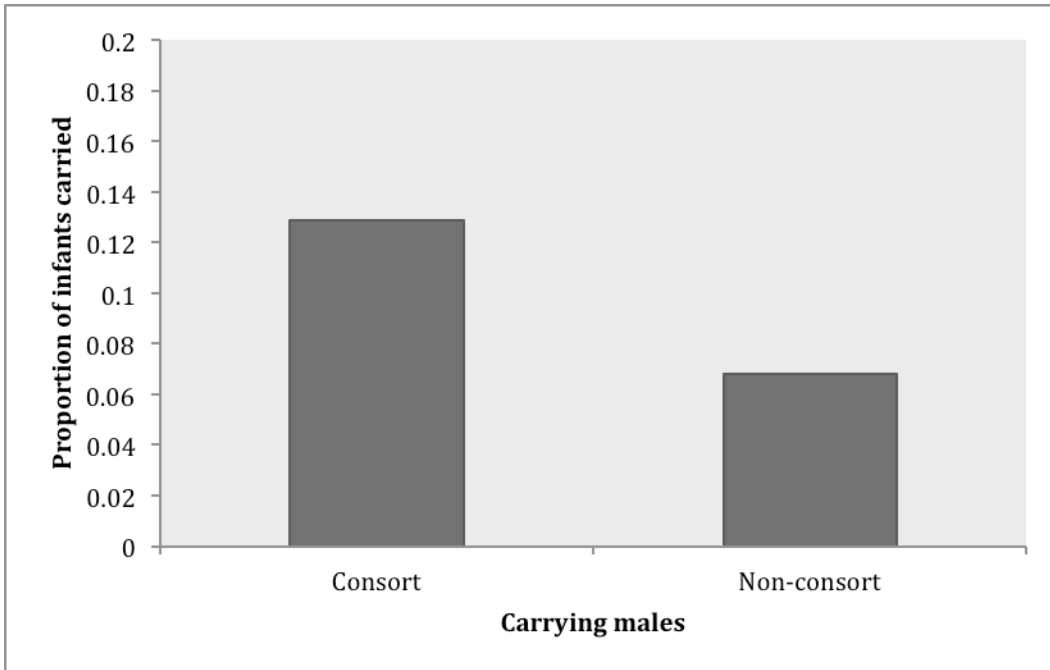
Figure 3-3: Comparison of A) the number and B) proportion of infant carries based upon male and opponent type.

A) The number of infant carries against consort, immigrant, and resident males by males observed in consortship with the carried infant's mother (consort males), resident males not seen in consortship (resident males), and males not present at conception (immigrant males). B) The proportion of total infant carries against consort, immigrant, and resident males by consort and resident males (immigrant males were only observed carrying infants once in observations in which both male identities were known; n.d. = insufficient data).

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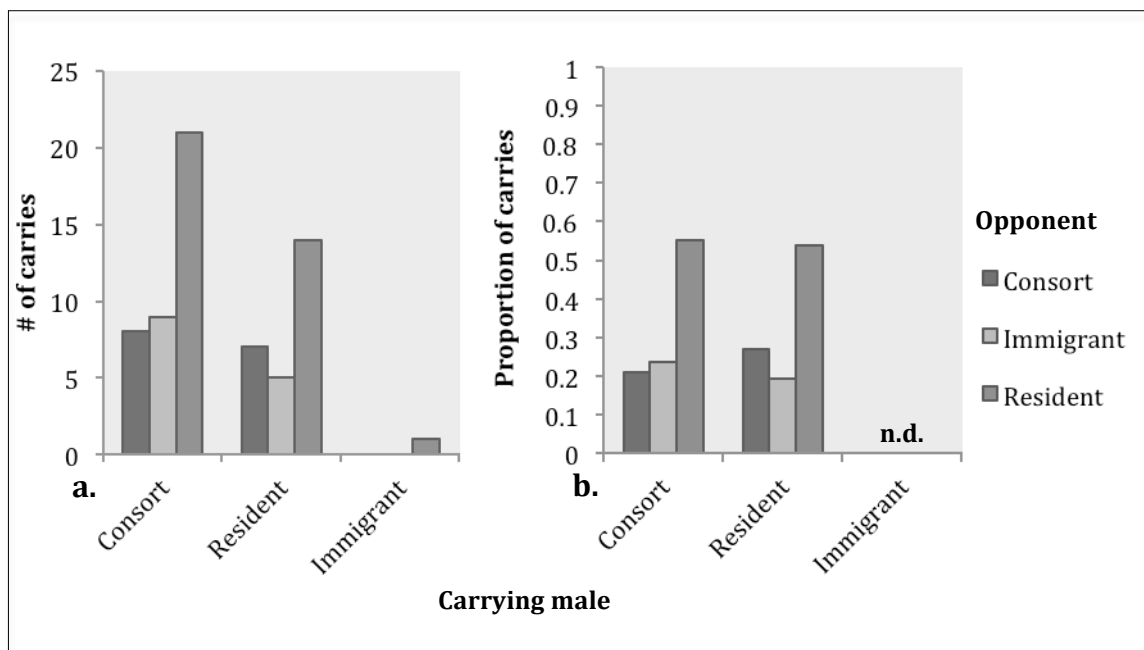
CONCLUSIONS

This dissertation addresses mechanisms by which female reproduction can be constrained by aggression from conspecifics and counterstrategies females may or may not employ. Chapter 1 suggests that pregnant female baboons utilize a color signal to reduce the amount of aggression they receive from non-kin female group members and hints at the possible role of kin and fathers. Chapter 2 shows that the role of kin may, in fact, be limited, and that superior, rapidly-ascending immigrant males are a large driving force in miscarriage patterns, especially in high-ranking females. Chapter 3 goes on to show that immigrant males as a whole, though apparently not infanticidal, still pose a risk to female reproduction by exploiting infants during contests with other males, ultimately increasing the hazard of death for those infants.

As expected, these findings raise a number of important questions for future research. Though the use of visual signals is well document across animal taxa (Baker and Parker 1979; Cooper and Greenberg 1992; Andersson 1994; Caro 2005; Clutton-Brock and McAuliffe 2009), this research highlights two relatively unexplored signal patterns: the adaptive use of color to signal pregnancy in a social mammal and the utilization of juveniles to communicate aggressive intent. The former suggests risks to pregnant individuals may be considerably higher and more widespread than originally believed and that, therefore, mammals may have developed a wide variety of strategies, including yet-to-be-recognized signals spanning different modalities, to mitigate these costs. The latter introduces a potential complexity to social interactions that involve the use of "living tools" to communicate intent. Chimpanzees utilize their environment as part of aggressive displays, shaking branches and pounding on trees (Goodall 1986; Nishida *et al.* 1998; Muller and Wrangham 2004). Elephants throw dirt and pull trees from their roots (Poole and Granli 2011). However, the use of conspecifics in agonistic displays appears relatively rare (Kitchen *et al.* 2009). Chapter 3 hypothesized the communicative intent of infant carrying amongst male baboons, but this signal still remains poorly understood and merits systematic investigation of the message such behavior conveys.

Chapter 2 highlights an important nuance in male reproductive strategy, suggesting fetal loss in response to a new male may be more prevalent than originally believed simply because it may be a strategy employed by a select few. This chapter also re-emphasizes the importance the environment plays in reproductive patterns and intimates its ability to mask patterns, accentuating our need for long-term studies in wild populations.

In this dissertation I aimed to identify the distinct ways intragroup aggression affects female reproductive output and how females mitigate these costs. Not only did this work highlight key factors that influence the survival of fetuses and infants in a social mammal, but it also suggested how such patterns may be widespread and, therefore, unexplored, across mammalian species.

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