Beyond infant death: the hidden costs of male immigration in geladas

India Schneider-Crease [a, b, *], Kenneth L. Chiou [a], Noah Snyder-Mackler [a], Thore J. Bergman [c, d], Jacinta C. Beehner [c, e], Amy Lu [b]

[a] Department of Psychology, University of Washington, Seattle, WA, U.S.A.
[b] Department of Anthropology, Stony Brook University, Stony Brook, NY, U.S.A.
[c] Department of Psychology, University of Michigan, Ann Arbor, MI, U.S.A.
[d] Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, U.S.A.
[e] Department of Anthropology, University of Michigan, Ann Arbor, MI, U.S.A.

ARTICLE INFO

The experience of traumatic events can catalyse physiological trade-offs that increase the vulnerability of organisms to disease and death. Among potential sources of trauma, the arrival of new males in female-philopatric species may be particularly salient due to the accompanying threat of infanticide. In such social systems, the killing of dependent offspring benefits these new males by accelerating females' return to receptivity. Despite widespread interest in the evolutionary drivers of infanticide, there is little known about the collateral effects of male immigration on other group members. That is, do the periods following male immigration act as 'windows of adversity' that carry costs for group members over and above the direct victims of infanticide? Here, we examined how the immediate aftermath of new male immigration in a female-philopatric species (*Theropithecus gelada*) was related to the risk of injury for all individuals. Analysing 139 injuries and 41 male immigration events across 9 years of data collection, we found that male immigration was accompanied by increases in injury risk for all natal individuals (adult males were excluded from the analysis), with the most severe effects for dependent infants and lactating females. Females with injuries had longer interbirth intervals, highlighting the reproductive consequences of injury. This study is among the first to quantify costs associated with male immigration beyond infant mortality and highlights that these periods can act as windows of adversity that may affect lifetime health and fitness outcomes.
© 2019 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Exposure to adversity can have negative consequences for lifetime health and fitness (Shonkoff et al., 2012; Tung, Archie, Altmann, & Alberts, 2016). Sources of adversity can range from the environmental (e.g. famine) to the social (e.g. abuse), and consequences can include increased mortality, decreased fecundity and disruption of psychosocial development (Lindström, 1999; Champagne, 2010; Fagundes et al., 2013; O'Rand & Hamil-Luker, 2005; Tung et al., 2016). The mechanisms that have been proposed to underlie the relationship between adversity and lifetime health centre on the dysregulation of core physiological processes, including the development of the immune system, DNA methylation and the activity of the hypothalamic—pituitary—adrenal (HPA) axis (reviewed in Fagundes et al., 2013). Elucidating these mechanisms has important implications for understanding the

interplay between environmental and social factors and animal behaviour, and requires identifying a model system in which individuals are regularly exposed to adverse events as a feature of their social structure or ecological niche.

In female-philopatric species, in which females remain in their natal groups and males disperse, the risk of experiencing adversity may be tied to the immigration of new adult males into stable groups. For species with high paternity certainty and prolonged lactation periods, males can attempt to kill unrelated fetuses (feticide) or infants (infanticide), and thereby hasten the return of amenorrheic females to receptivity (van Schaik & Jansen, 2000; Bellemain, Swenson, & Taberlet, 2006; Ebensperger, 1998; Hausfater &Hrdy 2017; Hrdy, 1974, 1977; Lewison, 1998; Knörnschild, Ueberschaer, Helbig, & Kalko, 2011; Packer & Pusey, 1983; Palombit, 2015; Zipple, Roberts, Alberts, & Beehner, 2019). The arrival of new males can also elicit pregnant females to spontaneously abort in certain taxa (Bruce, 1959; reviewed in; Zipple et al., 2019). This phenomenon, known as the 'Bruce effect', has been observed in voles, lemmings, hamsters, mice, rats, gerbils,

* Correspondence: I. Schneider-Crease, Department of Psychology, 119A Guthrie Hall, Box 351252, University of Washington, Seattle, WA, 98195, U.S.A.
E-mail address: indiaaugusta@gmail.com (I. Schneider-Crease).

marmots, dogs, lions, primates, zebra and domestic sheep and horses (Zipple et al., 2019). Premature termination of pregnancy is hypothesized to increase female reproductive success given the likelihood of eventual infanticide in these species. Thus, male immigration can pose an enormous threat to infants and pregnant females across taxonomic groups.

However, little is known about how male immigration affects individuals over and above the effects of sexually selected aggression. These periods may be generally chaotic, introducing novel stressors that may affect all group members. Indeed, the arrival of new males is associated with elevated glucocorticoid hormones (indicators of stress) in some species, such as chacma baboons, *Papio ursinus* (Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2005; Engh et al., 2006) and geladas, *Theropithecus gelada* (Tinsley Johnson, Snyder-Mackler, Lu, Bergman, & Beehner, 2018). Individuals engaged in energetically expensive processes, such as somatic development (infants), gestation (pregnant females) and lactation (adult females), should be particularly vulnerable to these stressors. If take-overs have negative consequences for individuals other than infants killed during infanticide, then these periods may act as major stressors with far-reaching lifetime effects.

Geladas, cercopithecine primates endemic to the Ethiopian highlands, provide a useful system in which to investigate the collateral consequences of male immigration. Take-overs and infanticide are common, with males competing for near-exclusive reproductive access to groups of related females (the reproductive unit; hereafter 'unit') (Beehner & Bergman, 2008; Snyder-Mackler, Beehner, & Bergman, 2012). These closed units provide males with high paternity certainty (Snyder-Mackler et al., 2012), increasing selection pressure for infanticide. Using 9 years of near-continuous data collected on a habituated gelada population, we assessed whether take-overs expose individuals other than the known victims of infanticide to adversity. Observing an impact of take-overs beyond infanticide would position geladas as a useful model for examining the impact and mechanisms of adversity.

Using this long-term data set on gelada injury, take-overs and infanticide attempts, we sought to examine two specific aims. First, we examined (Aim 1) the association between take-overs and injury across demographic categories to investigate whether the occurrence of take-overs in geladas increases the risk of physical injury for all group members. Second, we assessed (Aim 2) the relationship between injuries and interbirth interval length in adult females to investigate whether injuries arising from take-overs, and thus take-overs themselves, have direct fitness costs for affected females.

METHODS

Study Site and Overall Data Set

Our data come from a population of wild geladas inhabiting the Simien Mountains National Park, Ethiopia (13°10′60″N, 38°4′0″E, 3200 m above sea level). The Simien Mountains Gelada Research Project has collected near-daily data on 413 individuals since 2006, including 41 take-overs across 34 units between January 2008 and September 2017. Injuries were recorded ad libitum by observers and were defined as the novel and acute presence of an open wound, dislocated or ostensibly fractured limb, or limp or restricted mobility indicating new physical damage (Fig. 1). Recorded injuries spanned a range of severity, and the instance of injury was rarely observed. We excluded pathologies likely to be associated with illness, such as parasitic cysts or rashes. Injuries were only counted (presence/absence) in the first month that they were observed (even if the injury lasted longer than a month) to ensure that each occurrence was counted only once. Because the most severe

injuries probably resulted in death, and were not observed, we also compiled data on these deaths across the study population for separate analyses. Deaths for natal individuals (females and males of juvenile age and younger) were assigned based on sudden disappearances as these individuals are highly unlikely to leave their natal groups.

Ethical Note

All research followed the ASAB/ABS Guidelines for the use of animals in research, was approved by the University Committee on the Use and Care of Animals at the University of Michigan (UCUCA protocol number 09554) and followed all laws and guidelines in Ethiopia. All data were collected observationally, and observers never interacted with animals, even in the case of injury.

Aim 1 Data Set

We assembled our data set on the level of the month because exact dates of injuries were often unknown. We excluded adult males because their regular emigration from study groups following take-overs biases against observing injuries. Our complete injury data set included 13 951 'individual-months' (i.e. all months that each study individual was alive and observed) from natal individuals (i.e. infants, juveniles, adult females). Of the 413 individuals in the total data set, 251 were female and 162 were male. We observed 139 injuries and 131 deaths of natal animals over the study period, including three cases in which an injury was followed by a death within the same month. This data set included 157 adults, 49 juveniles and 61 infants. Fourteen injuries occurred in the same month as a take-over, with four observed on the same day as a take-over and the remaining 10 observed in the weeks following a take-over. While we cannot say with absolute certainty that the four injuries that occurred on the same day as the observed take-over followed the take-over, we think this is the most parsimonious explanation as there was no other observed event (e.g. predation attempt, rockfall) that could account for the sudden appearance of four injuries in the same group.

Because reproductive state may affect the likelihood that adult females are targeted by new males, we conducted an additional analysis focusing exclusively on adult females. For each individual-month, we assigned females the reproductive state (i.e. cycling, pregnant, lactating) recorded for them during the majority (>50%) of each individual-month. Reproductive state is based on validated measures: cycling based on assessments of sex skin or by elimination (i.e. not pregnant or lactating), pregnancy determined by backcalculating 180 days from the offspring's date of birth, and lactation based on the presence of a nursing infant (Roberts, Lu, Bergman, & Beehner, 2017). Because >80% of pregnant geladas abort immediately following take-overs (Roberts, Lu, Bergman, & Beehner, 2012), these females may be mistakenly classified as 'cycling' by our method of categorizing pregnancy as only the 180 days prior to an infant birth. Therefore, we removed females categorized as 'cycling' in the 6 months preceding a take-over ($N = 25$ females, 11 injuries) from our analyses. Outside of this window, we are confident in our assessment of pregnancy because 'background' abortion rates (i.e. those unrelated to take-overs) are low (2.0%, 1/50) (Roberts et al., 2012). This subset of our data included 93 injuries across 5433 individual-months in 133 females.

Aim 2 Data Set

We assessed whether injuries extended the interbirth interval (IBI) for females. We assembled a data set of IBI lengths, injury status across each IBI and take-over occurrence across each IBI. We

Figure 1. Injuries in geladas. (a) Skin pulled off of the skull of an adult female. (b) An open wound revealing facial muscles on a juvenile female.

took into account whether a take-over occurred during lactation, which may decrease IBI due to accelerated development, or during nonlactation, which may increase IBI due to spontaneous abortion (Zhao, Borries, & Pan, 2011). We eliminated IBIs in which an infant died ($N = 18$) because the timing of preweaning infant death is known to be positively correlated with IBI. However, examining whether or not injuries can temper this acceleration is not possible due to our small data set. This data set included 39 injuries across 204 independent IBIs from 107 adult females.

Statistical Analyses

Aim 1 analyses

For each individual-month, we designated injury presence/absence, whether the individual died that month (yes/no), categorical age (infant, juvenile, adult, based on known or estimated birth dates and validated maturational milestones; Barale, Rubenstein, & Beehner, 2015), sex and whether that individual-month was within 3 months after a take-over (yes/no), which is considered a 'recent take-over'. We selected the 3 months that follow a take-over based on prior work that identified this time frame as the period during which most infanticides occur (Tinsley Johnson et al., 2018). For all analyses in Aim 1, we used a logit link function and a binomial error distribution and performed Akaike's information criterion (AIC) model selection (Bartoń, 2009; Burnham, Anderson, & Huyvaert, 2011) in R (R Studio Team, 2018).

We first examined whether injury likelihood (i.e. the log odds of an injury) increased for all demographic categories following recent take-overs relative to respective baseline rates (i.e. outside of the 3 months following a take-over). Using a generalized linear mixed model (GLMM) ('lme4' R package; Bates, Mächler, Bolker, & Walker, 2014), we modelled injury likelihood as a function of recent take-over, age, their interaction, and individual identity (ID) as a random effect. We then examined whether mortality likelihood increased for all demographic categories following take-overs relative to respective baseline rates. We used a GLMM to model the likelihood of death as a function of recent take-over, age, and their interaction, with individual ID as a random effect. We performed an identical analysis on a metric that combined injuries and deaths to ensure the robustness of our analyses, since deaths

following take-over presumably represent the most severe form of injury.

Third, we assessed whether reproductive state affected injury likelihood following take-overs (relative to respective baseline likelihoods) in adult females. Here, we modelled injury likelihood as a function of recent take-over, reproductive state (cycling, pregnant, lactating) and their interaction. To correct for multiple hypotheses, we performed a Bonferroni correction on the *P* values included in the top model for the overall injury and reproductive state analyses, as the latter analysis was performed on a subset of the overall data set used in the former.

Aim 2 analyses

To assess whether injuries affected female fitness by elongating IBIs, we modelled IBI length (in days) as a function of the presence or absence of an injury during either the lactational (0/1) or nonlactational (0/1) components of the IBI, individual age at the start of the IBI and the presence of a take-over, which can independently either lengthen IBI through the (undetected) induction of abortions during the gestational IBI portion, or shorten it through accelerated weaning during the lactational IBI portion. However, the high likelihood of abortions following a take-over (>80%, Roberts et al., 2012) impedes our ability to distinguish between cycling and pregnancy prior to a take-over (since pregnancy is defined in our data set by backcalculating from birth). For this reason, our take-over predictor was coded as '0' (no take-over during the IBI), '1' (take-over during the lactating portion of the IBI) and '2' (take-over during the nonlactating portion of the IBI). For this analysis, we used a linear mixed model with a Gaussian distribution (IBI lengths were normally distributed) and performed AIC model selection (Bartoń, 2009; Burnham et al., 2011) in R (R Studio Team, 2018).

RESULTS

Aim 1

We found that injuries increased following take-overs, but that the overall injury rate across all observation days was low (~1%). Nevertheless, we found that the probability of injury (i.e. hereafter 'injury likelihood') was significantly predicted by the temporal proximity to a recent take-over and the age of the animal. Of the

9261 individual-months observed for females, 119 contained an injury (~1.3%). Of the 4507 individual-months observed for males, 20 contained an injury (~0.05%). Injury rates by age category were ~0.03% for infants (9/2891 individual-months), ~0.06% for juveniles (26/4536 individual-months) and ~1.6% for adults (26/6341 individual-months). In our examination of injury likelihood (i.e. the probability of an injury) in relationship to take-overs and age, we found that proximity to a recent take-over and age were the most important predictors of injury in our study gelada population. We identified a single top model (ΔAIC < 2) that included age, recent take-over, and their interaction as fixed effects, and individual ID as a random effect (Table 1). Overall, adults had the highest injury likelihood compared to infants and juveniles. This result is likely related to adult agonistic behaviour and high infant mortality, in which infant death may mask the true rate of injury and result in apparently higher relative adult injury rates. The interaction effect demonstrated that, controlling for the main effects of age category and take-over, infants had a five-fold higher increase in injury likelihood following a take-over compared to that of adults and a 10-fold higher injury likelihood compared to that of juveniles (Table 1, Fig. 2). Take-overs increased the overall likelihood of injury by 15-fold across the data set, indicating that individuals were more likely to be injured after the arrival of a new male and that this effect was largely driven by infants and lactating females.

In our examination of the effects of recent take-overs on the likelihood of death, we again found that proximity to a recent take-over and age were the most important predictors. Death rates were ~1.9% for infants (54/2863 individual-months), ~0.05% for juveniles (24/4546 individual-months) and ~0.08% for adults (53/6411 individual-months). We identified a single top model (ΔAIC < 2) that included recent take-over, age, and their interaction as fixed effects, and individual ID as a random effect (Table 1). Overall, infants had higher mortality likelihood than juveniles but not adults. The interaction effect demonstrated that, controlling for the main effects, infants had a seven-fold higher increase in mortality likelihood compared to that of adults following a take-over and a smaller increase compared to that of juveniles. Recent take-overs increased the overall likelihood of death by 2.7-fold.

In our analysis of the effect of take-overs and reproductive state on injury, we identified a single top model (ΔAIC < 2) that included reproductive state, recent take-over, and their interaction as fixed effects, and individual ID as a random effect (Table 2). Overall, injury likelihood for cycling females was 2.6-fold greater than that of pregnant females and 1.7-fold greater than that of lactating females. However, following a recent take-over, while all individuals were 6.7 times more likely to be injured, lactating females experienced a 4.4-fold higher increase in injury likelihood compared to that of cycling females (Fig. 3). Lactating females did not differ from pregnant females in the increase of injury likelihood following a
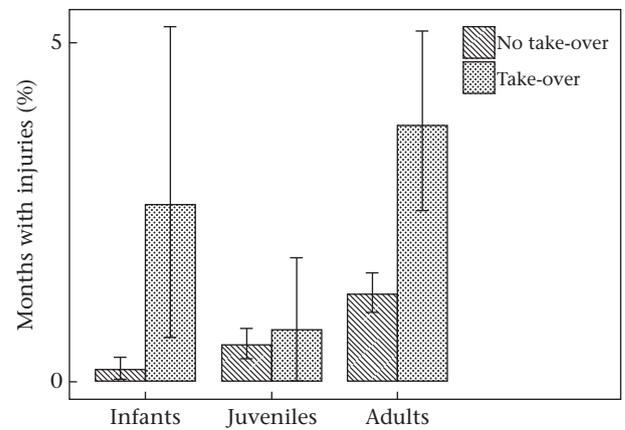

Figure 2. Percentage of months with an injury across age groups when no take-over occurred and 3 months following a take-over. Error bars represent bootstrapped 95% confidence intervals ($N = 10\,000$ iterations).

recent take-over, most likely because of our small sample size of pregnant females.

Aim 2

In our analysis of the effect of injury on IBI, we again identified a single top model (ΔAIC < 2) that included injury, take-over, and age as fixed effects, and individual ID as a random effect (Table 3). Older females had longer IBIs ($P = 0.01$). Injury increased the average IBI (868.1 days after surviving offspring, $N = 222$ unique IBIs from 107 unique females) by 121.9 days ($P = 0.003$; Fig. 4) or ~14.1%, while the occurrence of a take-over during the nonlactating portion of an IBI increased the average IBI by 218.2 days ($P < 0.001$) or ~25%.

DISCUSSION

The arrival of new males was associated with an increase in the likelihood of injury and death across the study gelada population, with infants and lactating females (presumably defending offspring) at the highest risk (Aim 1). Furthermore, injuries incurred by females were associated with longer interbirth intervals, demonstrating a concrete impact of injury on fitness (Aim 2). To our knowledge, this study is the first to demonstrate that male immigration functions as a window of injury risk—and possible adversity—for group members other than those killed in infanticidal attacks. Because the exact instance of injury is only occasionally observed, the provenance of injuries—and their connection to take-overs—remains unknown. However, our models provide substantial support for a strong association between take-over and injury. Our observation of group-wide

Table 1
Generalized linear mixed models for reproductive state data set

Model	Predictor	β	SE	P	P_{adj}
Injury ~ Take-over × Age + (1|ID)	Take-over : No take-over	2.71	0.68	0.03	0.06
	Adults : Infants	1.95	0.47	< 0.01	—
	Juveniles : Infants	1.12	0.50	0.03	—
	Take-over × Infants : × Adults	1.60	0.72	0.03	—
	Take-over × Infants : × Juveniles	2.33	0.92	0.01	—
Death ~ Take-over × Age + (1|ID)	Take-over: No take-over	1.01	0.45	0.03	—
	Infants : Juveniles	0.72	0.30	0.02	—
	Infants : Adults	0.38	0.28	0.18	—
	Take-over × Infants : × Adults	1.94	0.75	0.01	—
	Take-over × Infants : × Juveniles	1.77	1.13	0.12	—

The intercept (β), standard error (SE), P values and Bonferroni-adjusted P value (if appropriate) are given for all predictors in each model (reference intercept specified with ':').

Table 2
Generalized linear mixed models for reproductive state data set

Model	Predictor	β	SE	P	P_{adj}
Injury ~ Take-over × Reproductive state	Take-over : No take-over	1.90	0.35	<0.01	<0.01
	Cycling : Pregnant	0.94	0.39	0.02	—
	Cycling : Lactating	0.51	0.27	0.06	—
	Take-over × Lactating : Cycling	1.47	0.49	<0.01	—
	Take-over × Lactating : Pregnant	1.17	1.12	0.30	—

The intercept (β), standard error (SE), P value and Bonferroni-adjusted P value (if appropriate) are given for all predictors in each model (reference intercept specified with ':').
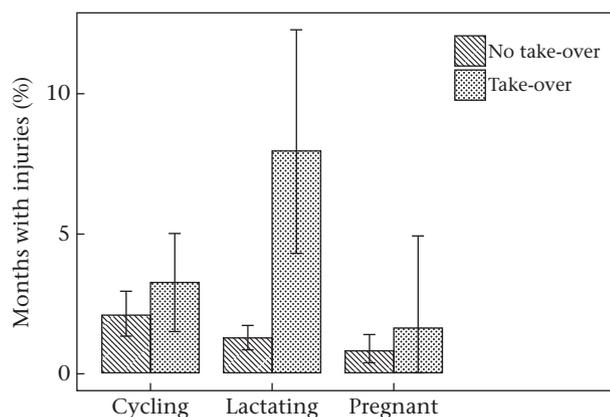

Figure 3. Percentage of months with injury across reproductive states when no take-over occurred and 3 months following a take-over. Error bars represent bootstrapped 95% confidence intervals (*N* = 10 000 iterations).

Figure 4. Each black point is a unique interbirth interval (IBI), with the mean IBI length and standard deviation for each category in red.

(excluding adult males) increases in injury following male immigration is in line with previous anecdotal reports on injuries following male immigration in chacma baboons, *P. ursinus* (Pereira, 1983), lions, *Panthera leo* (Packer & Pusey, 1983) and northern elephant seals, *Mirounga angustirostris* (Le Boeuf & Mesnick, 1991), and accompanying infanticide attempts in apes (summarized in Knott et al., 2019). In addition, the elongation of interbirth intervals following injuries in adult females suggests that the costs of take-overs are greater than the loss of infants directly to infanticide. One potential explanation for these patterns is that injuries are collateral damage due to proximity to infanticidal attacks by males. This explanation is plausible given the well-recorded occurrence of infanticide in geladas (Beehner & Bergman, 2008) and the strong increase in likelihood of injury and death demonstrated by our models. If injuries can be explained by proximity to infanticidal attacks, physical injury across group members would be an ancillary consequence of male aggression.

Because injury is the outcome of physical aggression, physiological stress associated with male immigration is most likely underestimated. Take-overs and their immediate aftermath should therefore be recognized as windows during which all individuals are most likely to be exposed to adversity. This is particularly salient during infancy, a critical time for the development of physiological processes that ensure survival and reproductive success (Champagne, 2010; O'Rand & Hamil-Luker, 2005; Shonkoff
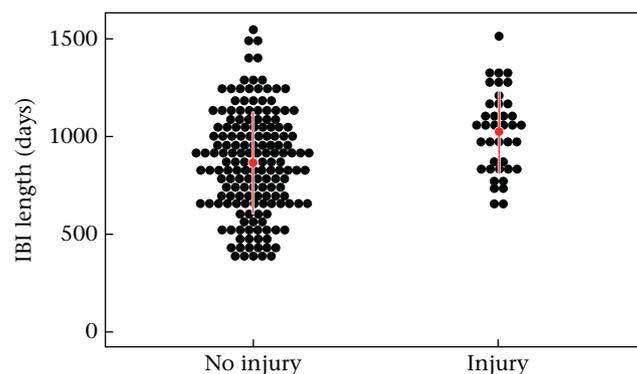
et al., 2012; Tung et al., 2016). Our results demonstrate that infants incur the most severe increase in both mortality and injury likelihood (presumably resulting from failed infanticidal attacks) following a take-over. Exposure to sharply increased threat of injury or death during infancy may catalyse trade-offs between essential physiological processes (Stearns, 1992) that ultimately give rise to decreased lifetime health and fitness (McDade, Georgiev, & Kuzawa, 2016).

If injuries are a physical proxy of physiological stressors, then infants and juveniles exposed to take-overs—or other forms of male immigration and accompanying aggression—may experience trauma not marked by injuries. Excluding the eight infants that died following a take-over in our study, the four infants observed with injuries following a recent take-over were less than 1 year old. Of these four, two died within 6 months of their injuries, one died at 18 months, and one survived to maturation. Fifty-one were exposed to at least one take-over before maturation but were not killed or injured. The continued monitoring of these individuals provides an unparalleled opportunity to investigate whether exposure to trauma in early life results in long-term negative health consequences and to explore potential mechanisms of this relationship.

Injuries to lactating females were generally associated with the deaths of their infants, which were most likely related to attacks from new males. Ten injuries in lactating females (out of 13) were associated with the death of the dependent infant, suggesting that, like female lions and chacma baboons (Packer & Pusey, 1983; Pereira, 1983), female geladas attempt to defend their offspring

Table 3
Generalized linear mixed models

Model	Predictor	β	SE	P
IBI ~ Injury + Age + Take-over + (1|ID)	Injury : No injury	121.91	40.53	<0.01
	Age	−628.5	240.77	0.01
	Take-over (Nonlactating): No take-over	218.23	39.24	<0.01
	Take-over (Lactating): No take-over	45.52	38.36	<0.01

The intercept (β), standard error (SE) and P value are given for all predictors in each model (with reference intercept specified with ':').

from infanticidal males. Our data suggest that injuries incurred in defence of infants were strongly associated with elongation of interbirth interval, a canonical metric of female fitness (Clutton-Brock, 1988). This suggests that injuries may demand energetic resources—for example, for wound healing (Archie, 2013)— to be diverted from the physiological processes necessary for reproduction. Attacks from males may have less obvious effects than physical injury, such as the activity budget and maternal care disruption observed in New Zealand sea lions, *Phocarctus hookeri*, or the increases in glucocorticoid hormones detected in chacma baboons (Beehner et al., 2005; Engh et al., 2006) and geladas (Tinsley Johnson et al., 2018). Because increased glucocorticoid activation generally suppresses the immune response (Archie, 2013; Walburn, Vedhara, Hankins, Rixon, & Weinman, 2009), females injured following a take-over may be less able to effectively repair their injuries and thus may suffer compounded damages to their reproductive success. Indeed, this phenomenon may underlie the reported elongation of IBIs following take-overs and/or male aggression in other species, such as hamadryas baboons (*Papio hamadryas*) (Swedell, Leedom, Saunders, & Pines, 2014).

The potential damage to reproductive success inflicted by infant loss and injury may place selective pressure on females to adopt mitigative counterstrategies in species that experience high levels of male aggression following immigration events. Various avian, rodent, pinniped and primate species exhibit potential maternal counterstrategies to male aggression or infanticide that range from increased aggression to sexual segregation and female dominance (reviewed in Palombit, 2015). For example, New Zealand sea lion females alter their land arrival and departure behaviour to avoid or defend against male aggression (Chilvers, Robertson, Wilkinson, Duignan, & Gemmell, 2005), while female house mice, *Mus domesticus*, launch pre-emptive attacks on new and potentially infanticidal males (Parmigiani, Palanza & Brain, 1989). In geladas, pregnant females spontaneously abort offspring in response to take-overs (Roberts et al., 2012), and lactating females produce situational signals of receptivity that may indicate deceptive fertility (Roberts et al., 2017) or accelerated weaning. Across taxonomic groups, counterstrategies generally mitigate, rather than prevent, the costs of male immigration (Beehner & Lu, 2013). Considering that the alternative, active infant defence, may actually compound potential costs, such compensatory strategies may be females' best option. However, these counterstrategies to male aggression may be accompanied by downstream impacts on health, reproductive success and survival.

Data Accessibility

Data and code are available at https://github.com/GeladaResearchProject/SchneiderCrease_Injury_2018.

Competing Interests

We have no competing interests.

Acknowledgments

References

Archie, E. A. (2013). Wound healing in the wild: Stress, sociality and energetic costs affect wound healing in natural populations. *Parasite Immunology, 35*(11), 374–385.
Barale, C. L., Rubenstein, D. I., & Beehner, J. C. (2015). Juvenile social relationships reflect adult patterns of behavior in wild geladas. *American Journal of Primatology, 77*(10), 1086–1096.
Bartoń, K. (2009). *MuMIn: Multi-model inference (R package, version 0.12.2)*. http://r-forge.r-project.org/projects/mumin/.
Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). *Fitting linear mixed-effects models using lme4*. arXiv preprint arXiv:1406.5823.
Beehner, J. C., & Bergman, T. J. (2008). Infant mortality following male takeovers in wild geladas. *American Journal of Primatology, 70*(12), 1152–1159.
Beehner, J. C., Bergman, T. J., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2005). The effect of new alpha males on female stress in free-ranging baboons. *Animal Behaviour, 69*(5), 1211–1221.
Beehner, J. C., & Lu, A. (2013). Reproductive suppression in female primates: A review. *Evolutionary Anthropology: Issues, News, and Reviews, 22*(5), 226–238.
Bellemain, E., Swenson, J. E., & Taberlet, P. (2006). Mating strategies in relation to sexually selected infanticide in a non-social carnivore: The brown bear. *Ethology, 112*(3), 238–246.
Bruce, H. M. (1959). An exteroceptive block to pregnancy in the mouse. *Nature, 184*(4680), 105.
Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology, 65*(1), 23–35.
Champagne, F. A. (2010). Early adversity and developmental outcomes: Interaction between genetics, epigenetics, and social experiences across the life span. *Perspectives on Psychological Science, 5*(5), 564–574.
Chilvers, B. L., Robertson, B. C., Wilkinson, I. S., Duignan, P. J., & Gemmell, N. J. (2005). Male harassment of female New Zealand sea lions, *Phocarctos hookeri*: Mortality, injury, and harassment avoidance. *Canadian Journal of Zoology, 83*(5), 642–648.
Clutton-Brock, T. H. (1988). *Reproductive success: Studies of individual variation in contrasting breeding systems*. Chicago, IL: University of Chicago Press.
Ebensperger, L. A. (1998). Strategies and counterstrategies to infanticide in mammals. *Biological Reviews, 73*(3), 321–346.
Engh, A. L., Beehner, J. C., Bergman, T. J., Whitten, P. L., Hoffmeier, R. R., Seyfarth, R. M., et al. (2006). Female hierarchy instability, male immigration and infanticide increase glucocorticoid levels in female chacma baboons. *Animal Behaviour, 71*(5), 1227–1237.
Fagundes, C. P., Glaser, R., & Kiecolt-Glaser, J. K. (2013). Stressful early life experiences and immune dysregulation across the lifespan. *Brain, Behavior, and Immunity, 27*, 8–12.
Hausfater, G., & Hrdy, S. B. (2017). *Infanticide: Comparative and evolutionary perspectives*. New York, NY: Routledge.
Hrdy, S. B. (1974). Male–male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatologica, 22*(1), 19–58.
Hrdy, S. B. (1977). Infanticide as a primate reproductive strategy. *American Scientist, 65*(1), 40–49.
Knörnschild, M., Ueberschaer, K., Helbig, M., & Kalko, E. K. (2011). Sexually selected infanticide in a polygynous bat. *PLoS One, 6*(9). e25001.
Knott, C. D., Scott, A. M., O'Connell, C. A., Scott, K. S., Laman, T. G., & Susanto, T. W. (2019). Possible male infanticide in wild orangutans and a re-evaluation of infanticide risk. *Scientific Reports, 9*(1), 7806.
Le Boeuf, B. J., & Mesnick, S. (1991). Sexual behavior of male northern elephant seals: I. Lethal injuries to adult females. *Behaviour, 116*(1), 143–162.
Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology & Evolution, 14*(9), 343–348.
McDade, T. W., Georgiev, A. V., & Kuzawa, C. W. (2016). Trade-offs between acquired and innate immune defenses in humans. *Evolution, Medicine, and Public Health, 2016*(1), 1–16.
O'Rand, A. M., & Hamil-Luker, J. (2005). Processes of cumulative adversity: Childhood disadvantage and increased risk of heart attack across the life course. *Journals of Gerontology Series B: Psychological Sciences and Social Sciences, 60*(Special Issue 2), S117–S124.
Packer, C., & Pusey, A. E. (1983). Adaptations of female lions to infanticide by incoming males. *American Naturalist, 121*(5), 716–728.
Palombit, R. A. (2015). Infanticide as sexual conflict: Coevolution of male strategies and female counterstrategies. *Cold Spring Harbor Perspectives in Biology, 7*(6). a017640.
Parmigiani, S., Palanza, P., & Brain, P. F. (1989). Intraspecific maternal aggression in the house mouse (*Mus domesticus*): A counterstrategy to infanticide by male? *Ethology Ecology & Evolution, 1*(4), 341–352.
Pereira, M. E. (1983). Abortion following the immigration of an adult male baboon (*Papio cynocephalus*). *American Journal of Primatology, 4*(1), 93–98.

Roberts, E. K., Lu, A., Bergman, T. J., & Beehner, J. C. (2012). A Bruce effect in wild geladas. *Science, 335*(6073), 1222–1225.

Roberts, E. K., Lu, A., Bergman, T. J., & Beehner, J. C. (2017). Female reproductive parameters in wild geladas (*Theropithecus gelada*). *International Journal of Primatology, 38*(1), 1–20.

RStudio Team. (2018). *RStudio: Integrated Development for R.* Boston, MA: RStudio, Inc. http://www.rstudio.com/.

van Schaik, C. P., & Janson, C. H. (Eds.). (2000). *Infanticide by males and its implications*. Cambridge, U.K.: Cambridge University Press.

Shonkoff, J. P., Garner, A. S., Siegel, B. S., Dobbins, M. I., Earls, M. F., McGuinn, L., et al. (2012). The lifelong effects of early childhood adversity and toxic stress. *Pediatrics, 129*(1), e232–e246.

Snyder-Mackler, N., Beehner, J. C., & Bergman, T. J. (2012). Defining higher levels in the multilevel societies of geladas (*Theropithecus gelada*). *International Journal of Primatology, 33*(5), 1054–1068.

Stearns, S. C. (1992). *The evolution of life histories*. Oxford, U.K.: Oxford University Press.

Swedell, L., Leedom, L., Saunders, J., & Pines, M. (2014). Sexual conflict in a polygynous primate: Costs and benefits of a male-imposed mating system. *Behavioral Ecology and Sociobiology, 68*(2), 263–273.

Tinsley Johnson, E., Snyder-Mackler, N., Lu, A., Bergman, T. J., & Beehner, J. C. (2018). Social and ecological drivers of reproductive seasonality in geladas. *Behavioral Ecology, 29*(3), 574–588.

Tung, J., Archie, E. A., Altmann, J., & Alberts, S. C. (2016). Cumulative early life adversity predicts longevity in wild baboons. *Nature Communications, 7*, 11181.

Walburn, J., Vedhara, K., Hankins, M., Rixon, L., & Weinman, J. (2009). Psychological stress and wound healing in humans: A systematic review and meta-analysis. *Journal of Psychosomatic Research, 67*(3), 253–271.

Zhao, Q., Borries, C., & Pan, W. (2011). Male takeover, infanticide, and female countertactics in white-headed leaf monkeys (*Trachypithecus leucocephalus*). *Behavioral Ecology and Sociobiology, 65*(8), 1535–1547.

Zipple, M. N., Roberts, E. K., Alberts, S. C., & Beehner, J. C. (2019). Male-mediated prenatal loss: Functions and mechanisms. *Evolutionary Anthropology: Issues, News, and Reviews, 28*, 114–125.