

Genital wounding in chimpanzees (*Pan troglodytes*): Targeted attacks or happenstance?

Abstract

Reports of primate violence frequently note wounds to the genital region, raising the possibility that attackers target genitals to eliminate the reproductive capacity of rivals. Alternatively, in chimpanzees (*Pan troglodytes*) and other species with prominent genitals, injuries may occur simply because large size makes them easy targets. To test these hypotheses, we compiled records of wounds suffered by chimpanzees in four communities at three long-term study sites (Gombe, Tanzania; Kibale, Uganda; Fongoli, Senegal), including both non-lethal (N=1,268 wounds; N=891 male wounds; N=377 female wounds) and lethal attacks (N=258 wounds), to determine whether genital wounding occurred more frequently than expected by chance. In non-fatal cases, wounds occurred in the genital region more often than expected for females (Kasekela: N=9/80 wounds, Mitumba: N=8/61 wounds, Fongoli: N=11/84 wounds, Kanyawara: N=31/152 wounds), but only in Kasekela did males suffer genital wounds more often than expected by chance (Kasekela: N=3/80 wounds, Mitumba: N=2/48 wounds, Fongoli: N=6/413 wounds, Kanyawara: N=4/350 wounds). In contrast, killings of males involved genital wounds more often than expected (N=12/258 wounds). Increased genital wounding may occur when genitals are more accessible, such as when females flee from male aggression, exposing their hindquarters, or when victims are immobilized during fatal attacks.

Keywords: Wounding; Contest competition; reproductive success; genitals

21 Meriones
22 pursued, and struck him with his spear and pierced
23 his navel, piercing through his genitals—
24 the worst affliction that the god of war gives
25 to poor unhappy mortals
26 –Homer, *The Iliad* 13.749-753
27

28 **Introduction**

29 Animals frequently compete over key resources and status, and sometimes injure their
30 opponents (Whitten & Smith, 1984; Ruehlmann et al., 1988; Drews, 1996; Macdonald et al.,
31 2004; Delahay et al., 2006; Forman & Brain, 2006; West et al., 2006; Mosser & Packer, 2009;
32 Williams et al., 2010; Beisner et al., 2012; MacCormick et al., 2012; Charpentier & Drea, 2013;
33 Archie et al., 2014; Leeds et al., 2021; Grimes et al., 2022). While in many cases, animals
34 appear to avoid injuring opponents, perhaps to avoid suffering the costs of escalated fighting
35 (Maynard Smith & Price, 1974), in other cases animals engage in violence, injuring or killing
36 opponents, and may gain fitness benefits by doing so, such as by eliminating rivals (Enquist &
37 Leimar, 1990).

38

39 Wounds inflicted to any part of an opponent's body may reduce their reproductive success.
40 Across taxa, wounding often occurs more frequently in one sex, suggesting a relationship
41 between wounding rates and species-specific patterns of reproductive competition (males:
42 stump-tailed macaques, *Macaca arctoides*, Whitten & Smith, 1984, Ruehlmann et al., 1988;
43 rhesus macaques, *Macaca mulatta*, Ruehlmann et al., 1988; pigtail macaques, *Macaca*
44 *nemestrina*, Ruehlmann et al., 1988; yellow baboon, *Papio cynocephalus*, Drews, 1996;
45 European badger, *Meles meles*, Macdonald et al., 2004; ring-tailed lemur, *Lemur catta*,
46 Charpentier & Drea, 2013; olive baboon, *Papio anubis*, MacCormick et al., 2017; orca, *Orcinus*

47 orca, Grimes et al., 2022; Females: water voles, *Arvicola terrestris*, Forman & Brain, 2006). In
48 some species, wounding increases during times of intense competition. For example, male
49 rhesus macaques (*Macaca mulatta*) suffer their highest rates of mortality and wounding during
50 the mating season (Hoffman et al., 2008). By inflicting wounds, competitors impose an
51 immunological cost on their rivals. Wounded individuals not only suffer risk of infection, physical
52 impairment, and death but expend energy that directly or indirectly compromises reproductive
53 success. For example, in a study of ornate tree lizards (*Urosaurus ornatus*), individual lizards
54 that suffered wounds exhibited reduced reproductive success when lizards were subjected to a
55 stress-inducing experimental treatment, but this difference was not evident in the absence of
56 induced stress (French et al., 2007). Among yellow baboons (*Papio cynocephalus*), wounds
57 healed more slowly when females were lactating relative to either pregnant or cycling females
58 (Archie et al., 2014).

59
60 When fighters cause injury, the location of the resulting wounds may depend mainly on
61 happenstance and opportunity, insofar as fighters injure whatever parts are accessible and/or
62 unprotected. However, the possibility exists that fighters may target specific locations to
63 maximize the impact of their attack. Descriptions of wounding resulting from fights among male
64 primates often note injury to the genitals or groin region (bonobos, *Pan paniscus*: Kano, 1984,
65 chimpanzees, *Pan troglodytes*: de Waal, 1986, Goodall, 1992, Watts et al., 2006, Kaburu et al.,
66 2013; rhesus macaques, *Macaca mulatta*: de Waal, 1986; crab-eating macaques, *Macaca*
67 *fascicularis*; de Waal 1986; chacma baboons, *Papio ursinus*: de Waal, 1986; olive baboons,
68 *Papio anubis*: de Waal, 1986). For example, in the Kasekela chimpanzee community in Gombe
69 National Park, Tanzania, adult male Wilkie overthrew the alpha male, Goblin, in a fight that
70 involved a Goblin biting Wilkie on the scrotum, inflicting a severe wound; researchers inferred
71 that the resulting infection likely would have been fatal without veterinary intervention (Goodall,
72 1992). Such wounding can end the victim's reproductive career; genetic tests have found no

subsequent offspring sired by Goblin (Wroblewski et al., 2009). Subsequent scrotal wounds to other former alpha males, including Frodo and Ferdinand (Massaro et al., in revision), as well as a severe attack on adult female Flirt's sexual swelling (Gombe Stream Research Centre, unpublished data) further invite the question of whether chimpanzees target their victims' genitals. In addition to injuries from non-fatal fighting, mutilated or severed genitals feature prominently in descriptions of conspecific killings by chimpanzees (de Waal, 1986; Goossens et al., 2005; Watts et al., 2006; Kaburu et al., 2013).

Researchers have proposed two main hypotheses to explain the prevalence of such genital wounds: (1) attackers target this region, perhaps to eliminate the reproductive capacity of rivals (Betzig, 2014), and (2) genitals may be injured frequently simply because they are large or easily accessible (Goodall, 1992). For example, Goodall speculated whether Wilkie "intentionally [bit] Goblin in his most vulnerable part," but concluded it was more likely luck: "the scrotum (so very large in wild chimpanzees) is an obvious thing to bite" (Goodall, 1992). Given that male primates frequently compete over reproductive opportunities, injuring an opponent's genitals would provide an effective way to eliminate a reproductive competitor. Additionally, wounds to the genital region can be catastrophic for other reasons. Passing near the groin, the femoral artery delivers blood to the lower extremities; severing this artery can cause massive blood loss and rapid death (Degiannis et al., 1995). Historical accounts indicate that in human societies, attackers targeted the genitals of victims as both a symbolic and practical means of disabling an opponent (Betzig 2014). While fights among non-human primates presumably lack a symbolic element, targeting the groin can be effective both for eliminating a rival's reproductive capacity and damaging their health.

For both male and female chimpanzees, genitals present a conspicuous target for attackers. Compared to other primates, chimpanzees have exceptionally large testes, both in absolute

terms (139 g combined mass (Harcourt et al., 1995; estimate based on multiple studies, weighted by sample size) and controlling for body mass (*ibid.*). Female chimpanzees exhibit estrogen-dependent swelling of the genital skin during the follicular phase of the menstrual cycle (Dixon, 1998). Chimpanzee menstrual cycles last approximately 36 days with full tumescence lasting from 2 to 19 days (Deschner et al., 2003; Emery & Whitten, 2003). Thus, the genitals of both male and female chimpanzees present large targets for damage during fights.

Distinguishing between the two hypotheses poses challenges, but we can make some inferences based on patterns such as sex differences in wounding and the locations of the wounds. Determining the intentionality of such targeting—and indeed, determining intentionality at all in observational studies of animals—poses severe challenges (Heyes & Dickinson, 1990). The records of wounds provide little direct evidence of the intentions of attackers. Nonetheless, the two hypotheses—targeted versus non-targeted attack—yield contrasting predictions. If attackers do not specially target genitals, then genital wounds should occur in proportion to relative surface area. In this case, the proportion of wounds suffered to genitals should approximate their relative proportion of total body surface area. In contrast, targeted attacks should result in a greater proportion of wounds suffered to genitals than predicted by surface area alone, particularly among males and during non-lethal attacks, as genital wounds to these individuals would have the greatest potential impact on future reproductive success.

Here, we test two alternative hypotheses: the frequency of wounds to the genital region in chimpanzees is best explained by either (1) targeting of this area by attackers, resulting in more genital wounds than expected by chance; or (2) incidental damage, such that genitals receive no more wounds than expected given the proportion of total body surface. To assess wounding patterns, we use a dataset compiled from the health monitoring records of three long-term chimpanzee field studies, in which research teams recorded the presence and location of any

newly observed chimpanzee wounds, noting additional details when able. We used these data to assess whether genital injury occurs more often than expected, given the proportion of the body surface represented by the genital region.

Methods

Data collection

To assess whether wounds to these areas occurred more frequently than expected, we examined wounding data recorded during a total of 611 months of observation of chimpanzees in four communities at three study sites: Gombe National Park, Tanzania: Kasekela community (N=190 months: 2004–2019) and Mitumba community (N=184 months: 2004–2019); Kibale National Park, Uganda: Kanyawara community (N=166 months: 2006–2019); and Fongoli, Senegal: (N=71 months: 2006–2014). The Kasekela and Mitumba communities occupy portions of Gombe National Park, a mosaic of forest, woodland, and grassland habitat along the mountainous shoreline of Lake Tanganyika in northwestern Tanzania (4°38' – 4°45'S, 29°36' – 29° 39'E; Wilson, 2021). The Kasekela community (47–62 individuals) consistently outnumbered the neighboring Mitumba community (20–29 individuals) throughout the study period (2004-2019). The Kanyawara community occupies a mosaic of forest, swamp, and grassland habitat along the western boundary of Kibale National Park (00°30'N, 30°24'E) in southwestern Uganda and numbered between 44 to 54 individuals during the study period (2006-2019; Emery Thompson et al., 2020). The Fongoli community occupies a savannah habitat featuring a mosaic of woodland, grassland, bamboo and gallery forests in the Kedougou region in southeastern Senegal (12°40'N, 12°13'W) and ranged in group size from 31 to 37 individuals through the present study (2006-2014; Pruetz et al., 2015).

During daily observations of chimpanzees, observers noted the location and other details of any wounds observed. While such wounds may be reported across multiple days when they remain

unhealed, we inspected these records to identify unique events. While minor differences exist across sites in the methods for collecting wound information, our analysis compares each site to itself. We compiled all reported wounds, excluding any cases in which we could infer that wounds were caused by members of another species (e.g., snare wounds, or wounds resulting from observed interspecies interactions). We also tallied the locations of wounds from nine cases of conspecific killings that provided sufficiently detailed accounts (Table 1). In total, we compiled 1,272 wounds suffered during non-lethal attacks (N=1,272 wounds; N=895 male wounds; N=377 female wounds) and 258 wounds suffered during lethal attacks (N=258 male wounds).

Table 1. Summary of fatal chimpanzee attacks with detailed accounts of wounds from Kibale, Uganda; Kalinzu, Uganda; Mahale, Tanzania; and Gombe Tanzania (2002–2017)

Community	Site	Victim identity	Number of wounds	Number of genital wounds	Publication
Ngogo	Kibale	Unknown male	26	1	Watts et al. 2006
Ngogo	Kibale	Unknown male	25	1	Watts et al. 2006
Ngogo	Kibale	Unknown male	16	0	Watts et al. 2006
Kanyawara	Kibale	Unknown male	54	2	Watts et al. 2006
M-Group	Mahale	Pimu	15	1	Kaburu et al. 2013
Kalinzu M-Group	Kalinzu	Unknown male	33	0	Wilson et al., 2014
Mitumba	Gombe	Fansi	22	2	Massaro et al., in revision
Mitumba	Gombe	Vincent	47	4	Massaro et al., in revision
Mitumba	Gombe	Ebony	20	1	Massaro et al., in revision

Estimations of surface area: Females

While sexual swellings change in size throughout the reproductive cycle of female chimpanzees, we calculate the surface area of a fully swollen sexual swelling to provide an upper bound to our estimate of genital surface area. To determine the percentage of a female chimpanzee's body covered by a fully tumescent sexual swelling, we started with the total surface area (1.64 m²) estimated by Cross & Collard (2011), based on measurements of body segments of a 47.1 kg adult female chimpanzee, reported by Crompton et al. (1996). We then used an estimate of the surface area of a full sexual swelling (0.0297 m²) from a study that used measurements of swelling height, width, and depth collected via photogrammetry (Emery & Whitten, 2003). Together, these figures indicate that a fully tumescent sexual swelling covers approximately 1.84% of a female chimpanzee's body surface.

Estimations of surface area: Males

We estimated the surface area of a male chimpanzee based on the ratio between male and female body mass. Dixon and Mundy (1994) reported a mean body mass of 58.8 kg for male chimpanzees, 1.25 times the mass of the female specimen used to calculate female surface area (Crompton et al., 1996; Cross & Collard, 2011). While these studies used chimpanzees raised in captivity, which are larger than some wild chimpanzees (e.g., Gombe: (females: 31.3 kg; males: 39 kg; Pusey et al., 2005), they have approximately the same 1.25 ratio of male to female body mass as wild chimpanzees, and presumably have similar body proportions to wild chimpanzees. We estimated male surface area, $A_M = A_F(m_M/m_F)^{2/3}$, where A_F = female surface area, m_M = male body mass, m_F = female body mass, with the ratio of body masses taken to the $2/3$ power because area increases with the square of linear dimensions, while volume and mass increase by the cube of linear dimensions. This calculation produced an estimated surface area of $(1.6413 \text{ m}^2)(1.25)^{2/3} = 1.87 \text{ m}^2$ for adult male chimpanzees.

We estimated the surface area of the chimpanzee scrotum based on the testes volume (mean=150.4 cm³) measured from 11 male chimpanzees (Dixon & Mundy, 1994). Assuming the scrotum is approximately spherical, this yields a radius of:

$$r = (3V/4\pi)^{1/3} = ((3 \times 150.4 \text{ cm}^3)/4\pi)^{1/3} = 0.0329 \text{ m} \text{ and an area } A = 4\pi r^2 = 0.0137 \text{ m}^2.$$

Next, we used Preview to measure the size in pixels of a flaccid chimpanzee penis depicted in a figure with accompanying centimeter scale (Dixon & Mundy, 1994: Figure 1) to estimate the approximate length (4.2 cm) and width (1.4 cm, radius of 0.7 cm). By treating the penis as a cylinder without one end, we calculated surface area ($A = 2\pi rh + \pi r^2$), yielding an estimated flaccid penis surface area of 0.00246 m², and a combined male genital surface area of 0.0161 m².

Data Analysis

For each study community, we calculated the expected number of genital wounds for males and females based on the percentage of the adult body surface covered by the genital region for males (0.86%) and females (1.84%). We then used exact binomial tests with a Bonferroni correction for multiple comparisons to assess whether observed genital wounding significantly differed from the expected values.

Ethical Note

All researchers complied with Institutional Animal Care and Use Committee (IACUC) guidelines of their respective institutions. We analyzed data collected through non-invasive observation of wild animals, which does not require IACUC approval. Researchers collected data with permission and oversight of the government organizations responsible for wildlife research at each field site.

Results

Across study sites, we documented a total of $n = 74$ genital wounds ($n = 59$ to females; $n = 15$ to males) in our set of non-fatal injuries (Figure 1). Male chimpanzees included in this dataset suffered $\bar{x} = 0.19 \pm 0.50$ wounds (mean $\pm$ standard deviation; $n=77$ males), while females included in the sample received $\bar{x} = 0.58 \pm 0.95$ genital wounds (mean $\pm$ standard deviation, $n=102$ females). Observers generally noted the presence and location of each wound but did not consistently provide additional details such as shape or size of the wound.

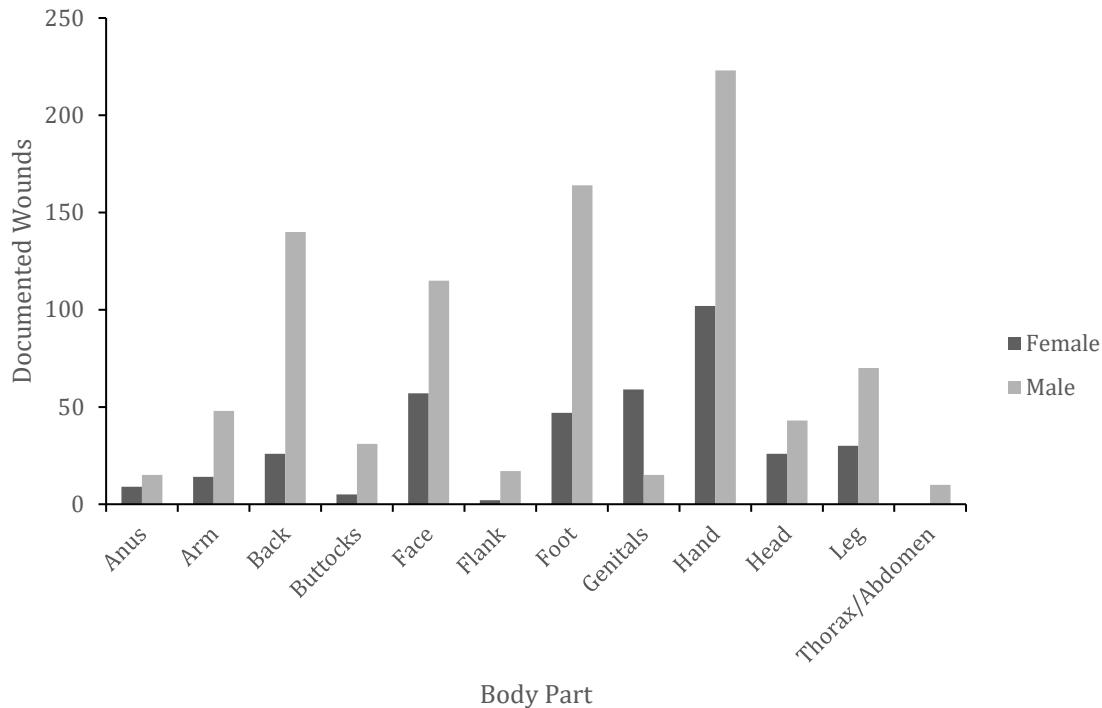


Figure 1. Distribution of documented non-fatal wounds suffered by chimpanzees across body part and sex. Researchers documented wounds at Fongoli, Senegal (2006–2014), Gombe, Tanzania (2004–2019), and Kibale, Uganda (2006–2019). Columns represent the sum of documented wounds divided by sex and body part.

230 In the nine fatal attacks, seven victims suffered genital wounds, for a total of $n = 12$ genital
231 wounds. In five of these cases, testes were removed from the scrotum of the killed chimpanzee.
232 In two cases, parts of the penis were removed. In one additional case, researchers documented
233 lacerations to the scrotum, but neither penis nor testes were removed from the body.

234

235 Females suffered wounds to their sexual swellings more often than expected in all four
236 communities (exact binomial test, Kasekela: $N=9/80$ wounds, $p<0.001$, Mitumba: $N=8/61$
237 wounds, $p<0.001$, Fongoli: $N=11/84$ wounds, $p<0.001$, Kanyawara: $N=31/144$ wounds,
238 $p<0.001$).

239

240 Male chimpanzees also received more genital wounds than the number expected by chance,
241 but this pattern was statistically significant only in one community (Kasekela; Table 2).

242 Even at Kasekela, the number of genital wounds recorded for males was small ($n = 3$), though
243 more than four times as many as the 0.69 genital wounds predicted by body surface area. The
244 three Kasekela males receiving genital wounds included two former alpha males (Frodo, 37
245 years old, and Ferdinand, 26 years old) and one younger male (Fundi, 19 years old).

246 Chimpanzees in the Mitumba community at Gombe also suffered a high number of genital
247 wounds, but not significantly more than expected ($p=0.083$). In contrast, killings of males
248 involved genital wounds more often than expected (exact binomial test, $N=12/258$ wounds,
249 $p<0.001$).

Table 2. Summary of wound locations documented at Fongoli, Senegal (2006–2014), Gombe, Tanzania (2004–2019), Kibale, Uganda (2006–2019), and reported fatal attacks.

Community	Site	Country	Victim's Sex	Total Wounded Individuals	Total Wounds	Total Genital Wounds	Expected Genital Wounds	Exact Binomial Test Corrected p-value
Non-fatal Cases – Males								
Kasekela	Gombe	Tanzania	Male	22	80	3	0.69	0.048
Mitumba	Gombe	Tanzania	Male	7	48	2	0.41	0.083
Fongoli	Fongoli	Senegal	Male	22	413	6	3.56	0.167
Kanyawara	Kibale	Uganda	Male	26	350	4	2.67	0.355
Non-fatal Cases – Females								
Kasekela	Gombe	Tanzania	Female	29	80	9	1.47	<0.001
Mitumba	Gombe	Tanzania	Female	14	61	8	1.12	<0.001
Fongoli	Fongoli	Senegal	Female	18	84	11	1.55	<0.001
Kanyawara	Kibale	Uganda	Female	41	152	31	2.80	<0.001
Fatal Cases – Males								
Fatal Attacks			Male	9	258	12	2.22	<0.001

Discussion

Overall, we found a higher-than expected proportion of genital wounds for female chimpanzees and in fatal attacks on male chimpanzees. In male chimpanzees, the number of genital wounds was also higher than expected, but only for one community (Kasekela) was this difference statistically significant. Even in Kasekela, this involved only three genital wounds to males in 190 months of observation. These results indicate that during fights, males rarely injure the genitals of rival males. In contrast, we found a high prevalence of wounds inflicted to the genitals of females, indicating that targeting may be occurring. We found this pattern consistently throughout our dataset despite making the conservative assumption that the injured swelling was fully tumescent at time of injury. If we were to adjust our analysis to account for the possibility of genital wounds when females were not fully tumescent, we would employ a smaller relative surface area for female genitals and thus only increase the extent to which females received wounds to this area more than expected and would not change the gist of our findings.

266

267 It might seem counterproductive for males to injure the genitals of their potential mating
268 partners. Two additional factors may increase the likelihood of genital injury for females. First,
269 males act aggressively toward females disproportionately during the time of their sexual cycles
270 when their genital skin is fully tumescent (Muller et al., 2009), when the skin is pulled taut by the
271 edema and rendered more vulnerable to injury. As a result, any bites or blows received to this
272 area may be more likely to result in noticeable injuries. Second, sex differences in body
273 orientation during aggressive incidents may result in a higher incidence of genital wounds for
274 females. Field observations suggest that males more frequently face one another when fighting,
275 whereas females more often flee male attackers or crouch to protect their underside (and
276 offspring), exposing their hindquarters to attack. Supporting this observation, analysis of
277 craniofacial trauma in chimpanzees found that females suffered a greater portion of lesions to
278 the rear of their skulls than did males (Novak & Hatch, 2009).

279

280 In killings of males, attackers damaged the genitals of victims in 7 of 9 cases, suggesting that
281 attackers targeted the genitals of their victims. While wounds to the genital region could involve
282 mortal wounds, such as severing the femoral artery, none of the genital injuries in our dataset
283 involved such catastrophic trauma. Instead, they generally involved more superficial injuries—
284 lacerations of the skin—or removal of tissue, which could preclude future reproduction had the
285 victim survived, but which otherwise seemed unlikely to be fatal in the absence of other injuries.
286 In one case at Kasekela, researchers noted that attackers caused a tear in the victim's scrotum,
287 exposing the testis (Massaro et al., in revision), yet the victim survived for 48 months after this
288 injury. Our finding that in fatal cases, genital wounding occurred more often than expected
289 suggests that attackers targeted this area. An additional factor to consider, however, is that
290 during fatal attacks, chimpanzees often pin the victim to the ground, exposing the victim's
291 ventral surface (e.g., Watts et al., 2006). Most wounds in our set of fatal cases occurred to the

extremities (hands and feet: 28.3%, $n=73/258$) or ventral surface (face, neck, chest, abdomen, groin: 39.9%, $n=103/258$), suggesting that attackers damage any readily accessible part of their victim. This finding leaves open the possibility that attackers intentionally expose the ventrum of victims to damage vulnerable body parts, including genitals.

We used health monitoring data to test our hypotheses. In most cases, observers did not record how these wounds were inflicted. Thus, we do not have data on the identity, community membership or number of attackers, nor do we have data on the true orientation during the duration of such attacks. Studies using direct observation or video recording of chimpanzee violence would provide opportunities to test these hypotheses further.

In summary, while for both sexes of chimpanzees, the number of genital wounds exceeded the number expected by surface area, this difference was only statistically significant for females; for living males in one of four study communities; and for males killed by other chimpanzees. Attackers may target genitals, but so long as males are unrestrained, they generally succeed in avoiding genital injury. Inflicting wounds, regardless of location, may either serve to alter conspecific behavior or diminish reproductive success of rivals due to energy tradeoffs between investment in healing wounds and mating effort.

Data Availability

The raw datasets generated during and/or analyzed during the current study are not publicly available due to ongoing studies at respective field sites but are available from the corresponding author on reasonable request. We report summary data in tabular format within the text. Summary data are sufficient to replicate the statistics reported in this analysis.

316 **References**

- 317 Archie, E. A., Altmann, J., & Alberts, S. C. (2014). Costs of reproduction in a long-lived female
318 primate: injury risk and wound healing. *Behavioral ecology and sociobiology*, 68, 1183-
319 1193.
- 320 Betzig, L. (2014). Suffodit inguinal: Genital attacks on Roman emperors and other primates.
321 Politics and the Life Sciences 33, 54-68. 10.2990/33_1_54.
- 322 Beisner, B. A., Jackson, M. E., Cameron, A., & McCowan, B. (2012). Sex ratio, conflict
323 dynamics, and wounding in rhesus macaques (*Macaca mulatta*). *Applied Animal*
324 *Behaviour Science*, 137(3-4), 137-147.
- 325 Charpentier, M. J., & Drea, C. M. (2013). Victims of infanticide and conspecific bite wounding in
326 a female-dominant primate: a long-term study. *PloS one*, 8(12), e82830.
- 327 Crompton, R.H., Li, Y., Alexander, R.M.N., Wang, W., and Gunther, M.M. (1996). Segment
328 inertial properties of primates: New techniques for laboratory and field studies of
329 locomotion. *American Journal of Physical Anthropology* 99, 547-570. 10.1002/(sici)1096-
330 8644(199604)99:4<547::aid-ajpa3>3.0.co;2-r.
- 331 Cross, A., and Collard, M. (2011). Estimating Surface Area in Early Hominins. *PLoS ONE* 6,
332 e16107. 10.1371/journal.pone.0016107.
- 333 Degiannis, E., Levy, R. D., Velmahos, G. C., Potokar, T., & Saadia, R. (1995). Penetrating
334 injuries of the femoral artery. *Journal of British Surgery*, 82(4), 492-495.
- 335 Delahay, R. J., Walker, N. J., Forrester, G. J., Harmsen, B., Riordan, P., Macdonald, D. W., ... &
336 Cheeseman, C. L. (2006). Demographic correlates of bite wounding in Eurasian

337 badgers, *Meles meles* L., in stable and perturbed populations. *Animal Behaviour*, 71(5),
338 1047-1055.

339 Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2003). Female sexual swelling size,
340 timing of ovulation, and male behavior in wild West African chimpanzees. *Hormones and*
341 *behavior*, 46(2), 204-215.

342 DeWaal, F.B.M. (1986). The brutal elimination of a rival among captive male chimpanzees.
343 *Ethology and Sociobiology* 7, 237-251. 10.1016/0162-3095(86)90051-8.

344 Dixson, A. F. (1998). *Primate sexuality: comparative studies of the prosimians, monkeys, apes,*
345 *and human beings*. Oxford University Press, USA.

346 Dixson, A.F., and Mundy, N.I. (1994). Sexual behavior, sexual swelling, and penile evolution in
347 chimpanzees (*Pan troglodytes*). *Archives of Sexual Behavior* 23, 267-280.
348 10.1007/bf01541563.

349 Drews, C. (1996). Contexts and patterns of injuries in free-ranging male baboons (*Papio*
350 *cynocephalus*). *Behaviour*, 133(5-6), 443-474.

351 Emery, M.A., and Whitten, P.L. (2003). Size of sexual swellings reflects ovarian function in
352 chimpanzees (*Pan troglodytes*). *Behavioral Ecology and Sociobiology* 54, 340-351.
353 10.1007/s00265-003-0648-6.

354 Emery Thompson, M., et al. (2020). "The Kibale Chimpanzee Project: Over thirty years of
355 research, conservation, and change." *Biological conservation* 252: 108857.

356 Enquist, M., & Leimar, O. (1990). The evolution of fatal fighting. *Animal Behaviour*, 39(1), 1-9.

Feldblum, J. T., Wroblewski, E. E., Rudicell, R. S, Hahn, B. H., Paiva, T., Cetinkaya-Rundel, M., Pusey, A. E., and Gilby, I. C. (2014). Sexually coercive male chimpanzees sire more offspring. *Current Biology* 24, no. 23: 2855-2860.

Forman, D. W., & Brain, P. F. (2006). Agonistic behaviour and bite wound patterns in wild water voles (*Arvicola terrestris* L.). *Aggressive Behavior: Official Journal of the International Society for Research on Aggression*, 32(6), 599-603.

Goodall, J. (1991). Unusual violence in the overthrow of an alpha male chimpanzee at Gombe. In *Topics in primatology: Human origins*, T. Nishida, W.C. McGrew, P. Marler, M. Pickford, F. de Waal, eds, University of Tokyo Press (Vol. 1, pp. 131-142).

Goossens, B., Setchell, J.M., Tchidongo, E., Dilambaka, E., Vidal, C., Ancrenaz, A., and Jamart, A. (2005). Survival, interactions with conspecifics and reproduction in 37 chimpanzees released into the wild. *Biological Conservation* 123, 461-475.
10.1016/j.biocon.2005.01.008.

Grimes, C., Brent, L. J., Weiss, M. N., Franks, D. W., Balcomb, K. C., Ellifrit, D. K., ... & Croft, D. P. (2022). The effect of age, sex, and resource abundance on patterns of rake markings in resident killer whales (*Orcinus orca*). *Marine Mammal Science*, 38(3), 941-958

Harcourt, A. H., Purvis, A., & Liles, L. (1995). Sperm competition: mating system, not breeding season, affects testes size of primates. *Functional Ecology*, 468-476.

Homer. (2023). *The Iliad* (E. R. Wilson, Trans.; First edition.). W.W. Norton and Company. Book 13, lines 749-753

Heyes, C., & Dickinson, A. (1990). The intentionality of animal action. *Mind & Language*, 5(1), 87-103.

Hoffman, C. L., Ruiz-Lambides, A. V., Davila, E., Maldonado, E., Gerald, M. S., & Maestriperi, D. (2008). Sex differences in survival costs of reproduction in a promiscuous primate. *Behav Ecol Sociobiol*, 62, 1711-1718.

Kaburu, S.S.K., Inoue, S., and Newton-Fisher, N.E. (2013). Death of the Alpha: Within-Community Lethal Violence Among Chimpanzees of the Mahale Mountains National Park. *American Journal of Primatology* 75, 789-797. 10.1002/ajp.22135.

Kano, T. (1984). Observations of physical abnormalities among the wild bonobos (*Pan paniscus*) of Wamba, Zaire. *American Journal of Physical Anthropology*, 63(1), 1-11.

Leeds, A., Boyer, D., Ross, S. R., & Lukas, K. E. (2021). Patterns of wounding in mixed-sex social groups of western lowland gorillas (*Gorilla gorilla gorilla*). *Applied Animal Behaviour Science*, 236, 105226.

MacCormick, H.A., MacNulty, D.R., Bosacker, A.L., Lehman, C., Bailey, A., Collins, D.A., and Packer, C. (2012). Male and female aggression: lessons from sex, rank, age, and injury in olive baboons. *Behavioral Ecology* 23, 684-691. 10.1093/beheco/ars021.

Macdonald, D. W., Harmsen, B. J., Johnson, P. J., & Newman, C. (2004). Increasing frequency of bite wounds with increasing population density in Eurasian badgers, *Meles meles*. *Animal Behaviour*, 67(4), 745-751.

408 Massaro, A., Wroblewski, E., Mjungu, D., Feldblum, J., Boehm, E., Desai, N., Kamenya, S.,
409 Lonsdorf, E., Lipendi, I., Mwacha, D., Terio, K., Kinsel, M., Kimaro, E.W., Foerster, S.,
410 Rudicell, R., Hahn, B., Pusey, A., and Wilson, M.L. (in revision). Severe within-group
411 violence amongst chimpanzees at Gombe National Park.
412

413 Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African
414 lion, *Panthera leo*. *Animal Behaviour*, 78(2), 359-370.
415

416 Muller, M. N., Kahlenberg, S. M., & Wrangham, R. W. (2009). Male aggression against females
417 and sexual coercion in chimpanzees. *Sexual coercion in primates and humans: An*
418 *evolutionary perspective on male aggression against females*, 184-217.
419

420 Novak, S.A., and Hatch, M.A. (2009). Intimate wounds: craniofacial trauma in women and
421 female chimpanzees. *Sexual coercion in primates and humans: An evolutionary*
422 *perspective on male aggression against females*, 322.
423

424 Pruetz, J.D. (2015), et al. "New evidence on the tool-assisted hunting exhibited by chimpanzees
425 (*Pan troglodytes verus*) in a savannah habitat at Fongoli, Sénégal." *Royal Society Open*
426 *Science* 2.4: 140507.

427 Pusey, A.E., Oehlert, G.W., Williams, J.M., and Goodall, J. (2005). Influence of Ecological and
428 Social Factors on Body Mass of Wild Chimpanzees. *International Journal of Primatology*
429 26, 3-31. 10.1007/s10764-005-0721-2.

430 Ruehlmann, T. E., Bernstein, I. S., Gordon, T. P., & Balcaen, P. (1988). Wounding patterns in
431 three species of captive macaques. *American journal of primatology*, 14(2), 125-134.

432 Watts, D.P., Muller, M., Amsler, S.J., Mbabazi, G., and Mitani, J.C. (2006). Lethal intergroup
433 aggression by chimpanzees in Kibale National Park, Uganda. *American Journal of*
434 *Primatology* 68, 161-180. 10.1002/ajp.20214.

435 West, P. M., MacCormick, H., Hopcraft, G., Whitman, K., Ericson, M., Hordinsky, M., & Packer,
436 C. (2006). Wounding, mortality and mane morphology in African lions, *Panthera*
437 *leo*. *Animal Behaviour*, 71(3), 609-619.

438 Whitten, P. L., & Smith, E. O. (1984). Patterns of wounding in stumptail macaques (*Macaca*
439 *arctoides*). *Primates*, 25, 326-336.

440 Williams, R. C., Nash, L. T., Scarry, C. J., Videan, E. N., & Fritz, J. (2010). Factors affecting
441 wounding aggression in a colony of captive chimpanzees (*Pan troglodytes*). *Zoo*
442 *biology*, 29(3), 351-364.

443 Wilson, M.L. (2021). "Insights into human evolution from 60 years of research on chimpanzees
444 at Gombe." *Evolutionary human sciences* 3: e8.

445 Wilson, M.L., et al. (2020). "Research and conservation in the Greater Gombe Ecosystem:
446 Challenges and opportunities." *Biological conservation* 252 (2020): 108853.

447 Wilson, M.L., Wallauer, W.R., and Pusey, A.E. (2004). New cases of intergroup violence among
448 chimpanzees in Gombe National Park, Tanzania. *International Journal of Primatology*
449 25, 523-549. 10.1023/b:ijop.0000023574.38219.92.

450 Wroblewski, E.E., Murray, C.M., Keele, B.F., Schumacher-Stankey, J.C., Hahn, B.H., and
451 Pusey, A.E. (2009). Male dominance rank and reproductive success in chimpanzees,
452 *Pan troglodytes schweinfurthii*. *Animal Behaviour* 77, 873-885.
453 10.1016/j.anbehav.2008.12.014.