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Lethal aggression in *Pan* is best explained by adaptive strategies, not human impacts

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1 **Observations of chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) provide**
2 **valuable comparative data for understanding the significance of conspecific killing. Two**
3 **kinds of hypothesis have been proposed. Lethal violence is sometimes concluded to be**
4 **the result of adaptive strategies, such that killers ultimately gain fitness benefits by**
5 **increasing their access to key resources, such as food or mates.¹⁻⁵ Alternatively, it has**
6 **been argued to be a non-adaptive result of human impacts, such as habitat destruction**
7 **or provisioning of food.⁶⁻⁹ To discriminate between these hypotheses we compiled long-**
8 **term information from 18 chimpanzee communities and 4 bonobo communities. Our**
9 **data include 152 killings (N=58 observed, 41 inferred, and 53 suspected killings) by**
10 **chimpanzees in 15 communities and one suspected killing by bonobos. We found that**
11 **males had the greatest involvement as attackers (92% of participants) and victims**
12 **(73%); most killings (66%) involved intercommunity attacks; and attackers greatly**
13 **outnumbered their victims (median 8:1 ratio). Variation in rates of killing among**
14 **communities depended on demographic variables but was unrelated to measures of**
15 **human impacts. These results from all major study populations over the last five**
16 **decades are consistent with previously proposed adaptive explanations for killing by**
17 **chimpanzees but not with the human impact hypothesis.**

18

19 Conspecific killing has been documented at multiple chimpanzee study sites,^{2-5,10-12} but rates
20 vary greatly among sites. The human impact hypothesis and the adaptive strategies
21 hypothesis yield contrasting predictions, which we test here (Tables 1, 2). The human impact
22 hypothesis states that killing occurs mainly as an incidental outcome of aggression,
23 exacerbated by human activities such as providing a concentrated food resource,
24 deforestation-induced crowding, anthropogenic diseases or hunting. Accordingly, lethal
25 aggression should be high where human disturbance is high.⁸

26

27 In contrast, the adaptive strategies hypothesis views aggression as an evolved strategic
28 response by which aggressors tend to increase their fitness through increased access to
29 territory, food, mates or other benefits.^{1-5,10-17} Within this overall framework, arguments from
30 kin selection¹⁸ and evolutionary game theory¹⁹ yield a set of specific predictions for how
31 benefits and costs should vary with the context, age, sex, and genetic relatedness of the
32 attackers and targets. Killing is expected when benefits exceed costs.²⁰ Intercommunity
33 killing is part of a male reproductive strategy, in which males attempt to maximize the size of
34 their feeding territories^{3,5,10,13} and/or acquire females from other communities.^{4,11} Larger
35 territories yield more food, as indicated by larger party size¹³ and heavier body mass,²¹ which
36 yields fitness benefits for males and their mates by increasing female reproductive rate.¹³
37 Attackers are proposed to kill, rather than merely repel, rivals because the costs of killing are
38 reduced by fission-fusion dynamics (in which community members travel in parties of
39 variable size), which sometimes allow attackers to greatly outnumber victims.² Killing rivals
40 enables males to expand their territories.⁵ Males may kill male infants of foreign females to
41 reduce the future size of rival coalitions³, and killing foreign infants of either sex may reduce
42 competition for food by inducing foreign females to avoid contested regions.¹³
43 Intracommunity killing has received less attention. Males may kill other grown males due to
44 intense competition for mating opportunities.^{15,16} Males may kill infants of females in their
45 own communities in an effort to coerce females to mate more exclusively with them.²²
46 Intracommunity infanticide by females may result from intense competition among females
47 for the best feeding areas.¹⁷ Population differences in rates of killing are accordingly
48 expected to result from socioecological factors such as differences in grouping patterns^{2,11}
49 and/or demography.¹⁴ Lethal aggression thus occurs within a diverse set of circumstances,
50 but is expected to be most commonly committed by males; directed towards males; directed

51 towards non-kin, particularly members of other groups; and committed when overwhelming
52 numerical superiority reduces the costs of killing.

53

54 Previous studies have developed and tested these specific hypotheses^{2,5,11-17}; the present study
55 represents the first effort to test multiple hypotheses simultaneously with a comprehensive
56 dataset. To do so, we assembled data from 18 chimpanzee communities from both eastern
57 (N=12) and western (N=6) clades²⁴ of chimpanzees studied over 426 years (median = 21
58 years; range: 4—53) and from 4 bonobo communities studied for 92 years (median = 21;
59 range: 9—39; Figure E1). We rated each case of killing as observed, inferred, or suspected
60 (see Online Methods; Tables E1-E4). We examined contrasting predictions relating to overall
61 patterns of killings (Table 1) and variation among communities (Table 2).

62

63 **Differences among taxa.** Bonobos are widely recognized to be more peaceful than
64 chimpanzees,^{2,23} and previous studies have noted that western chimpanzees kill less
65 frequently than eastern chimpanzees.^{2,11} The human impact hypothesis attributes such
66 differences to “local custom” and different “socialization for gender roles.”⁸ Proponents of
67 this view have not provided detailed predictions regarding which circumstances should favor
68 aggressive customs, but if human impacts cause chimpanzees to be aggressive, then
69 presumably they should induce violent behavior in bonobos as well. In contrast, in behavioral
70 ecology, distinct populations are expected to respond to prevailing ecological circumstances
71 through biological evolution and/or phenotypic flexibility. For bonobos and western
72 chimpanzees, ecological factors appear to favor higher levels of gregariousness, reducing
73 opportunities for low-cost coalitionary killing.^{2,11} Our dataset includes observations in a
74 range of settings for both species of *Pan*, including sites with and without a history of
75 provisioning, and with high and low levels of *disturbance*, a qualitative rating of human

76 impacts estimated independently by each site's director(s) (Online Methods; Figures E1a,
77 E2a).

78

79 For chimpanzees, we compiled accounts of 58 observed killings, 41 inferred killings, and 53
80 suspected killings (Tables E1-E4), with 15 of 18 communities having evidence of committing
81 at least one killing (Figure 1). In contrast, for bonobos, we documented only a single
82 (suspected) case, which occurred at Lomako, a never-provisioned site with a low disturbance
83 rating. No killings were recorded at other bonobo sites, including one with a history of
84 provisioning and a high disturbance rating (Wamba). Controlling for years of observation,
85 chimpanzees had a higher rate of killing than bonobos; this difference was statistically
86 significant for eastern but not western chimpanzees (Poisson regression: N=22 communities;
87 estimated coefficients±SE for chimpanzees compared to bonobos: $\beta_0 = -4.5 \pm 1.0$;
88 $\beta_{east} = 3.4 \pm 1.0$, $z = 3.3$, $P = 0.0008$; $\beta_{west} = 0.65 \pm 1.2$, $z = 0.56$, $P = 0.57$; overall effect of clade:
89 $\chi^2 = 80.8$, $df = 2$, $P < 0.0001$).

90

91 **Variation among sites.** We limited the remaining analyses to chimpanzees, using an
92 information theoretic approach²⁵ to investigate which variables best explained the number of
93 killings per community, controlling for years of observation. To be conservative, we included
94 only observed and inferred cases. We considered three variables for the human impact
95 hypothesis: *provisioned* (whether or not the community had been artificially fed on a regular
96 basis); *area* (the size of the protected area in which the apes lived, on the assumption that
97 smaller areas experience more impacts); and *disturbance*. We also considered three variables
98 for the adaptive strategies hypothesis: *clade* (eastern and western chimpanzees may have
99 experienced different histories of selection for violence); *males* (the number of adult males,
100 which may increase rates of killing due to increased reproductive competition and/or

101 increased fighting ability of large male coalitions), and *density* (number of individuals per
102 km², which may increase rates of killing through increased intercommunity encounter
103 frequency and/or increased competition for available resources). We consider *density* relevant
104 to adaptive strategies, rather than human impacts, because in our dataset *density* was
105 unrelated to *disturbance* (general linear model, $F_{1,16}=1.4$, $P=0.26$) but instead appeared to
106 reflect food abundance. For example, at Ngogo (4.5 chimpanzees/km²), vegetation sampling
107 revealed high forest productivity²⁶ and chimpanzees have high C-peptide levels,²⁷ indicating
108 high energy balance, and thus abundant food per capita; whereas at Fongoli (0.37
109 chimpanzees/km²), chimpanzees range widely across a dry savanna to feed from sparsely
110 available fruit trees.²⁸

111

112 Of the 16 models we considered (Table 3), four of the five models in the resulting 95%
113 confidence set included various combinations of the three adaptive variables; the fifth model
114 included the three human impact variables. The best model included only *males* and *density*,
115 and was supported 6.8 times more strongly than the human impact model (evidence ratio =
116 $w_i/w_j = 0.40/0.059=6.8$). Considering model-averaged parameter estimates,²⁵ increases in
117 *males* and *density* increased the number of killings; for all other parameter estimates, the 95%
118 CI included zero (Table 3; Figure 2). Opposite to predictions from the human impact
119 hypothesis (Table 2), *provisioned* and *disturbance* both had negative effects; the estimates for
120 these parameters included zero in the 95% CI (Table 3; Figure E2b). Excluding one
121 community (Ngogo) that had both an unusually high killing rate and unusually many males
122 resulted in similar values for model averaged parameters, but somewhat different model
123 rankings; only the estimate for *density* excluded zero from the 95% CI (Table E5a; $N = 17$).

124

125 In confirmation that high levels of human impacts are neither necessary nor sufficient to
126 explain killing rates, the highest rate of killing occurred at a relatively undisturbed and never-
127 provisioned site (Ngogo); chimpanzees at the least disturbed site (Goualougo) were suspected
128 of one killing and inferred to have suffered an intercommunity killing; and no killings
129 occurred at the site most intensely modified by humans (Bossou).

130

131 **Killings over time.** According to the human impact hypothesis,⁸ recent increases in reported
132 killings reflect increasing levels of human impacts. However the number of communities
133 under long-term observation increased from just one (1960-1964) to 16 (2000-2013).

134 Controlling for changes in the number of communities observed per year (*communities*), the
135 rate of killing has not changed over time (*year*). Using an information theoretic approach²⁵ to
136 compare three different models (*year*; *communities*; and *year + communities*), the best model
137 contained only *communities*; considering model averaged parameters, the 95% CI excluded
138 zero for *communities*, but not *year* (Poisson regression: N=52 years; model averaged
139 parameters and 95% CI: $\beta_0=10$ (-38—58); $\beta_{year}=-0.0058$ (-0.022—0.010); $\beta_{communities}=0.18$
140 (0.10—0.26); Table E5b).

141

142 **Sex bias among attackers.** Killings involved a median of five male attackers (range: 0—19)
143 and no female attackers (range: 0—6). Considering all cases for which the number of
144 attackers was observed (N=58) or could be inferred (N=6), males constituted 92% of
145 participants in attacks (338/366). Controlling for observation time and community
146 composition, males were much more likely to participate in killings than females (negative
147 binomial mixed model: N = 36 observations (fixed effects: *sex* with 2 levels; random effects:
148 *community* with 18 levels); $\beta_0=-6.9\pm 0.98$; $\beta_{males}=2.6\pm 0.59$, $z=4.42$, $P<0.0001$). Females

149 sometimes joined males in attacking grown individuals, but when acting without males,
150 females killed only young infants (N=8).

151

152 **Bias in sex and age of victims.** Controlling for observation time and community
153 composition, the probability of being killed was highest for infants and males (Poisson
154 regression; N=203 combinations of *sex*, *age class* and *community*; fixed effects: *sex* with two
155 levels; *age class* with four levels; random effects: 26 levels of *community*, including 8
156 unhabituated communities; log-likelihood = -123; estimated coefficients \pm SE: $\beta_0 = -8.1 \pm 0.62$;
157 comparisons with adolescents: $\beta_{infant} = 1.7 \pm 0.56$, $z = 3.2$, $P = 0.003$; $\beta_{juvenile} = -0.97 \pm 0.88$; $z = -1.1$,
158 $P = 0.27$; $\beta_{adult} = 0.87 \pm 0.54$, $z = 1.6$, $P = 0.11$; males compared to females: $\beta_{male} = 1.4 \pm 0.29$, $z = 4.7$,
159 $P < 0.0001$). We confirmed the statistical significance of the fixed effects by comparing the
160 full model with the null model (with just the random effects: $\chi^2 = 32.7$, $df = 4$, $P < 0.0001$) and a
161 reduced model with sex, but not age-class, as a fixed effect ($\chi^2 = 14.4$, $df = 3$, $P = 0.002$).
162 Notably, during infanticides, attackers typically removed infants from mothers under
163 circumstances in which they appeared capable of killing the mother as well, but did not do so.
164 The number of grown females killed (N=9) was much smaller than the number of infants
165 killed (N=58), suggesting that attackers usually targeted infants, but not mothers.

166

167 **Community membership.** Most victims were members of different communities from the
168 attackers (N = 62 of 99 cases; 63%) and thus not likely to be close kin.²⁹ This difference is
169 particularly striking given that chimpanzees could potentially attack members of their own
170 community on an almost daily basis, but encounter members of other communities only
171 rarely (e.g., 1.9% of follow days at Kanyawara³⁰).

172

173 **Numerical asymmetries.** Intercommunity killings mainly involved parties with many males
174 (median = 9 males, range: 2—28, N=36 cases with known numbers of attackers) attacking
175 isolated or greatly outnumbered males or, more often, mothers with infants (median = 0
176 males, range: 0—3, N=30; median = 1 female, range: 0—5, N=31). For 30 cases in which the
177 number of attackers and defenders (= number of adult and adolescent males and females on
178 each side) were known, attackers outnumbered defenders by a median factor of 8 (range: 1—
179 32; Table S11). Most intercommunity killings thus occurred when attackers overwhelmingly
180 outnumbered victims.

181

182 We conclude that patterns of killing in *Pan* are best explained by adaptive factors, not human
183 impacts. Killing was most common in eastern chimpanzees and least common among
184 bonobos. Among chimpanzees, killings increased with more males and higher population
185 density, whereas none of the three human impact variables had an obvious effect. Male
186 chimpanzees killed more often than females, and killed mainly male victims; attackers most
187 frequently killed unweaned infants; victims were mainly members of other communities (and
188 thus unlikely to be close kin); and intercommunity killings typically occurred when attackers
189 had an overwhelming numerical advantage. The most important predictors of violence were
190 thus variables related to adaptive strategies: species; age-sex class of attackers and victims;
191 community membership; numerical asymmetries; and demography.

192

193 **Methods Summary**

194

195 See Online Methods.

196

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198

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205

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213 KZ provided data on site characteristics and human disturbance ratings; MLW coordinated
214 the contributions of all authors; MLW wrote the paper with JCM, DPW, RWW and input
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216

217 **References**

218

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285 Figure 1: Number of victims killed per year by members of study communities (N=22). Bars
286 indicate the annual rate of observed (black), inferred (grey), and suspected (white) killings by
287 each community for bonobos (B; N=4), eastern chimpanzees (E; N=12), and western
288 chimpanzees (W; N=6). Communities with a history of provisioning are indicated by (P).
289

290 Figure 2: Number of killings per year for each community versus (a) number of males and (b)
291 population density (individuals/km²). Rates for each community are indicated by black
292 diamonds (chimpanzees; N=18) and open squares (bonobos; N=4). Black lines indicate
293 simple linear regression for chimpanzee data for illustrative purposes only; statistical tests
294 were done using Poisson regressions.

295 **Table 1. Predicted patterns of lethal aggression**

No.	Variable	Human Impact Hypothesis	Adaptive Strategies Hypothesis
1.	Chimpanzees kill more than bonobos	None	+
2.	Rate of killing over time	+	None
3.	Sex bias: attackers	None	Mainly males
4.	Sex bias: victims	None	Mainly males
5.	Age of victims	None	Mainly young infants (most vulnerable and/or reduce time to mother's next estrus)
6.	Genetic relatedness of attackers and victims	None	Mainly non-relatives (e.g., members of other communities)
7.	Numerical asymmetries	None	Victims greatly outnumbered

296

297

298 **Table 2. Predicted correlates of number of killings per study community**

No.	Variable	Human Impact Hypothesis	Adaptive Strategies Hypothesis
1.	Provisioning (<i>provisioned</i>)	+	None
2.	Size of protected area, km ² (<i>area</i>)	-	None
3.	Disturbance Rating (<i>disturbance</i>)	+	None
4.	Eastern vs. western chimpanzees (<i>clade</i>)	None	+
5.	Mean number of adult males (<i>males</i>)	None	+
6.	Mean population density (<i>density</i>)	None	+

299

300 **Table 3. Summary of model selection: number of killings per community.**

#	<i>b</i>	<i>clade</i>	<i>males</i>	<i>density</i>	<i>area</i>	<i>prov.</i>	<i>dist.</i>	<i>k</i>	Δ_i	w_i
1	-3.6		0.081	0.21				4	0.00	0.40
2	-2.3	-1.9	0.073					4	0.61	0.30
3	-3.1	-1.4	0.073	0.15				5	1.8	0.16
4	-2.7		0.087					3	3.4	0.07
5	7.1				-0.0016	-1.4	-0.63	5	3.8	0.06
6	-2.2	2.4	0.10	0.42	-0.00083	1.3	-0.27	8	10	0.00
7	3.7				-0.0011		-0.40	4	12	0.00
8	-2.0	-2.1		0.17				4	17	0.00
9	-1.2	-2.7						3	18	0.00
10	-2.8			0.28				3	21	0.00
11	-1.1				-0.00042			3	24	0.00
12	-1.1				-0.00042	-0.12		4	28	0.00
13	-1.5							2	34	0.00
14	-1.6					0.19		3	36	0.00
15	-1.4						-0.011	3	37	0.00
16	-1.6					0.18	-0.0046	4	40	0.00
<i>MAP</i>	-2.4	-0.78	0.073	0.11	-0.00010	-0.078	-0.038			
2.5%	-5.0	-1.8	0.053	0.00029	-0.00027	-0.24	-0.11			
97.5%	0.12	0.25	0.093	0.22	0.000083	0.082	0.033			

301

302 Parameters include the intercept (*b*); impact of western relative to the eastern *clade* of
303 chimpanzees; mean number of adult males per community (*males*); mean population density
304 per community (*density*); size of protected area in km² (*area*); history of regular provisioning
305 with food (*prov.*); disturbance rating (*dist.*); the number of free parameters (*k*) including the
306 dispersion parameter (\hat{c}); the difference in Akaike information criterion (corrected for
307 overdispersion: QAICc) between the *i*th model and the best model (Δ_i); and model weight
308 (w_i). Models are arranged in order from best (lowest Δ QAICc_{*i*}) to worst (highest Δ QAICc_{*i*}).
309 The weight of the model (w_i) is the probability that a given model is the best model in a given
310 set of models. Model averaged parameters (*MAP*) with upper (97.5%) and lower (2.5%)
311 bounds of the 95% confidence intervals are given in the bottom rows.

312

313 **Online Methods**

314

315 **Rating of cases.** We rated a case as *observed* if observers directly witnessed the attack. We
316 rated a case as *inferred* if the attack was not directly witnessed, but compelling evidence
317 indicated that the victim was killed by chimpanzees (such as a body found with multiple bite
318 wounds, and/or skeletal trauma consistent with a chimpanzee attack). We rated other cases as
319 *suspected*; for example, disappearances of chimpanzees that appeared healthy prior to their
320 disappearance (with the exception of adolescent females, who generally disperse from their
321 natal community), or individuals known to have died from wounds that may have been
322 inflicted by chimpanzees.

323

324 **Demographic data.** For each community, we used the number of individuals known to be
325 alive in each age-sex category on 01 January of each year to obtain the mean number of
326 individuals in each category and summed to obtain the mean total group size. We calculated
327 the mean number of males and females in four age categories: ≥ 12 (old enough to participate
328 in intergroup fighting and reproductive competition); $\geq 8, < 12$ (older juveniles to young
329 adolescents); $\geq 3, < 8$ (older infants to young juveniles); and < 3 years (young, vulnerable,
330 unweaned infants). For each community, the number of individuals known to be alive in each
331 age-sex category on 01 January of each year was averaged to obtain the mean number of
332 individuals in each category and summed to obtain the mean total group size.

333

334 **Human disturbance scores.** We scored human disturbance as the sum of five separate
335 ratings adapted from³¹, each scored on a 1 to 4 point scale, giving a possible range of 5–20
336 points: (1) disturbance to habitat; (2) degree of harassment of study animals by people; (3)
337 amount of hunting of study animals; (4) degree of habituation to human observers at

338 beginning of studies; and (5) whether major predators have been eliminated (on the
339 assumption that the elimination of major predators by humans is associated with higher levels
340 of human impact). The different measures of disturbance were not strongly inter-correlated.
341 Of the 10 pairwise comparisons among the 5 measures, the median correlation coefficient for
342 the 22 study communities was 0.24 (range: -0.06—0.78). The two pairs that had a correlation
343 coefficient higher than 0.5 were (home range)(harassment)=0.78, and
344 (harassment)(predators)=0.52. Thus, communities with high disturbance to their home range
345 habitat also suffered more harassment by people, and communities with more harassment by
346 people also had fewer natural predators remaining in their habitat. The median variance
347 among the 5 measures was 1.0 (range: 0.7—1.4). None of these variances differed
348 significantly from the others (F-tests: $P > 0.05$).

349

350 **Statistical tests.** We conducted statistical tests using *R* 3.0.2.³² To test for differences in rate
351 of killing between bonobos and the two clades of chimpanzees (eastern and western²⁴), we
352 conducted Poisson regressions with $\log(\text{years of study})$ as an offset. The fact that bonobos
353 had the same response for all communities (zero observed/inferred killings) resulted in a
354 complete separation problem.³³ We addressed this by doing a series of four Poisson
355 regressions, each time replacing the 0 killings for one of the four bonobo communities with 1
356 killing to make the data less extreme, and averaging the results. This provides a conservative
357 estimate of the difference in rates of killing between chimpanzees and bonobos.

358

359 To investigate which factors best explained the number of killings per chimpanzee
360 community, we examined a set of *a priori* specified models, based on hypothesized effects of
361 six independent variables: *clade*; *males* (mean number of males ≥ 12 years old), *density* (mean
362 number of individuals per community/home range (km^2); *protected area* (size (km^2) of

363 national park or reserve in which community resided); *provisioned* (whether the community
364 had a history of being regularly provisioned with food by researchers) and *disturbance* (sum
365 of five four-point ratings, based on²²). Each model consisted of a Poisson regression with the
366 total count of observed/inferred killings committed by each community as the dependent
367 variable, and $\log(\text{years of study})$ as an offset. We recognize that *years of study* is a rather
368 coarse-grained measure of observation time, but finer grained measures such as total number
369 of observation hours were not available for all communities. We selected models to
370 distinguish between the predictor variables most closely associated with the adaptive
371 strategies hypothesis (*clade*, *males*, and *density*) and the human impact hypothesis (*protected*
372 *area*, *provisioned* and *disturbance*), including the null model, models with each variable by
373 itself, combinations of up to three variables associated with each hypothesis, and the full
374 model. We limited the number of variables per model to avoid over-fitting, and limited the
375 number of models tested to reduce the risk of finding spurious correlations. We corrected for
376 overdispersion and small sample size using QAICc, ranked models according to QAICc score
377 (lowest=best), and used results from all models to calculate model-averaged estimates of
378 parameters.²³

379

380 To test for sex differences in participation in lethal aggression, we conducted a GLMM with
381 negative binomial error structure using the glmmADMB package.³⁴ For the dependent
382 variable, we used the number of *participations* in killings by each sex for each community.
383 We defined *participation* as the active involvement of an individual during a lethal attack
384 (e.g., making or attempting to make direct aggressive contact with the victim). For each case
385 for which the attackers were observed directly, or could be inferred with confidence, we
386 counted the number of attackers of each sex. For each community, we summed the number of
387 attackers across all cases to obtain the number of times individuals of each sex participated in

388 attacks. Independent variables consisted the fixed effect *sex* (2 levels: *male* and *female*) and
389 the random effect *community* (18 levels). To control for community composition, we used
390 $\log(\text{chimp-years})$ for each sex in each community as an offset. *Chimp-years* was defined for
391 each age-sex class as *years of study* multiplied by the mean number of individuals of that
392 age-sex class present in the victim's community.

393

394 To test for patterns in the age-sex class of victims, we conducted a GLMM with Poisson error
395 structure using the lme4 (1.0-5) package.³⁵ To control for possible sex differences in
396 motivation for killing, we excluded from analysis the 8 cases that were known to have been
397 committed solely by females. For the dependent variable, we used the number of observed
398 and inferred victims of each age-sex class for each community. Independent variables with
399 fixed effects were *sex* (2 levels) and *age-class* (four levels, as categorized above
400 (Demographic Data)) and the random effect *community* (26 levels: 18 habituated
401 communities and 8 unhabituated communities (victims of intercommunity killings by study
402 communities). Because one community (Kahama) had zero adolescent males, and the number
403 of infants and juveniles were not specified for another (Kalinzu), the total number of age-sex
404 class and community combinations in our analysis (N=203) was less than would be if all age-
405 sex classes were represented for each community $((2 \text{ sexes}) \times (4 \text{ age classes}) \times (26$
406 $\text{communities}) = 208$). To control for the composition of the different communities, we used
407 $\log(\text{chimp-years})$ as an offset. For unhabituated communities, for which demographic
408 information was not available, we defined *chimp-years* as the number of years of observation
409 of the focal community (the community being observed when the killing occurred),
410 multiplied by the median number of individuals of that age-sex class present in the median
411 chimpanzee community. Because the range size and membership of unhabituated
412 communities was not known, we assigned victims to no more than one unhabituated

413 community per study community; this undoubtedly underestimates the total number of
414 communities involved, but should not affect the goal of this analysis, which was to estimate
415 the effect of age and sex class on the risk of being killed, given the proportion of each age-
416 sex class in the population. For chimp-years for victims of unknown sex, we used the mean
417 number of males and females present for that age class. To keep type I error rate at the
418 nominal level of 5% we included random slopes of each level of the fixed effects *sex* and
419 *age-class* within the random effect *community*.^{36,37}

420

421 Additional citations for Online Methods

422

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437

438 **Extended Data**

439

440 **Figure E1. Summary data and location of study sites. a.** Summary data for each
441 community. *Clade*: bonobos (B), eastern chimpanzees (E), western chimpanzees (W);
442 *Community*: mean total size of the community; *Males*: mean number of males ≥ 12 years old;
443 *Females*: mean number of females ≥ 12 years old; *Home range*: mean size of the
444 community's home range (km^2); *Density*=(community)/(home range); *Area*: size of protected
445 area inhabited by the community; *Provisioned*: whether community was regularly
446 provisioned with food; *Disturbance*: sum of the disturbance rating scores. **b** Location of
447 chimpanzee (circles; N=10) and bonobo (squares; N=3) study sites in Africa.

448

449 **Figure E2. Disturbance ratings. a.** Disturbance ratings for each site: disturbance to habitat
450 (black bars); harassment of study animals by people (vertical lines); amount of hunting of
451 study animals (grey); degree of habituation to people at start of study (diagonal hatching);
452 and whether major predators have been eliminated (white). *Clade* is indicated by letters
453 following community name: bonobos (B), eastern chimpanzees (E), and western
454 chimpanzees (W). **b.** Number of killings per year vs. disturbance. Rates for each community
455 are indicated by black diamonds (chimpanzees; N=18) and open squares (bonobos; N=4).

456

457 **Table E1: Intercommunity killings of weaned victims.** For Tables E1-E4, *Ref.*

458 (*References*) refers to references in Table E7.

459

460 **Table E2: Intercommunity infanticides**

461

462 **Table E3: Intracommunity killings of weaned victims**

463

464 **Table E4: Intracommunity infanticides**

465

466 **Table E5: Summary of model selection statistics.** **a.** Effects of including different subsets
467 of the data on rates of killing per community. **b.** The number of killings reported per year has
468 increased, but only because the number of communities under observation has increased;
469 controlling for this, there is no overall effect of *year* on the number of killings reported.

470

471 **Table E6: Number of attackers and defenders on each side for intercommunity killings.**

472

473 **Table E7: References for data in tables E1-E4.**



