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Costs of reproduction in a long-lived female primate: injury risk and wound healing

Elizabeth A. Archie · Jeanne Altmann · Susan C. Alberts

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Summary Reproduction is a notoriously costly phase of life, exposing individuals to injury, infectious disease, and energetic trade-offs. The strength of these costs should be influenced by life history strategies, and in long-lived species, females may be selected to mitigate costs of reproduction because life span is such an important component of their reproductive success. Here, we report evidence for two costs of reproduction that may influence survival in wild female baboons—injury risk and delayed wound healing. Based on 29 years of observations in the Amboseli ecosystem, Kenya, we found that wild female baboons experienced the highest risk of injury on days when they were most likely to be ovulating. In addition, lactating females healed from wounds more slowly than pregnant or cycling females, indicating a possible trade-off between lactation and immune function. We also found variation in injury risk and wound healing with dominance rank and age: Older and low-status females were more likely to be injured than younger or high-status females, and older females exhibited slower healing than younger females. Our results support the idea that wild nonhuman primates experience energetic and immune costs of reproduction and they help illuminate life history trade-offs in long-lived species.

Keywords Aging · Social status · Ecoimmunology · Lactation · Reproductive effort

Introduction

Reproduction can be dangerous and energetically costly, exposing individuals to physical harm, infectious disease, and reduced immunity (Hamilton and Zuk 1982; Gustafsson et al. 1994; Nordling et al. 1998). The degree to which individuals tolerate these costs is thought to be influenced by life history strategies (Stearns 1992). For instance, in short-lived, fast-reproducing species, individuals are predicted to tolerate high risks and strong trade-offs during reproduction because such species maximize fitness by investing in current reproductive opportunities and discounting future opportunities. However, in long-lived, slow-reproducing species, individuals should experience strong selection to mitigate costs of reproduction that compromise survival (Stearns 1992; Rolff 2002; Zuk and Stoehr 2002).

Within this framework, long-lived female mammals represent an interesting group because female mammals exhibit several adaptations that may help mitigate the high costs of reproduction. Gestation and lactation are energetically demanding and may often constrain the resources that females can devote to maintenance or immunity (Gittleman and Thompson 1988;

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E. A. Archie (✉)
Department of Biological Sciences, University of Notre Dame,
137 Gavin Hall, Notre Dame, IN 46556, USA
e-mail: earchie@nd.edu

E. A. Archie · J. Altmann · S. C. Alberts
Institute of Primate Research, National Museums of Kenya,
Nairobi, Kenya

J. Altmann
Department of Ecology and Evolutionary Biology,
Princeton University, Princeton, NJ 08544, USA

J. Altmann
Department of Veterinary Anatomy and Physiology, University of
Nairobi, Chiromo Campus, Post Office Box 30197, 00100 Nairobi,
Kenya

S. C. Alberts
Department of Biology, Duke University, Durham, NC 27708, USA

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Konig et al. 1988; Clutton-Brock et al. 1989; Festa-Bianchet 1989; Houdijk 2008). However, female mammals also often have stronger immune responses than males (Zuk and McKean 1996; Moore and Wilson 2002; Nunn et al. 2009), and during pregnancy and lactation, females often eat more or higher-quality foods, store fat as an energy reserve, and increase their metabolic efficiency, alleviating some of the intense energetic costs of reproduction (Dufour and Sauther 2002). To date, the extent to which the energetic costs of female reproduction in long-lived mammals create trade-offs with other energetically expensive activities is relatively unknown (but see Graham et al. 2010).

Here, we test for costs of reproduction in a long-lived, slow-reproducing primate. We do so using a 29-year data set of natural injuries from the wild Amboseli baboon population in Kenya (Alberts and Altmann 2012). Among long-lived species, female baboons represent a useful system for testing energetic and immune costs of reproduction because so much is known about their reproductive physiology. Baboons live in multimale, multifemale social groups and reproduce year-round. In Amboseli, females reach menarche at around age 4.5 and usually have their first birth by age 6 (Charpentier et al. 2008). Gestation lasts 6 months and is followed by approximately 12 months of lactation if the infant survives. Female baboons lead long reproductive lives, typically producing one infant about every 2 years into their early twenties (Altmann 1983; Altmann et al. 2010). Baboons should be sensitive to costs of reproduction that jeopardize survival as about 50 % of the variation in their lifetime fitness is explained by variation in life span (Altmann and Alberts 2003; Cheney et al. 2004).

We focus on two costs of reproduction that may influence female survival: injury risk and delayed wound healing. Injury risk is linked to mortality risk in a range of species (e.g., Wilson 1992; Chilvers et al. 2005). Wound healing is sensitive to energetic reserves and reflects inflammatory and cell-mediated aspects of innate immunity (Martin 1997; Singer and Clark 1999). Experimental studies of mice and humans have shown that wound healing can be altered by social circumstances, stress, and life history strategies (e.g., Kiecolt-Glaser et al. 1995; Padgett et al. 1998; Glasper and DeVries 2005; Martin et al. 2006a; Martin et al. 2006b). Similar research in natural populations is challenging, especially when researchers are constrained to noninvasive methods (Archie 2013). However, despite these challenges, wound healing has important functional consequences for animals: If animals fail to recover efficiently from injuries, they are likely to experience higher risk of bacterial or viral infection, higher predation risk, and problems acquiring resources (Glass et al. 1988; Wilson 1992; Marucha et al. 1998; Rojas et al. 2002; Demas et al. 2011; Archie 2013).

Predictions For injury risk, we predicted that females would be wounded more often during ovarian cycling than during pregnancy or lactation. Males typically engage in mate guarding of females during ovarian cycling, placing cycling females at the center of male-male competition and potentially making them a focus of female-female competition as well (Wasser and Starling 1988; Huchard and Cowlishaw 2011; Cheney et al. 2012; MacCormick et al. 2012). Furthermore, a previous study on wound incidence in female baboons in Gombe, Tanzania, found that females were more likely to be wounded during ovarian cycling than at other times (MacCormick et al. 2012). We further predicted that low-ranking females would experience higher rates of injury than high-ranking females, because low-ranking females would be more often the target of aggression from other group members. In addition, we predicted that injury risk would be elevated during periods of group fission, i.e., when a baboon social group permanently divides into two or more smaller groups. Fissions have occurred six times during the course of the study, and a group fission may last from weeks to several months, potentially resulting in periods of high social tension (Van Horn et al. 2007). We predicted that injury rates would not change systematically with age, group size, or season, but we included these variables in our analyses of injury risk because many aspects of physiology and life history in mammals, and Amboseli baboons in particular, are sensitive to age, social density, and season (Bulger and Hamilton 1987; Altmann and Alberts 2003; Altmann et al. 2004, 2010; Gesquiere et al. 2008; Bonenfant et al. 2009; Gesquiere et al. 2010).

Our predictions for wound healing stemmed from previous research showing that the energetic and immune costs of reproduction can slow wound healing in vertebrates, although such data are rare (reviewed in Archie 2013). To date, the strongest evidence comes from work in tree lizards, where females experience suppressed wound healing during vitellogenesis, which is the phase of egg production with the highest energetic costs (French and Moore 2008). The magnitude of these costs is sensitive to reproductive effort and energetic resources; female lizards experienced the most severe delays in wound healing when they were subjected to restricted diets or to experimentally elevated reproductive effort (French et al. 2007a, b). The energetic costs of reproduction in female baboons, too, are considerable and may be difficult to mitigate. After birth, females bear the double burden of milk production and of carrying infants, which they do almost constantly for the first 2 months of life, over average daily distances of 8–10 km (Altmann and Samuels 1992). Females continue to carry their infants intermittently until they are 8 months or older, by which time they may weigh 15 % of their mother's body mass (Altmann and Samuels 1992). The costs of lactation and infant carrying appear to be partly met by metabolizing body tissues, which in turn delays future reproduction; lactating females weigh less than cycling females, and lactating females with the lowest body masses take longer to achieve their next conception (Bercovitch 1987).

Given these intense energetic demands, we predicted that females would experience slower healing during lactation (Bercovitch 1987; Clutton-Brock et al. 1989; Altmann and Samuels 1992). We also predicted that older females would heal more slowly than younger females, because older females are expected to tolerate higher costs during reproduction because of their declining reproductive value (Williams 1966; Stearns 1992). Moreover, age has well-known negative effects on immune function, and human females commonly experience suppressed wound healing in old age (Ashcroft et al. 2002; Routley and Ashcroft 2009; Emmerson and Hardman 2012). With respect to social status, we predicted that high-ranking females would heal more rapidly than low-ranking females because they spend less time carrying their infants and are less likely to be interrupted while feeding (Post et al. 1980; Altmann and Samuels 1992; Barton 1993). As with injury rate, we predicted that wound healing would not change systematically with group size or with season, but we included these variables in our analyses of injury risk because previous research in mammals has shown that healing can be sensitive to social circumstances and season (reviewed in Archie 2013).

Materials and methods

Study subjects

Study subjects were wild adult female baboons living the Amboseli ecosystem in Kenya. Since 1971, the Amboseli Baboon Research Project (ABRP) has been collecting continuous, individual-based data on the members of several social groups (Alberts and Altmann 2012). The baboons are individually known, and several types of data are collected throughout the year by full-time; experienced observers during half-day observation visit two to three times per week per group. To maximize consistency and minimize differences in interobserver reliability, almost all data are collected by three permanent, full-time field assistants, who have been collecting data at ABRP for 32, 26, and 19 years, respectively, and who typically confer on wound healing status and other aspects of wound monitoring. Relevant to this study, observers collected information on the incidence and recovery from naturally occurring injuries, as well as a variety of data on life history and social relationships (Alberts and Altmann 2012).

Observations of injuries

The injuries in this study were observed between 1982 and 2011. They were not clinical diagnoses; instead, observations were collected noninvasively by watching the animals at a distance of a few meters. Whenever a baboon displayed signs of injury (e.g., limping, bleeding from a wound), observers used an established protocol and data sheet to record the type of injury and whether it impaired the animal's locomotion. For cutaneous wounds, observers also recorded the location of the wound on the body and, whenever possible, a visual estimate of its size in centimeters. Because the data were collected noninvasively, our observations probably exclude many mild injuries.

Once an injury occurred, observers monitored its progress toward healing during subsequent visits to the animal's social group. Prior to 1991, healing was monitored every few days until the injury healed. After 1991, ABRP changed its methods, and all injuries were systematically monitored on the last observation day of each month. Consequently, prior to 1991, observers updated records on average once every 5 days, while after 1991, these records were updated on average every 14 days. Because we could not measure healing in a controlled setting, we utilized healing metrics that focused on functional consequences to animals—specifically, wound closure, which reduces risk of infection, and individual mobility, which addresses an individual's ability to obtain resources and keep up with the group. Hence, cutaneous wounds were considered "healed" when a scab was no longer visible on the wound site, leaving only healed skin or scar tissue. In cases where the injury impaired locomotion, an individual was considered healed when it was no longer limping.

Measuring predictor variables

We tested whether the incidence of injury and healing rates was predicted by female reproductive state and several other variables, including the following: (1) the female's age at the time she was injured, (2) her dominance rank at the time she was injured, (3) her group size, (4) whether she lived in a wild-feeding group or in a group that foraged part-time at the refuse pit of a nearby tourist lodge, (5) whether the female's social group was experiencing a permanent group fission, and (6) the season in which the injury was observed. Here, we briefly describe data collection on each of these variables (see Supplementary methods for more details).

Reproductive state For most analyses, females were assigned to one of the three reproductive states: ovarian cycling, pregnancy, or lactation as defined in Altmann (1973), Wildt et al. (1977), Shaikh et al. (1982), Beehner et al. (2006), and Gesquiere et al. (2007). In one analysis, we also tested whether cycling females experienced the highest risk of injury during the putative period of ovulation in each cycle (i.e., the 5-day period prior to deturgescence of her sexual swelling), termed the periovulatory period (Gesquiere et al. 2007). Data on each female's reproductive state were recorded on each observation day, based on the color of her paracallosal skin, characteristics of her sexual swelling (e.g., turgescent vs deturgescent and visual estimates of swelling size), and the presence of menstrual bleeding. This near-daily tracking allowed us to assign reproductive state on the day she was seen injured with high confidence (see Supplementary methods for more details).

Age For 93 % of the subjects (215 of 231 females), we knew their birth dates within a few days and could calculate their ages accordingly. The remaining 16 females were born prior to the initiation of observations, and so, their ages were estimated. Most had ages that were estimated to be accurate within 1 year (N=9), and the remaining had ages estimated to be accurate within 2 (N=2), 3 (N=4), or 4 years (N=1).

Dominance rank Dominance ranks were assigned on a monthly basis using agonistic interactions recorded as part of the regular observation visits as described in Hausfater (1975). We constructed dominance matrices where each female was assigned an ordinal rank ranging from 1 (the highest rank) to n, where n was the number of adult females in the female's group. In modeling the effects of dominance rank, we used both ordinal and proportional dominance ranks. Proportional ranks (sometimes called relative ranks) are commonly used in the literature to address the problem that ordinal rank is somewhat collinear with group size (i.e., the lowest ordinal ranks can only occur in the largest groups). Proportional rank was calculated as a female's ordinal rank divided by the number of adult females in the group. Proportional ranks range from near 0 to 1, with high-ranking females holding the smallest proportional ranks (e.g., ordinal rank 1 in a group of 10 represents a proportional rank of 0.1).

Group size and foraging condition We tested whether group size (the number of adult males and females present in the group) created a density effect. Group size is known from near-daily censuses of all group members conducted during each observation visit. In addition, 14 % of injuries were observed in females living in a group that sometimes foraged at a refuse site at a nearby tourist lodge. Because this supplemented feeding might influence healing, we also included feeding regime (wild-feeding or lodge-feeding) in our models of healing rates.

Group fission Since 1982, six of our study groups have experienced natural, permanent fission events, where the group divided from one stable social group into two groups (Van Horn et al. 2007). Fissions are sometimes accompanied by high rates of conflict and may lead to injuries. Fission events were defined as described in Van Horn et al. (2007). The effect of group fissions was modeled as the presence or absence of a fission event on the date the injury was incurred.

Season Season can influence wound healing (Martin et al. 2008). Amboseli experiences a predictable, 5-month dry season from June through October when the ecosystem receives no rain and when food and water are relatively scarce. In the remaining 7 months of the year (November through May), the ecosystem receives highly variable amounts of rain (yearly average=350 mm, range=141–757 mm).

Multivariate analyses of the incidence of injury

Analyses of incidence were based on 707 observations of injuries incurred by 160 of 231 adult females studied over the 29-year period. To test which variables predicted the risk of injury, we built generalized linear mixed models (GLMMs) in *R*, using the lme4 package. Prior to constructing models, we tested for colinearity among predictor variables; no such correlations were detected. The risk of injury was modeled on a monthly basis for each female using a binomial error structure. For the analysis of the effects of the periovulatory period, the risk of injury was modeled on a daily basis considering only cycling females, and days were assigned as either inside or outside the periovulatory period. For all models, female identity and year were included as random factors. For the models of injury risk, we attempted to enter the following variables into the model: female reproductive state, age, dominance rank (proportional or ordinal, depending on the model), group size, group foraging condition, group fission status, and season. We also tested for interaction effects between group size and rank and between reproductive state and either rank or age. For all analyses, we chose the "best" model (i.e., the one that provided the best fit to the data) by sequentially dropping the parameter with the highest P value and testing for significant improvement via likelihood ratio tests.

Multivariate analyses of variation in healing rates

We tested predictors of healing rates using a subset of 501 injuries observed in adult females. This data set was smaller than the total number of injuries observed since 1982 because we excluded some injuries where our estimate of the time to heal was especially poor. These included injuries where the animal died or disappeared shortly after the injury occurred (N =33), injuries composed of mixed types, making it difficult to measure the time to heal for any single injury (N=35), and injuries where observers missed one or more monthly observations prior to the injury being marked as healed (N=138). These exclusions were not skewed toward any particular female reproductive state, rank, or age. In the final set of 501 injuries, there were 71 cases that were right-censored, i.e., recent injuries in that had not healed by the final observation.

We used Cox proportional hazard models to test whether any of our predictor variables were significantly associated with time to heal, controlling for differences in injury type (limps, punctures, slashes, and amorphous wounds) and differences in monitoring frequency. Cox proportional hazard models use a nonparametric approach that depends on the ranks of event times, not their numerical value, making this approach robust to uncertainty in event times and variation in the underlying hazard function (Allison 2010). Each model was stratified by the study period (before or after 1991, when we changed monitoring frequency). We attempted to enter the following variables into the model: female reproductive state, age, dominance rank (proportional or ordinal depending on the model), group size, group foraging condition, group fission status, and season. We also tested for significant interaction effects among reproductive state and rank or age. We constructed models by sequentially dropping parameters with the highest *P* value and testing for significant improvement in the model via likelihood ratio tests. Proportional hazard models produce hazard ratios, which can be used to understand the size of an effect. In terms of this study, hazard ratios represent the relative probabilities that baboons in a given category will heal at time *t*, compared to baboons in other categories.

In the course of our study, we found that lactation significantly predicted healing rates (see "Results" section). We tested whether observer bias or differences in injury severity could explain these results (see Supplementary methods). We found no evidence for these effects (see "Results" section).

Results

Between 1982 and 2011, we observed 707 injuries in 160 adult female baboons. Injuries included cutaneous wounds (slashes, puncture wounds, or scrapes) and limps, which impaired locomotion but had no visible wound. In our data set, females were injured about once every 2 years; the rate of observed injuries was 0.46 injuries per female per year.

Cycling females, low-ranking females, and older females experienced the highest rates of injury

Risk of injury in females was predicted by ovarian cycling, dominance rank, age, and whether the group was experiencing a fission (Table 1 and Supplementary Table 1). Cycling females were significantly more likely to be injured than noncycling (i.e., pregnant and lactating) females (Table 1 and Supplementary Table 1; Fig. 1a, b), while pregnant and lactating females experienced similar risks of injury (Supplementary Table 2; pregnant vs lactating females: β=0.21, Z=1.735, P=0.083). In addition, the risk of injury was highest in low-ranking and older females (Table 1 and Supplementary Table 1). We did not find significant interaction effects between reproductive state and either rank or age, indicating that youth and high rank were equally protective for cycling versus noncycling females.

When we modeled the effects of dominance rank using proportional rank, we did not find any additional effects of group size or significant interaction effects between proportional rank and group size (Table 1). Hence, females with similar proportional ranks in different-sized groups seemed to experience similar risks of injury (Fig. 2a). For instance, two females living in different-sized groups, each dominated by ~50 % of female group members (e.g., rank 3 of 7 or rank 10 of 21), experienced similar risk (Fig. 2a). However, when we modeled injury risk using ordinal rank, we found a significant interaction between ordinal rank and group size (Supplementary Table 2; Fig. 2b) such that females with the same ordinal rank number (e.g., rank 5) living in a small and a large group, respectively, differed in their injury risk. Specifically, a female ranked 5 in a small group experienced higher injury risk than a female ranked 5 in a large group (Fig. 2b).

Aside from rank, age, and cycling, the only other significant predictor of injury risk in females was whether her social group was fissioning into two (or three) distinct groups (Fig. 1c, d). Females were more likely to be injured during group fissions, indicating that fission events can be costly in terms of injury risk.

Cycling females faced the highest risk of injury during putative ovulation

Injuries in cycling females are thought to occur in the context of reproductive competition. Hence, we performed a second analysis of injury risk only in cycling females to test whether the daily risk of injury was highest during the periovulatory period when females are most likely to conceive. In support, we found that injury risk in cycling females was not evenly distributed across female ovarian cycles; rather, periovulatory females were about twice as likely to be wounded as females in less fertile days of their cycle (Table 2, median risk of injury

Table 1 Best supported GLMM predicting the monthly risk of injury in adult female baboons, modeling dominance rank using proportional ranks

Fixed effects	β	SE	Z	P
Age	0.047	0.011	4.492	<0.0001
Proportional dominance rank	0.606	0.187	3.246	0.0012
Reproductive state (cycling vs noncycling)	0.854	0.089	9.566	<0.0001
Fission period	1.672	0.367	4.554	<0.0001

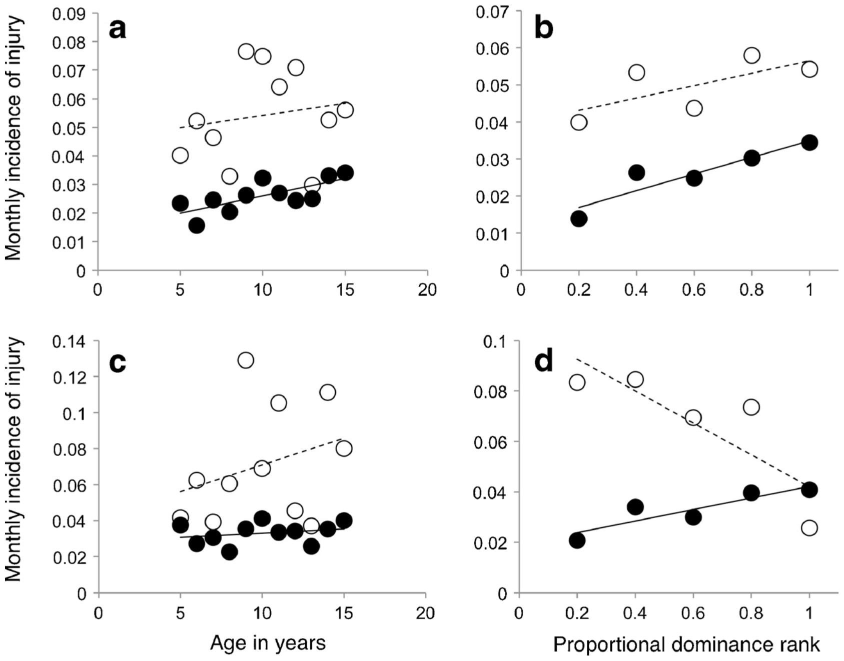

Fig. 1 Observed monthly incidence of injury in adult female baboons. Plots **a** and **b** depict the relationships between the incidence of injury and **a** age or **b** proportional dominance rank as a function of whether a female was cycling (*dashed line*) or not cycling (*solid line*). Plots **c** and **d** depict the relationships between the incidence of injury and **c** age or **d** proportional dominance rank as a function of whether the female's social group was experiencing a permanent fission (*dashed line*) or not (*solid line*). *Lines* represent linear regressions. Note that the negative relationship between injury risk and proportional rank for females during a group fission was not significant, and we found no significant interaction effect for the relationship between proportional rank and group fission

in periovulatory females=0.0030 injuries per day, median risk of injury in the rest of the cycle=0.0016 injuries per day).

Lactation and old age were associated with delayed wound healing

If the costs of reproduction create trade-offs with wound healing, or if females experience age-related delays in healing, we would expect to observe slower healing in lactating and/or older females. In support, the best Cox proportional hazard model of female healing indicated that lactation and old age were associated with delayed healing (Table 3). While we found no significant differences in healing rates between cycling and pregnant females ($\beta=-0.064$, Wald=0.262, $P=0.601$), lactating females were about 21 % less likely to heal in a given time period than nonlactating females (Table 3,

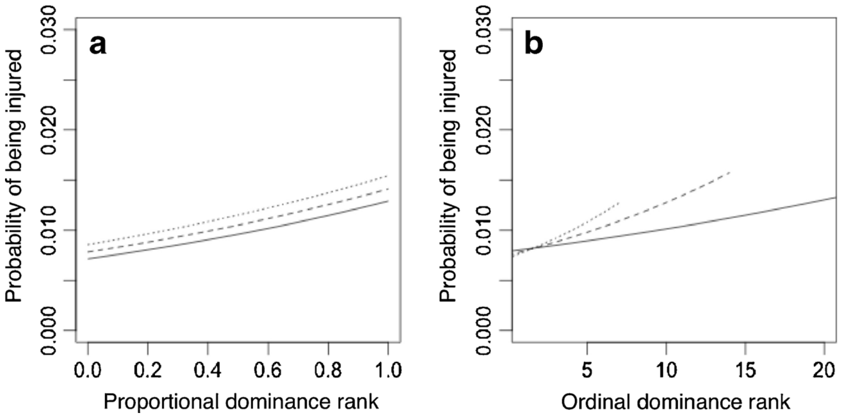

Fig. 2 Predicted probability of injury as a function of **a** proportional dominance rank and **b** ordinal dominance rank. In both plots, the *solid line* depicts the predicted relationships for a large group size of 21 females, the *medium dashed line* depicts predicted effects for a group size of 14 females, and the *fine dashed line* depicts the predicted relationship for a small group of 7 females. Plot **a** depicts fitted model values based on the parameter estimates from a GLMM including all the factors in Table 1, plus a nonsignificant term for group size ($\beta=-0.01$, $Z=-1.1$, $P=0.27$). Note that the addition of group size did not significantly improve the model in Table 1 ($\chi2=1.17$, $df=1$, $P=0.28$). Plot **b** depicts fitted model values based on the parameter estimates from the GLMM in Supplementary Table 1

Table 2 Best supported GLMM predicting the daily risk of injury in cycling female baboons

Fixed effects	*β*	SE	*Z*	*P*
Age	0.038	0.012	3.139	0.0017
Proportional dominance rank	0.545	0.224	2.432	0.0150
Periovulatory period versus other cycle phases	0.628	0.128	4.887	<0.0001

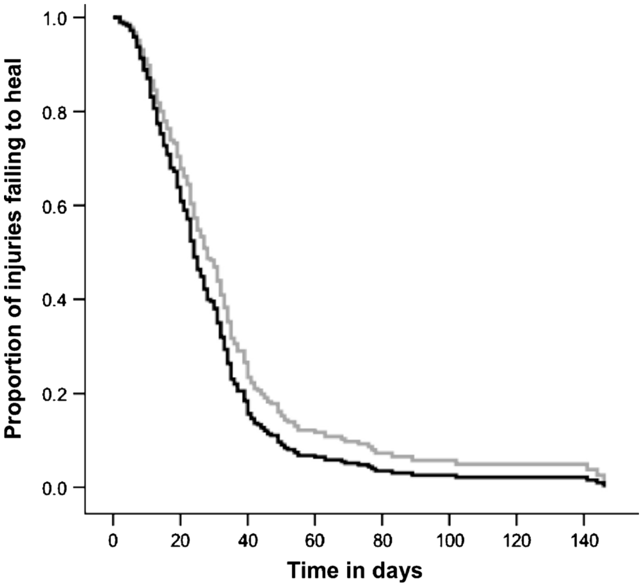

Fig. 3 Survival curves depicting the proportion of females' injuries failing to heal as a function of time in days. *Curves* shown here are derived from the set of 305 injuries observed since 1991. The *black line* represents injuries observed in nonlactating females (i.e., those who were pregnant or cycling), and the *gray line* represents injuries in lactating females. Statistics are in Table 3

Fig. 3; hazard ratio=0.786). These results were not explained by variation in injury severity; lactating females did not receive larger injuries than cycling or pregnant females ($N=75$, $F=1.00$, $P=0.373$) nor were they more likely to receive injuries that impaired locomotion ($N=501$, $\chi^2=0.19$, $P=0.910$).

Aside from reproductive state, the only other significant predictors of female healing rates were age and the type of injury; females healed from cutaneous wounds more slowly than from limps, and older females healed more slowly than younger females, indicating that females experienced immunosenescence that affected wound healing. We further tested for interactions between age or rank and reproductive state on wound healing; however, we found no evidence that youth or high rank mitigates the association between lactation and slower healing.

Discussion

Reproduction in female mammals can be dangerous and energetically costly (e.g., Gittleman and Thompson 1988; Clutton-Brock et al. 1989; Bowen et al. 2001; Stockley and Bro-Jorgensen 2011). Identifying these costs is an important step to understanding how patterns of female reproduction have been shaped by selection. Strategies that mitigate the survival costs of reproduction should be especially favored in long-lived species (Stearns 1992; Rolff 2002; Zuk and Stoehr 2002). Here, we report evidence for two costs of reproduction that may influence survival in female baboons—injury risk and delayed wound healing. Female baboons were most likely to be injured on days when they were most likely to conceive, and females experienced the slowest healing during lactation. As yet, it is unclear if these costs influence female survival, but in many species, injuries and slow healing have important functional consequences, including reduced mobility and greater risk of infection or predation (Glass et al. 1988; Wilson 1992; Marucha et al. 1998; Rojas et al. 2002; Archie 2013). Below, we discuss the implications of our results, starting with variation in injury risk.

Variation in the risk of injury

The increased risk of injury to female baboons during cycling may result from reproductive competition. Indeed, in Gombe National Park, Tanzania, female baboons were most likely to be injured during cycling as compared to lactation or pregnancy (MacCormick et al. 2012). We found the same pattern

Table 3 Best supported Cox proportional hazard model predicting the time to heal from naturally occurring injuries

Predictors	*β*	Hazard ratio (95 % CI)	Wald	*P*
Age	-0.037	0.963 (0.946-0.981)	15.463	<0.0001
Type of injury (limps, punctures, slashes, and amorphous wounds)	NA	NA	14.078	0.003
Reproductive state (lactating vs nonlactating)	−0.241	0.786 (0.633–0.975)	4.797	0.029

in Amboseli, and we further found that cycling females were most likely to be injured during the few days of their cycle when they were likely to be ovulating, as compared to days outside the periovulatory period. While it is difficult to assign direct causes to most injuries, in Gombe, causes were known for 23 injuries, and 70 % of these were attributed to adult males (MacCormick et al. 2012). Hence, interactions with adult males in the context of mate guarding or male-male competition are probably dangerous for females. However, interactions with adult females around mating may also lead to injury. Female baboons compete for access to mates and paternal investment, and cycling females, especially females with sexual swellings, are often targets of female aggression (Wasser and Starling 1988; Huchard and Cowlishaw 2011; Cheney et al. 2012). Hence, interactions with both adult males and females may lead to injuries for cycling females.

In addition to the risks of reproductive competition, we also found that older and low-ranking females experienced higher rates of injury than younger and high-ranking females. It is unclear why the risk of injury is higher in older females; one explanation is that older females take greater risks during reproduction, as predicted by their declining reproductive value (Williams 1966; Stearns 1992). However, higher rates of injury in older females may simply be a consequence of overall declines in health and resilience (Altmann et al. 2010). For instance, an older female may exhibit more severe symptoms (e.g., stiffness, limping) over a longer period, as compared to a comparable injury in a younger female, making injuries in older females more obvious to observers. In terms of social status, the observation that low-ranking females experienced higher injury risk than high-ranking females is not surprising. Prior research has shown that low-ranking female baboons receive more aggression and are less likely to receive support in conflicts than high-ranking females (Seyfarth 1976). However, one surprising feature of rank-related differences in injury in Amboseli is that in the model using proportional rank, social status predicted injury risk without an additional significant effect of group size or an interaction between proportional rank and group size. In other words, females who were dominated by a similar proportion of adult female group members experienced similar risks of injury no matter the number of females in their hierarchy. In contrast, when social status was modeled using ordinal rank, we found a significant interaction between rank and group size. Specifically, while the risk of injury was similar among females with high ordinal ranks (e.g., ranks 1–3), females with moderate or low ordinal ranks experienced relatively lower risk of injury in larger groups. This pattern suggests that rank-related differences in injury risk operate as a frequency-dependent, rather than a density-dependent process. That is, while low-ranking females in large groups have the potential to receive aggression from many more animals than low-ranking females in a small group, there are also more targets for a given dominant individual to direct aggression toward; hence, the rate of injuries probably does not vary much across individuals with similar proportional ranks. Similarly, if females receive most of their aggression from animals directly above or below them in the hierarchy, then the absolute number of animals dominating a given female may not be an important predictor of injury risk.

Variation in wound healing

Our results support the idea that the energetic costs of reproduction affect wound healing; specifically, wounds in lactating females healed more slowly than wounds in either pregnant or cycling females. Variation in wound healing is often interpreted as variation in immune function (e.g., Cohen et al. 1987; Glasper and DeVries 2005; Martin et al. 2006a; Martin et al. 2007; French et al. 2009). Indeed, efficient wound healing draws on several immune components, including inflammatory responses, cell-mediated aspects of innate immunity, and some Th2-mediated processes (Martin 1997; Singer and Clark 1999; Wynn 2004; Seno et al. 2009). However, in wild populations, differences in healing might also reflect other processes besides immunity, including variation in tissue proliferation or in social mediators of healing such as grooming, which is thought to promote wound healing (Hart and Powell 1990; Hart 2011). However, lactating female baboons receive more grooming than female baboons in other reproductive states (e.g., Silk et al. 2003); hence, it seems unlikely that grooming influences wound healing in lactating female baboons in the direction we observed.

Instead, we think that the most likely explanation for our results is that females experience reduced physical condition and energetic resources during lactation. These in turn create trade-offs with wound healing, either directly through the resources available to repair tissues or indirectly via variation in immune response. In support, prior studies have found that wound healing is sensitive to trade-offs with other immune processes and it suffers under energy restriction (de Groot et al. 2002; Martin et al. 2006b; French and Moore 2008). For instance, in female tree lizards, the energetic costs of yolk deposition in egg follicles are associated with compromised wound healing (French et al. 2007b, 2011; French and Moore 2008). The energetic costs of lactation in female baboons are quite high; in Amboseli, they include milk production in an arid environment and near-constant infant carrying for the first few months of life (Altmann et al. 1978; Altmann 1983; Roberts et al. 1985; Bercovitch 1987; Altmann and Samuels 1992; Rosetta et al. 2011). While female baboons have several adaptations to compensate for the energetic demands of reproduction (e.g., increased metabolic and foraging efficiency; Altmann 1980; Roberts et al. 1985; Silk 1986, 1987; Muruthi et al. 1991), our results suggest that these strategies are not sufficient to prevent trade-offs with wound healing. Interestingly, in male baboons, the energetic costs of reproduction do not compromise healing, and high-ranking males, who generally experience higher reproductive effort than low-ranking males, healed faster than low-ranking males (Alberts et al. 1996; Gesquiere et al. 2011; Archie et al. 2012). These results support the idea that females pay relatively higher energetic costs of reproduction than do males and/or that males have evolved mechanisms to mitigate energetic trade-offs between reproductive effort and wound healing.

If delayed wound healing in lactating female baboons is caused by energy restriction and/or reduced immunity, then our results support the idea that, even in long-lived species, females may experience costs of reproduction that influence survival. To date, most evidence for such trade-offs come from relatively short-lived species that exert reproductive effort over intense breeding seasons (Ots and Horak 1996; Nordling et al. 1998; Ardia 2005; French and Moore 2008; Cox and Calsbeek 2010). However, there is mounting evidence that the costs of reproduction also create considerable trade-offs for long-lived species. For instance, high levels of autoantibody responsiveness in sheep are linked to lower reproductive rates (Graham et al. 2010). In common eiders, females experience reduced adaptive immunity during incubation (Hanssen et al. 2005). Finally, in wild and domesticated ungulates, females experience a well-known increase in susceptibility to gastrointestinal nematode parasitism at the onset of lactation, which is probably caused by protein deficiency (Festa-Bianchet 1989; Houdijk 2008; Jones et al. 2011; Sakkas et al. 2011). Hence, long-lived species may often be forced to balance the energetic costs of reproduction against other energetically intensive activities that promote survival.

In addition to the effects of reproduction, we also found age-related effects on wound healing, such that older females healed more slowly than younger females. If these differences in wound healing are caused by differences in immune function, then they comprise evidence for immunosenescence (Nussey et al. 2012, 2013). Wound healing commonly declines with age in humans and lab animals. In women, declining levels of sex steroids, especially estrogen, are often cited as the primary driver of slower wound healing with age (Routley and Ashcroft 2009; Emmerson and Hardman 2012). Specifically, the reduction in sex steroids that occurs as a consequence of menopause is associated with higher inflammation and less effective macrophage activation. Estrogen replacement therapy can partially reverse the effects of menopause on wound healing (Emmerson and Hardman 2012). Interestingly, female baboons in Amboseli do not experience age-related declines in estrogen or progesterone (Altmann et al. 2010). Hence, the age-related delays that we observed in wound healing occurred in the absence of declines in these hormones. This result suggests that other age-related changes in immunity can delay wound healing, even without changes in sex steroids.

In sum, we found multiple social, physiological, and life history factors that predicted injury risk and wound healing in female baboons. Conflict during reproductive competition led to elevated rates of injury, and the energetic costs of lactation may create trade-offs with wound healing. These costs are mitigated or exacerbated by social status and age, and older females appear to pay substantially higher costs than younger females in terms of injury risk and immune function. In the future, it will be interesting to learn whether these costs influence survival, especially whether females who engage in extraordinary reproductive effort lead shorter lives. Our results contribute to a growing understanding of the costs of reproduction in long-lived species.

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Data accessibility Data sets on observations of injuries and rates of wound healing will be deposited in Dryad (http://datadryad.org/).

Ethical standards All protocols were noninvasive and adhered to the laws and guidelines of Kenya (Kenya Research Permit numbers NCST RRI/12/1/SS011/1543 to EAA, NCST 5/002/R/777 to SCA, and NCST 5/002/R/776 to JA). All protocols were approved by the Animal Care and Use Committees at the University of Notre Dame (13-030), Duke University (A0840903), and Princeton University (1689).

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