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Original Article

Male and female aggression: lessons from sex, rank, age, and injury in olive baboons

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Aggression is ubiquitous, influencing reproduction through inter- and intraspecific effects in ways that reflect life-history strategies of species. In many social mammals, females remain in their natal group for life, whereas males emigrate and compete for rank in other social groups. Competition for rank is inherently risky. Therefore, it has long been hypothesized that risks of injury depend on an individual's sex, rank, and age in ways that maximize an individual's reproductive output. However, studies quantifying such risks have been lacking. We analyzed 20 years of long-term data on wounds among olive baboons (*Papio anubis*) in Gombe National Park, Tanzania. Males received significantly more wounds than female baboons, and both sexes received the most wounds at ages when they competed most intensely for rank. Immature females received more wounds than immature males in their natal groups, and immature females were more likely to be wounded by females than were immature males. Males in their natal group were wounded less often than immigrant males of the same age. The risk of wounding did not depend on rank in females but rose with rank in immigrant males. Lastly, females received significantly more wounds when cycling (not pregnant or lactating). This study is among the first to quantify the risk of injury for competitors of different sexes, ages, and ranks in social groups. Our results support the prediction that individuals target aggression toward present and future competitors and suggest that sexual coercion increases the risk of wounding in cycling females. **Key words:** competition, injury, life history, olive baboon, *Papio anubis*, rank. [*Behav Ecol* 23:684–691 (2012)]

INTRODUCTION

Competition and sex are inextricably linked. This linkage broadly spans taxa and affects the very structure and evolutionary dynamics of species. In social species, the relationship between competition and sex depends on such factors as reproductive strategies of the sexes, age and social rank of individuals, and the life history of the species. Studies of related phenomena include primates (Clutton-Brock and Harvey 1977; Muller and Wrangham 2009), birds (Wiley 1974; Arcese 1989), rodents (Dobson 1982; Edelman 2011), carnivores (Bekoff et al. 1984), ungulates (Andersen et al. 2000), insects (Kemp and Alcock 2003), and arachnids (Ulrich and Henschel 1999). However, comparatively few studies have directly quantified the risks of competition by linking competition with the incidence of physical wounding. Social mammals, specifically primates, provide an excellent system to explore this question because of differences between the sexes that apply to many social mammalian species; females remain in their natal group

for life (i.e., “female philopatry”), whereas males immigrate into preexisting groups at puberty (i.e., “male-biased natal dispersal”) (Packer 1979a; Greenwood 1980; Dobson 1982; Waser and Jones 1983).

In many female-philopatric species, female rank is largely determined by birth order and maternal rank (Kawamura 1958; Koford 1963; Koyama 1967; Cheney 1977; Holekamp and Smale 1991). In contrast, male rank rises or falls according to the outcome of pairwise interactions between males that reflect the competitor's body size and physical condition (Hausfater 1975; Packer 1979b; van Noordwijk and van Schaik 1988; Haley et al. 1994; Pelletier and Festa-Bianchet 2006). High-ranking males have preferential access to females in many social mammalian species with dominance hierarchies (e.g., LeBoeuf 1974; Clutton-Brock et al. 1982; Moore et al. 1995; Constable et al. 2001; Alberts et al. 2003; Natoli et al. 2007; Altmann et al. 2010). However, individuals in their natal group often show reduced sexual attraction toward close kin (Packer 1979a; Pusey 1980; Bolhuis et al. 1988; Simmons 1991; Manson and Perry 1993; Sterck et al. 2005). Thus, males typically do not engage in intra-sexual competition for females until dispersing to new groups (Packer 1979a; Pusey and Packer 1987). As physical condition declines with age, older male baboons rely less on direct confrontation with high-ranking peers to obtain mating opportunities and instead adopt alternative strategies such as forming

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coalitions with other subordinate males and cultivating relationships with individual females (DeVore 1965; Packer 1977; Smuts 1985; Bercovitch 1986, 1988; Noë and Sluiter 1990; Alberts et al. 2003). Thus, direct aggressive competition is often most intense between young, high-ranking immigrant males (Packer 1979b; Yoccoz et al. 2002; Mainguy and Côte 2008).

Competition among females generally involves access to resources rather than mates (Trivers 1972). Female per capita reproductive success often declines with increasing group size (van Noordwijk and van Schaik 1999 [macaques]; Packer et al. 2000 [olive baboons]; Altmann and Alberts 2003 [*Papio* spp.]). Thus, infant females often represent future competition for adult females, whereas infant males will eventually disperse to compete elsewhere. Therefore, adult females are expected to employ behaviors that limit the survival of unrelated juvenile females, though documented examples of adult females selectively harassing immature females remain rare (for toque [*Macaca s. sinica*] and bonnet [*Macaca radiata*] macaques, e.g., Dittus 1979; Silk et al. 1981).

Studies of intersexual aggression suggest that males are the predominant aggressor and disproportionately wound females (Muller and Wrangham 2009). Smuts (1985) found that female olive baboons were the targets of male aggression approximately once every 17 h. Adult male olive baboons are formidable opponents, and males are approximately twice as large as females and have canines about a third longer and wider than females (Virgadamo et al. 1972). Male olive baboons are also formidable relative to other animals. Male baboons have canine teeth whose relative size can exceed those of felids, and primates in general can have canine teeth that are as long as carnivores, relative to their body size (Lucas 1982; Plavcan and Ruff 2008). Females may be at greater risk of wounding during particular times if their reproductive state (e.g., cycling, consorting with males, etc.) alters their frequency and/or type of interactions with males. Olive baboons are one of many species that exhibit sexual dimorphism; therefore, the potential costs of mating are of particular interest given the disparities between male and female body size and weaponry and the potential for males to monopolize and sexually coerce females (Clutton-Brock and Parker 1995; Muller and Wrangham 2009).

Agonistic interactions between individuals inevitably involve risks of physical injury (Clutton-Brock et al. 1979; Blanchard et al. 1988; Drews 1996). Aggressive encounters are potentially the most costly between young adult males that are fully grown and have not yet worn down their weapons (Packer 1979b). Yet, measuring the costs of agonistic interactions in natural populations is difficult (Smuts BB and Smuts RW 1993; Mitani et al. 1996). In this paper, we analyze the age-, sex-, and rank-specific risks of wounding in a long-term field study of olive baboons (*Papio anubis*) in Gombe National Park, Tanzania, to test the following hypotheses: 1) If wounding differs between sexes, males should receive more wounds than females. 2) If wounding differs among individuals of different ages, males should receive most wounds during ages that correspond to times when males compete most intensely for dominance rank and receptive females; females should receive most wounds when their rank is first determined as juveniles. 3) If competition, dominance rank, and wounding are linked, rank should predict wounding for males because male dominance rank is determined by direct competition. Note, we do not expect to see a clear relationship between wounding and rank in females because once a female's rank is established, it remains relatively stable for life, reducing female–female competition, and because injuries from males could potentially obscure any possible effect of rank on risk of wounding. 4) If female injuries are inflicted by sexual coercion, adult females should receive most wounds when they are cycling.

METHODS

Study area and population

Gombe National Park, Tanzania, is comprised of a chain of steep valleys flanked by Lake Tanganyika to the west and a rift escarpment to the east (van Lawick-Goodall 1968; Packer 1979a). A total of 671 male and 471 female baboons from 12 different groups (hereafter “troops”) have been studied since 1967; demographic data have been recorded daily since 1972 (Packer et al. 1998).

Wounding and dominance data

Data on wounding and dominance rank are available from January 1983 to November 2001. Tanzanian field assistants collected all data under the supervision of D.A.C. with assistance from A.B. “Wounds” are defined as gashes, cuts, or punctures of the skin. Monthly reports provide details on the date and number of wounds for each baboon and indicate the cause of wounding when witnessed (93 of 2078 cases of wounding). In addition to monthly reports, daily demographic records also note the number of fresh wounds. Analyses where the sex of the attacker is known, and those assessing sexual coercion, are done separately for the number of wounding events and the number of wounds received in a year. “Wounding events” are defined as the occurrence of one or more wounds on a single day. A distinction is drawn between annual wounding events and the annual number of wounds because the likelihood of receiving a wounding event versus several wounds at once may vary for individuals of different sexes, ages, and ranks. An individual may receive many wounds in a single aggressive encounter or may receive few wounds in multiple aggressive encounters over the course of several different days. In all other analyses, wounding was scored as a binary outcome (yes/no) for every individual, for each year of the study.

Injuries typically persisted for weeks or months, although the act of wounding was rarely observed. Contact with humans is minimal at Gombe: all study troops have restricted home ranges in the center of the national park and are completely isolated from local villagers. Human contact was limited to the Jane Goodall Institute research staff, Tanzania National Park staff, tourists, and itinerant local fisherman. All staff were strictly prohibited from harassing the baboons, and tourists must maintain a distance of at least 10 m from wildlife. Although human-caused injuries were recorded, they were easily identifiable (e.g., by gunshot, snare) and extremely rare: only 10 cases out of 2078 wounding events. Of these 10 wounds, 3 baboons were killed after humans had been attacked, 2 were injured after stealing food and destroying property, 2 were injured after stealing fish from fisherman, 1 was shot by park rangers, and the remaining 2 were injured for unknown reasons. Although, chimpanzee-inflicted wounds can be similar to baboon-inflicted wounds, the Gombe chimpanzees are subject to such intensive observation that chimpanzee attacks on baboons are well documented and could be excluded from the analysis. Although present in Gombe, leopards are rare: In more than 20 years of daily field observations, there is no definitive evidence of a leopard attack on either olive baboons or chimpanzees (Wilson et al. 2004; Gombe Stream Research Center, unpublished data). Wounds caused by accidents (e.g., falling from a tree) were typically described as scrapes, swelling of limbs, and limping. To minimize the inclusion of such injuries, we only included wounds that involve a break in the skin, cut, or puncture in the total data set of 2047 wound events. Thus, the vast majority of injuries in our analysis could be inferred to have resulted from bites by conspecifics.

Annual dominance ranks were determined by the outcomes of pairwise interactions involving displacements from food

Table 1

The number of injured females and the total number of wounds recorded for cycling (i.e., menstruating, with or without sexual swellings, consorting), pregnant, or lactating females

	Cycling	Pregnant	Lactating
Wound events			
Adolescent females	35	2	1
Adult females	252	38	105
Total	287	40	108
Expected wound events			
Adolescent females	9.9	9.9	18.2
Adult females	103.0	103.0	188.9
Total	113.0	113.0	207.1
Wound counts			
Adolescent females	64	2	2
Adult females	432	72	170
Total	546	74	174
Expected wound counts			
Adolescent females	17.7	17.7	32.5
Adult females	175.8	175.8	322.3
Total	193.6	193.6	354.9

Analyses were conducted separately for adult (>7 years of age) and adolescent (females that had reached menarche but were ≤6 years of age) females. Expected ratios for each of the categories were calculated according to average duration of time females spend in each reproductive state: 6 months of cycling, 6 months of gestation, and 11 months of lactation. Please note that the 35 of adolescent female cycling wound events are the sum of the following categories: flat ($N = 10$), sexual swelling ($N = 21$), consort ($N = 1$), and menses ($N = 3$). The 252 adult female cycling wound events are the sum of the following categories: flat ($N = 116$), sexual swelling ($N = 108$), consort ($N = 20$), and menses ($N = 16$). The 64 adolescent female cycling wound counts are the sum of the following categories: flat ($N = 13$), sexual swelling ($N = 45$), consort ($N = 2$), and menses ($N = 4$). The 432 adult female cycling wound counts are the sum of the following categories: flat ($N = 217$), sexual swelling ($N = 159$), consort ($N = 35$), and menses ($N = 22$).

sources or overt aggression. Summaries of these interactions consistently revealed linear rankings where the top-ranking male/female dominated all other like-sexed individuals in his/her troop, the second ranking male/female dominated the remainder, and so on. Each individual's annual numerical rank was converted to a "relative rank" by finding $D/(N - 1)$, where D = the number of like-sexed animals dominated by that individual and N = number of like-sexed individuals in that troop that year. Thus, top-ranked individuals would have relative ranks of 1.0, whereas bottom-ranking individuals would have 0.0. These scores were sorted into 5 categories: 0.0–0.199, 0.2–0.399, 0.4–0.599, 0.6–0.799, and 0.8–1.0.

Female reproductive state

To address when females were at greatest risk of injury, we noted both the number of injured females and number of wounds to females that were cycling, pregnant, or lactating. Note that the visual assessment of the presence of a sexual swelling when females are sexually receptive could be imperfect, especially during times of transition between reproductive stages. Therefore, the "cycling" category consisted of females that 1) had sexual swellings, 2) were consorting with males (this occurred when females also had sexual swellings), 3) did not have obvious sexual swellings but were neither lactating nor pregnant, and 4) were menstruating (there were comparatively few females in this category, see Table 1). We then calculated an expected ratio of injured females and wounds according to the typical time females spent in each reproductive state: the interbirth interval is about 23 months, including

approximately 6 months of cycling, 6 months of gestation, and 11 months of lactation. Female olive baboons reach menarche around 4–5 years of age, and cycle until approximately 23 years of age, when their fertility declines and eventually ceases around 24 years of age (Smuts and Nicholson 1989; Packer et al. 1998). Females included in the female reproductive state analysis were between 3 and 22 years of age. Analyses were conducted separately for adult (>7 years of age) and adolescent females (females that had reached menarche but were ≤6 years of age) because females typically reach menarche and then cycle for about 1–2 years before their first pregnancy (i.e., "adolescent sterility") (Smuts and Nicholson 1989).

Statistical Analysis

Annual wounding rates were scored repeatedly (up to 21 consecutive years for some animals) for 887 individuals and analyzed using generalized linear mixed models (GLMMs) with a binomial error distribution and with individual identity fitted as a random effect. All models included a compound symmetric correlation structure, which assumed that all observations within individuals were equally correlated on average. Models were estimated with adaptive Gaussian quadrature with parameters estimated from maximum likelihood, and significance of effects was determined by an approximate z -test.

We used piecewise linear splines to test for nonlinear effects of age (as measured in discrete 1-year increments) on the probability that an individual was wounded in a given year. Piecewise splines consist of a covariate (e.g., age) defined over specified segments (e.g., > and <4 years old) and a response variable (wounding) that is a continuous function of the covariate over all segments, but with different slopes in each segment (Marsh and Cormier 2002). Each line segment does not have its own intercept; rather, a spline regression model includes only a single intercept that is adjusted by the spline variable to accommodate a change in slope. This keeps the regression line continuous (i.e., no breaks) even as the regression line pivots to change direction at the points (knots) where the segments join. We used splines to identify the threshold age beyond which the probability of wounding abruptly changes, similar to the way knot location is used in epidemiology to identify "the threshold value of a risk factor for which the probability of disease occurring suddenly changes" (Bessaoud et al. 2005, p. 2).

To determine the presence and position of age-specific thresholds in wounding, we evaluated a set of competing GLMMs for each of 3 demographic classes: female, natal male, and immigrant male. Each set included models with a single knot placed at 6–10 different ages (females 3–12 years; natal males 2–7 years; immigrant males 6–15 years) and a model with no knot, representing the hypothesis of no threshold in wounding. We selected knots a priori according to the age distribution of each demographic class, which was consistent with guidelines for the efficient use of knots (Wold 1974; Eubank 1984). By definition, knots selected a priori are fixed (i.e., not random variables) and are therefore not estimated as parameters in models. We created variables containing a linear spline for age with the MKSPLINE command in STATA 10.1. The variables were constructed so that the estimated coefficients measure the slopes for each segment before and after a given knot.

We conducted all analyses in STATA 10.1 and compared GLMMs using information-theoretic statistics (Burnham and Anderson 2002). Our scope of inference concerned the population, so we performed model selection using marginal likelihoods. The most parsimonious model was the one with the lowest Akaike information criterion (adjusted for small sample, AIC_c) and smallest ΔAIC_c . ΔAIC_c equals the AIC_c

for the model of interest minus the smallest AIC_c for the set of models being considered. The best model has a ΔAIC_c of zero, and models with $\Delta AIC_c < 2$ are plausibly the best. We calculated population-averaged fitted values from best fit GLMMs by deriving marginal expectations of the responses averaged over the random effects but conditional on the observed covariates. We also used likelihood ratio statistics to test specific hypotheses among nested models, and results were considered significant at $P < 0.05$.

To minimize effects of small sample size at advanced ages, we restrict the analysis to ages where the sample size exceeded 20 individuals. Thus, the maximum age for females was 23 years, the maximum for natal males was 9 years, and the age of immigrant males ranged from a minimum of 4 years to a maximum of 20 years.

RESULTS

Context of wounding

Wounding was observed at the time it occurred in 93 of 2078 wound events. Of the wounds of known cause, 66% were due to bites from other baboons ($N = 62$), 14% to attacks by chimpanzees ($N = 13$), 11% to attacks by humans ($N = 10$), and 9% to accidents (e.g., falling from a tree, $N = 8$). Wounding was not observed in the remaining 1985 wound events; however, human-caused injuries were both easily identifiable (i.e., a gunshot or snare) and, moreover, were likely to be rare due to very limited contact between humans and baboons. The Gombe chimpanzees were subject to far more intensive observation than the baboons; thus, the percentage of chimpanzee-inflicted wounds was likely an overestimate (see METHODS). All baboon wounds known to be caused by chimpanzees, humans, or accidents were excluded from subsequent analyses leaving a total of 2047 wound events in the data set. Male baboons were wounded more often (wound events where an “event” is a 24-h day: males $N = 1197$, females $N = 850$) and received more wounds overall than females (wounds: males $N = 1440$, females $N = 1063$).

Wounding for all analyses was scored as a binary outcome. This is a conservative measure as approximately 65% of all wounded baboons suffered exactly 1 wound event per year. Of ranked individuals that received 2 or more wound events per year, females received similar proportions of wounding events for all rank classes, whereas the highest quintile of males suffered the most wounding events per year (39%).

The sex of the attacking baboon was known for 44 of the 62 observed baboon-inflicted wounding events; the identity was known for 42 of 62 events, where 21 injured baboons were male and 23 were female. With the exception of one case where a mother wounded her son, these 21 males were wounded only by other males. On the other hand, the 23 females were wounded by both males ($N = 16$) and females ($N = 7$). For individuals < 6 years of age, females were more likely to be wounded by females (4 of 8 cases) than were males (1 of 9 cases) ($P = 0.02$, binomial test with $p = q = 4/8$). The relatively small number of total female injuries in the < 6 years of age class may be attributed to stochasticity in a small sample size.

Age versus rank

The sex-specific relationship between dominance rank and age confirmed prior studies of this same population (Packer et al. 1995). Specifically, an intercept-only model provided the best fit ($\Delta AIC_c = 0.00$) to the female data ($N = 155$ ranked females), indicating that rank was constant across all ages in females. The next best model ($\Delta AIC_c = 1.71$), which included a linear term for age, was not significantly different from the intercept-only model ($\chi^2 = 0.33$, degrees of freedom [df] = 1, $P = 0.57$,

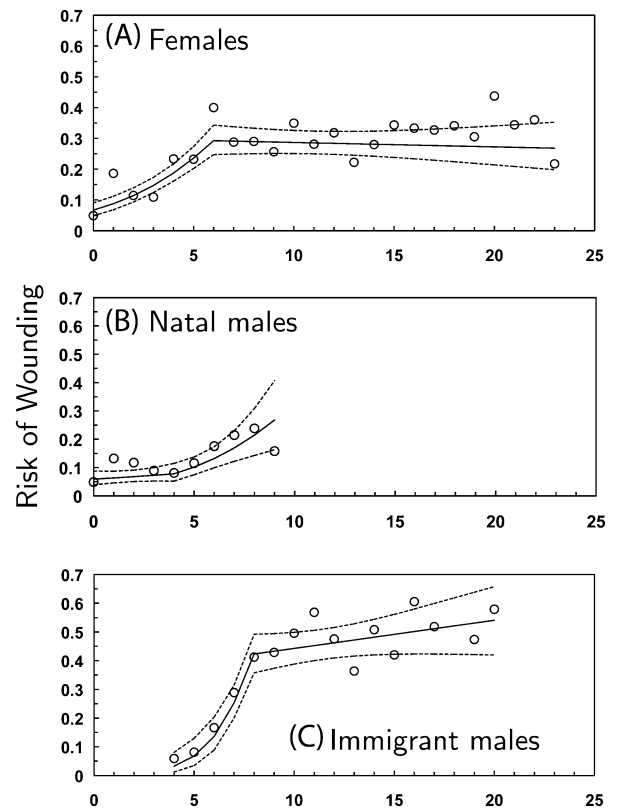


Figure 1

Age-specific risk of wounding for (A) female, (B) natal male, and (C) immigrant male baboons. The number of individuals in each analysis is (A) 327, (B) 300, and (C) 260. Solid lines are population-averaged fitted values from best fit GLMM models, with dotted lines indicating pointwise 95% confidence intervals. The estimated coefficients before and after each spline knot are (A) 0.29 ± 0.04 ($P < 0.001$) and -0.01 ± 0.02 ($P = 0.63$); (B) 0.07 ± 0.07 ($P = 0.31$) and 0.29 ± 0.09 ($P = 0.001$); and (C) 0.77 ± 0.13 ($P < 0.001$) and 0.04 ± 0.03 ($P = 0.13$). Circles are observed frequencies across individuals within each age class and are provided merely as a visual aid; analyses were performed on the raw binary data.

Supplementary Material). None of the spline models fit the female data well ($\Delta AIC_c \geq 3.00$). By contrast, spline models with knots at age 9 and 10 provided the best and second best ($\Delta AIC_c = 1.11$) fit, respectively, to the immigrant male data ($N = 192$ ranked immigrant males), indicating that immigrant male rank peaks at age 9–10. Models with knots at ages < 9 and > 10 performed poorly ($\Delta AIC_c > 14.00$, Supplementary Material). Before 9 years of age, the rank of immigrant males increased with age (slope = 0.75 ± 0.09 , $P < 0.001$); after 9 years, immigrant male rank declined with age (slope = -0.18 ± 0.02 , $P < 0.001$).

Wounding versus age

The annual risk of wounding changed with age for all 3 age–sex classes. For females, the best model is given by a change in slope at 6 years of age: before the age of 6, risk of injury increased by 34% per year; thereafter, risk does not significantly change with age (Figure 1A, Supplementary Material). Models of female wounding with knots before or after age 6 did not perform well ($\Delta AIC_c > 3.50$). For males in their natal troop, the best model is given by a change in slope at 4 years of age: risk of injury is constant before the age of 4 and risks increased by 34% per year thereafter (Figure 1B, Supplementary Material). However, models of natal male wounding with either no knot or knots at 3, 5, and 6 years of age also performed well

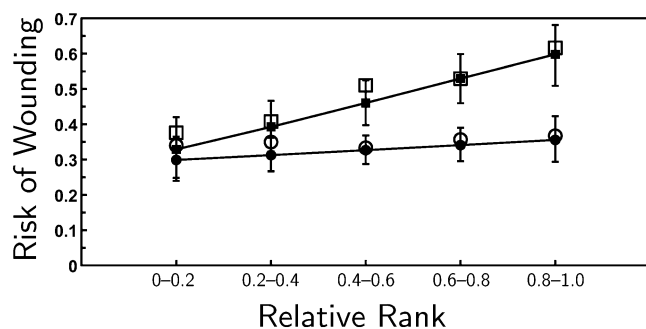


Figure 2

Relationship between relative rank and the risk of wounding for males (squares) and females (circles). Open symbols are observed frequencies across individuals with each rank and are provided as a visual aid; analyses were performed on the raw binary data. Solid symbols are fitted values with 95% confidence intervals from a GLMM model.

($\Delta AIC_c < 2.00$), indicating substantial uncertainty about the presence and location of any age-specific change in the risk of injury for natal males. For immigrant males, the best model is given by a change in slope at 8 years of age: risk of injury more than doubles each year from 4 to 8 years and is constant thereafter (Figure 1C, Supplementary Material). The next best model of immigrant male wounding included a knot at age 9 years ($\Delta AIC_c = 2.56$), whereas models with knots at ages <8 or >9 years did not score well ($\Delta AIC_c > 6.00$).

Immature individuals: males and females

For all injuries in animals less than 6 years of age, females ($N = 291$ individuals) were nearly twice as likely to be wounded each year as same-aged natal males ($N = 300$ individuals) (odds ratio = 1.91 ± 0.33 , $P < 0.001$).

Males: immigrants versus natal males

For all injuries in males between 4 and 9 years of age, immigrants ($N = 177$ individuals) were 70% more likely to be wounded each year than same-aged natal males ($N = 148$ individuals) (odds ratio = 1.70 ± 0.42 , $P = 0.03$). Note that this analysis is based on a total of 264 individuals. Of these, 61 males were measured both as natal and immigrant males, having transferred from one study troop to another.

Wounding versus rank

The risk of wounding each year was constant across female rank categories (odds ratio = 1.07 ± 0.06 , $P = 0.26$, $N = 155$ ranked females ≤ 23 years old; Figure 2) but increased by 32% for each rank quintile in immigrant males (odds ratio = 1.32 ± 0.09 , $P < 0.001$, $N = 192$ ranked immigrant males 4–20 years old) (Figure 2).

Sexual coercion

Adult and adolescent females were far more likely to be wounded and received the most wounds while cycling than when they were pregnant or lactating (Table 1, $N = 433$ wounded females; $N = 742$ wounds, chi-square test, adult females' wound events $\chi^2 = 294$, $df = 2$, $P \ll 0.001$; adult females' number of wounds $\chi^2 = 507$, $df = 2$, $P \ll 0.001$; adolescent females' wound events $\chi^2 = 86$, $\chi^2 = 64$, $df = 2$, $P \leq 0.001$; adolescent females' wound counts $\chi^2 = 163$, $df = 2$, $P \ll 0.001$).

DISCUSSION

Life-history theory posits that individuals will employ reproductive strategies to maximize the number of offspring. Classical examples of extremes in life-history strategies are semelparous species that reproduce once and then die versus iteroparous species that reproduce periodically throughout a longer lifetime (Stearns 1976). This is not restricted to animals. For example, perennial plant species can develop long-lived roots and stems as investments for repeated seed crops, each crop of moderate size, whereas annuals spend all the year's accrued energy in a single large seed crop. The extremes can be thought of as long-term versus short-term reproductive strategies. Between the extremes, life histories can be categorized by means and variances of parameters such as ages of first and last reproduction, juvenile and adult survival, and fertility (Oli and Dobson 2003). They are also conveniently summarized as varying degrees of "capital" versus "income" strategies (Stephens et al. 2009), where they often apply to stores of nutrients and body tissues but can also apply to behaviors.

Life-history strategies are evolutionary responses to the pervasive problem of maximizing reproductive success. They become particularly complex in social animals such as primates, where they can manifest as dominance hierarchies and persistent agonistic behaviors. Agonistic behaviors may seem maladaptive because injuries can reduce reproductive success. Yet, aggressive behavior can be evolutionary adaptive if the risk of injury is countered by benefits such as preferential access to resources and/or mates, immediately or in the future. Despite recognition that life-history theory and its evolutionary origins can influence agonistic behaviors, empirical studies are few, and studies quantifying the risks of aggressive behavior are largely theoretical (Smuts BB and Smuts RW 1993; Clutton-Brock and Parker 1995).

In olive baboons, 2 life-history strategies are female philopatry and male dispersal. Females remain in their natal group for life, whereas males immigrate into preexisting groups at puberty. Juvenile females largely inherit their place in the dominance hierarchy by acquiring a rank similar to that of their mother. Once established, a female's rank remains relatively stable for life. In contrast, male olive baboons disperse to new troops as juveniles and obtain and maintain their position in the dominance hierarchy via direct competition between males. The ability of rank to predict reproductive success varies among different species of social animals (Pusey et al. 1997). Smuts (1987) noted a positive relationship between high rank and reproductive success in many cercopithecine primates, and a study by Pusey et al. (1997) found that high-ranking female chimpanzees have "higher infant survival, faster maturing daughters, and more rapid production of young." However, both Smuts (1987) and Pusey et al. (1997) note that this is not true of all social mammals, citing a possible trade-off between the benefits and costs of high rank (Pusey et al. 1997).

In olive baboons, high-ranking females have shorter inter-birth intervals (Smuts and Nicholson 1989). However, no relationship was found between a female's dominance rank and infant survival, adult female mortality, or sex ratio at birth (Smuts and Nicholson 1989). In contrast, high-ranking male olive baboons father significantly more offspring, likely because they are better able to compete for and monopolize estrous females (Packer 1979b). These studies suggest that male reproductive success may be more tightly coupled to their position in the dominance hierarchy because higher rank affords greater access to mates in males. For these reasons, males are hypothesized to compete intensely for rank and access to females, whereas females are hypothesized to compete most aggressively when females first establish rank as

juveniles and are predicted to be the target of injury via sexual coercion from males.

The findings of our study have direct counterparts in life-history theory and its evolutionary origins. Immigrant males suffered more wounds than same-aged natal males. A male baboon's initial attempts to transfer into a new troop are often met with intense aggression by the new troop's resident males (Packer 1979a; Packer and Pusey 1979; Henzi and Lucas 1980; Cheney and Seyfarth 1983; van Noordwijk and van Schaik 1985; Zhao 1994). These new immigrants not only represent increased competition for resources and mates they may also be infanticidal (Palombit 1999), creating high fitness stakes for residents. Once wounded, transferring males may briefly return to their natal troop before attempting to immigrate again (Packer 1979a). This period of dispersal corresponds to an increased risk of wounding for natal males above 4–5 years of age. Immigrant males that have already dispersed are wounded most often. Among immigrant males, the highest ranking males suffer approximately twice as many wounds as the lowest ranking males. Interestingly, the highest risk of wounding was at 8 years of age, although males typically attain the highest rank of their life at 9 years of age. That suggests that young males are at the greatest risk of injury when they first begin competing for top rank, not when they actually attain the highest rank of their life.

The subset of our data where the sex of the attacker was known is relatively small (21 injured males and 23 injured females), and we would like to have more data for the light it would shed on differences in aggression by sex. Nonetheless, 70% of observed injured females were wounded by males. Sexually cycling females suffered by far the most wound events and the most wounds of any reproductive stage, suggesting that increased interactions with males during periods of sexual receptivity account for the disproportionate risks of wounding. Dominance rank does not appear to influence the risk of wounding for females, a result that is somewhat surprising given that prior studies of primates and other social mammals indicate subordinate females often receive more aggression (Seyfarth 1976; Silk et al. 1981; Clutton-Brock and Parker 1995; Perry 1996; Clutton-Brock et al. 2006) and are supported less often in agonistic encounters (Prud'Homme and Chapais 1993; Silk et al. 2004) than high-ranking females. This result may be due to the fact that females establish rank prior to reaching adulthood (Cheney 1977), and female hierarchies often remain stable for prolonged periods decreasing the need to maintain rank through intense aggression.

Males are wounded more often than females at most ages, and immigrant males are wounded most often. For females, most wounds occur in juveniles prior to the onset of menarche. Beyond adolescence (6 years of age and up), there is little relationship between wounding and dominance in females. However, data on wounds to females during different reproductive stages did provide a way to quantify the potential costs of mating, and there is a strong relationship between cycling females and wounding, supporting the sexual coercion hypothesis. These findings suggest that increased interactions with males when females are sexually receptive account for the disproportionate number and frequency of wounds to females. This result is particularly striking because the cycling stage is short, less than one-third of all reproductive stages combined.

Our findings are consistent with the predictions based on olive baboon life-history patterns and social structure. Females invest more heavily in parental care; therefore, females are the limiting sex. As such, males are predicted to, and do, compete more intensely for access to females. This is evident by the greater frequency and severity of wounds received by males. The fact that female rank is largely inherited—something competition can do little to change—and dominance hierar-

chies are relatively stable reduces the need for competition among females. This may be an evolutionary adaptation to enhance reproductive success in species where infant survival depends heavily on the consistency of maternal care.

Asymmetries in male–male versus female–female aggression cross the boundaries of taxa, possibly reaching even to humans. Studies of human females suggest that women tend to engage in aggressive behavior and competition less than men (Campbell 1999). A common theme among mammals is that females provide the majority of parental care (Clutton-Brock 1991). Given the benefits of a stable dominance hierarchy which reduces the need for competition, a greater investment in parental care, and a possible evolutionary adaptation toward self-preservation for the sake of higher infant survival, it is somewhat unsurprising that female olive baboons are wounded less frequently and with less severity than males and have a life-history strategy that helps ensure that. Moreover, in more than 20 years of field observations, competition among females was a low-level, more chronic occurrence than that of male–male agonistic interactions (Gombe Stream Research Center, unpublished data). These observations are consistent with the patterns of wounding observed in this study. Wounds are fairly evenly distributed across all female rank classes. From an evolutionary adaptive standpoint, the smaller female body size and unexaggerated weaponry further suggest that competition and the ability to fight are not of paramount importance for females. Indeed, the opposite is important, the ability to avoid fighting and maintain continuous intervals of parental care.

In contrast, male dominance hierarchies are more dynamic than that of females, owing to the influx of immigrant males and the movement of adult males between troops. The lack of stability in dominance hierarchy perpetuates the need to frequent competition to establish and reestablish the order of male rank. A less stable dominance hierarchy; the continual influx of new males; females as a limiting resource; more formidable weaponry; a greater link between male reproductive success, rank, and access to females; and perhaps a greater ability to adopt a more cavalier attitude toward survival beyond mating (as infant survival depends less on paternal care) all promote male competition that is of greater frequency and intensity than that of females.

In some species, life-history strategies and reproductive strategies are one and the same. In primates, life-history strategies (e.g., female philopatry and male dispersal) and reproductive strategies are intertwined. Baboons and other social mammals do not employ a single such strategy. In olive baboons, competition between males for increased rank represents a long-term capital breeding strategy—an immediate risk of injury in exchange for possibilities of future breeding. Concomitantly, coercive attempts by males consorting with receptive females are a short-term income breeding strategy, with immediate risks of injury providing the possibility of immediate breeding success. In contrast, the largely inherited dominance hierarchy of females is more representative of a different breeding strategy entirely. Female reproductive success depends heavily on females surviving in good condition to give parental care and therefore aggression is less favored altogether. Thus, the diametric breeding strategies of olive baboons both maximize reproductive fitness but in different ways with respect to competition and wounding; the males' strategies tolerate wounds whereas the females' strategy avoids them.

This empirical study has provided some connections between the dual themes of behavior and life history in a primate species. What may seem to be idiosyncratic primate behavior, studied for its subtle intricacy and fascinating complexity, resides within a life-history perspective as a special case in the general theme of organic reproduction and evolution, applying broadly across taxonomic groups from animals to plants.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

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