

# Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts

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**Observations of chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) provide valuable comparative data for understanding the significance of conspecific killing. Two kinds of hypothesis have been proposed. Lethal violence is sometimes concluded to be the result of adaptive strategies, such that killers ultimately gain fitness benefits by increasing their access to resources such as food or mates<sup>1–5</sup>. Alternatively, it could be a non-adaptive result of human impacts, such as habitat change or food provisioning<sup>6–9</sup>. To discriminate between these hypotheses we compiled information from 18 chimpanzee communities and 4 bonobo communities studied over five decades. Our data include 152 killings ( $n = 58$  observed, 41 inferred, and 53 suspected killings) by chimpanzees in 15 communities and one suspected killing by bonobos. We found that males were the most frequent attackers (92% of participants) and victims (73%); most killings (66%) involved intercommunity attacks; and attackers greatly outnumbered their victims (median 8:1 ratio). Variation in killing rates was unrelated to measures of human impacts. Our results are compatible with previously proposed adaptive explanations for killing by chimpanzees, whereas the human impact hypothesis is not supported.**

Substantial variation exists in rates of killing across chimpanzee study sites<sup>2–5,10–12</sup>. The human impact and adaptive strategies hypotheses both seek to explain this variation, but have contrasting predictions, which we test here (Tables 1 and 2). The human impact hypothesis states that killing is an incidental outcome of aggression, exacerbated by human activities such as deforestation, introducing diseases, hunting or providing food. Accordingly, lethal aggression should be high where human disturbance is high<sup>8</sup>.

In contrast, the adaptive strategies hypothesis views killing as an evolved tactic by which killers tend to increase their fitness through increased access to territory, food, mates or other benefits<sup>1–5,10–17</sup>. Kin selection<sup>18</sup> and evolutionary game theory<sup>19</sup> yield a set of specific predictions for how benefits and costs should vary with the context, age, sex, and genetic relatedness of the attackers and targets. Lethal aggression occurs within a diverse set of circumstances, but is expected to be most commonly committed by males; directed towards males; directed towards non-kin, particularly members of other groups; and committed when overwhelming numerical superiority reduces the costs of killing. Previous studies have developed and tested these specific hypotheses<sup>2,5,11–17</sup>; the present study represents the first effort to test multiple hypotheses simultaneously with a comprehensive data set. We assembled data from communities of eastern ( $n = 12$ ) and western ( $n = 6$ ) chimpanzees<sup>20</sup> studied over 426 years (median = 21 years; range: 4–53) and from 4 bonobo communities studied for 92 years (median = 21; range: 9–39; Extended Data Fig. 1). We rated each case of killing as observed, inferred, or suspected (see Methods; Extended Data Tables 1–4). To be conservative, we limited our analyses to those rated ‘observed’ and ‘inferred’ unless otherwise noted. We examined contrasting predictions relating to overall patterns of killings (Table 1) and variation among communities (Table 2).

Bonobos are consistently found to be less violent than chimpanzees<sup>2,21</sup>, and lower rates of killing are reported for western than eastern chimpanzees<sup>2,11</sup>. The human impact hypothesis could in theory ascribe these variations to different levels of disturbance. In contrast, in behavioural ecology, distinct populations are expected to respond to prevailing ecological circumstances through biological evolution and/or phenotypic

**Table 1 | Predicted patterns of lethal aggression**

Variable	Human impact hypothesis	Adaptive strategies hypothesis
Chimpanzees kill more than bonobos	None	+
Rate of killing over time	+	None
Sex bias: attackers	None	Mainly males
Sex bias: victims	None	Mainly males
Age of victims	None	Mainly young infants (most vulnerable and/or reduce time to mother's next estrus)
Genetic relatedness of attackers and victims	None	Mainly non-relatives (for example, members of other communities)
Numerical asymmetries	None	Victims greatly outnumbered

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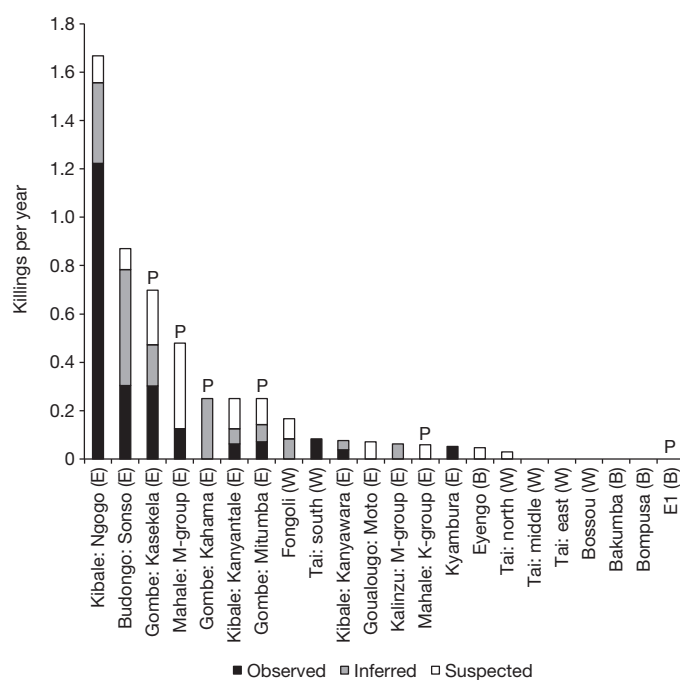
**Table 2 | Predicted correlates of number of killings per study community**

Variable	Human impact hypothesis	Adaptive strategies hypothesis
Provisioning (provisioned)	+	None
Size of protected area, km <sup>2</sup> (area)	–	None
Disturbance rating (disturbance)	+	None
Eastern vs. western chimpanzees (clade)	None	+
Mean number of adult males (males)	None	+
Mean population density (density)	None	+

flexibility. For bonobos and western chimpanzees, ecological factors apparently allow relatively high gregariousness, which reduces the risk of experiencing a lethal attack<sup>2,11</sup>. Our data set covers all major studies of both species of *Pan*, which include sites with and without a history of provisioning, and with high and low levels of human disturbance, a rating estimated independently by each site's director(s) (Methods; Extended Data Figs 1a and 2a).

We documented killings by chimpanzees in 15 of 18 communities (58 observed, 41 inferred, and 53 suspected cases; Extended Data Tables 1–4) (Fig. 1). For bonobos, we documented only a single (suspected) case, which occurred at Lomako, a never-provisioned site with a low disturbance rating. No killings were recorded at other bonobo sites, including one with a history of provisioning and a high disturbance rating (Wamba). Controlling for years of observation, chimpanzees had a higher rate of killing than bonobos; this difference was statistically significant for eastern but not western chimpanzees (Poisson regression:  $n = 22$  communities; estimated coefficients  $\pm$  s.e. for chimpanzees compared to bonobos:  $\beta_0 = -4.5 \pm 1.0$ ;  $\beta_{\text{east}} = 3.4 \pm 1.0$ ,  $z = 3.3$ ,  $P = 0.0008$ ;  $\beta_{\text{west}} = 0.65 \pm 1.2$ ,  $z = 0.56$ ,  $P = 0.57$ ; overall effect of clade:  $\chi^2 = 80.8$ ,  $df = 2$ ,  $P < 0.0001$ ). This difference persisted when 'suspected' cases were included (Extended Data Table 5a).

To investigate which factors best explained variation in killing rates among chimpanzee communities, we used an information theoretic approach<sup>22</sup>, controlling for years of observation. We considered three variables for the human impact hypothesis: provisioned (whether the



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

community had been artificially fed); area (size of protected area, with smaller areas assumed to experience more impacts); and disturbance. We also considered three variables for the adaptive strategies hypothesis: clade (eastern and western chimpanzees may have different histories of selection for violence); males (number of adult males, which may influence rates of killing via intensity of reproductive competition and/or coalitional fighting power), and density (number of individuals per km<sup>2</sup>, which may affect frequency of intercommunity encounter and/or intensity of resource competition). We consider density to reflect natural food abundance. For example, at Ngogo (4.5 chimpanzees per km<sup>2</sup>), vegetation sampling revealed high forest productivity<sup>23</sup> and chimpanzees have high C-peptide levels<sup>24</sup>, indicating high energy balance; whereas at Fongoli (0.37 chimpanzees per km<sup>2</sup>), chimpanzees range widely across a dry savannah with sparse food<sup>25</sup>. Density was unrelated to disturbance (general linear model,  $F_{1,16} = 1.4$ ,  $P = 0.26$ ).

Of the 16 models we considered (Table 3), four of the five models in the resulting 95% confidence set included combinations of the adaptive variables; the fifth model included the three human impact variables. The best model included only males and density, and was supported 6.8 times more strongly than the human impact model (evidence ratio =  $w_i/w_j = 0.40/0.059 = 6.8$ ). Considering model-averaged parameter estimates<sup>22</sup>, increases in *males* and *density* increased the number of killings; for all other parameter estimates, the 95% confidence intervals included zero (Table 3 and Fig. 2). Excluding one community (Ngogo) that had both an unusually high killing rate and unusually many males resulted in similar values for model-averaged parameters, but only the estimate for density excluded zero from the 95% confidence interval (Extended Data Table 5b;  $n = 17$ ).

Opposite to predictions from the human impact hypothesis (Table 2), provisioned and disturbance both had negative effects; the estimates for these parameters included zero in the 95% confidence intervals (Table 3 and Extended Data Fig. 2b). The highest rate of killing occurred at a relatively undisturbed and never-provisioned site (Ngogo); chimpanzees at the least disturbed site (Goualougo) were suspected of one killing and inferred to have suffered an intercommunity killing; and no killings occurred at the site most intensely modified by humans (Bossou).

As a test of confidence, we investigated the effects of including suspected cases and data from bonobos. Including suspected cases changed western and provisioned from negative to positive (Extended Data Table 5b). Nonetheless, even with these suspected cases, none of the estimates for human impact variables excludes zero from the 95% confidence interval. Including bonobo data widened the confidence intervals for density (Extended Data Table 5b), probably because two bonobo communities had high densities (Extended Data Fig. 1a). With either suspected cases or bonobo data added, only for males did the 95% confidence intervals exclude zero (Extended Data Table 5b). Thus, although demographic variables explain variation in rates of killing better than human impact variables, the confidence intervals are sensitive to including suspected cases or data from another species (bonobos).

These analyses combine killings committed for varied reasons by individuals in different age–sex classes. A full explanation of these events requires a finer grained analysis. To this end, we examined variation over time and among different categories of attacker and victim.

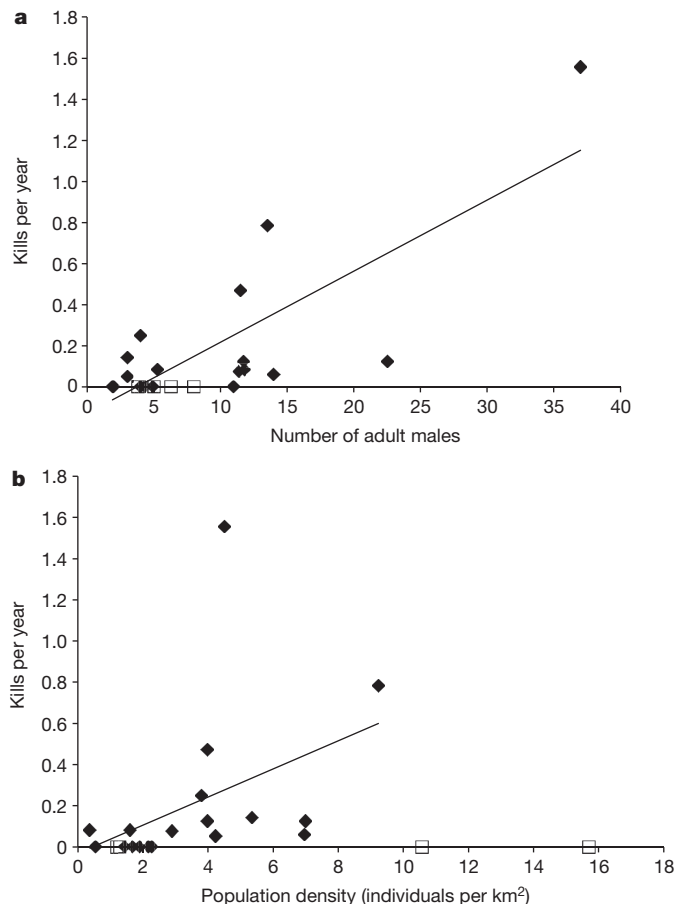
Increasing human impacts have been proposed to cause increasing numbers of killings in recent years<sup>8</sup>. However, controlling for changes in the number of communities observed per year (communities), the rate of killing has not changed over time (year). Using an information theoretic approach<sup>22</sup> to compare three different models (year; communities; and year plus communities), the best model contained only communities; considering model-averaged parameters, the 95% confidence interval excluded zero for communities, but not year (Poisson regression:  $n = 52$  years; model-averaged parameters and 95% confidence interval:  $\beta_0 = 10$  (–38 to 58);  $\beta_{\text{year}} = -0.0058$  (–0.022 to 0.010);  $\beta_{\text{communities}} = 0.18$  (0.10–0.26); Extended Data Table 5c).

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

	<i>B</i>	Clade	Males	Density	Area	Prov	Dist	<i>K</i>	$\Delta_i$	$w_i$
	-3.6		0.081	0.21				4	0.00	0.40
	-2.3	-1.9	0.073					4	0.61	0.30
	-3.1	-1.4	0.073	0.15				5	1.8	0.16
	-2.7		0.087					3	3.4	0.07
	7.1				-0.0016	-1.4	-0.63	5	3.8	0.06
	-2.2	2.4	0.10	0.42	-0.00083	1.3	-0.27	8	10	0.00
	3.7				-0.0011		-0.40	4	12	0.00
	-2.0	-2.1		0.17				4	17	0.00
	-1.2	-2.7						3	18	0.00
	-2.8			0.28				3	21	0.00
	-1.1				-0.00042			3	24	0.00
	-1.1				-0.00042	-0.12		4	28	0.00
	-1.5							2	34	0.00
	-1.6					0.19		3	36	0.00
	-1.4						-0.011	3	37	0.00
	-1.6					0.18	-0.0046	4	40	0.00
MAP	-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			

Parameters include the intercept (*B*); impact of western relative to the eastern clade of chimpanzees; mean number of adult males per community (males); mean population density per community (density); size of protected area in km<sup>2</sup> (area); history of regular provisioning with food (prov); disturbance rating (dist); the number of free parameters (*k*) including the dispersion parameter ( $\hat{c} = 2.8$ ); the difference in Akaike information criterion (corrected for overdispersion: QAICc) between the *i*th model and the best model ( $\Delta_i$ ); and model weight ( $w_i$ ). Models are arranged in order from best (lowest  $\Delta$ QAICc) to worst (highest  $\Delta$ QAICc). The weight of the model ( $w_i$ ) is the probability that a given model is the best model in a given set of models. Model-averaged parameter estimates (MAP) with upper (97.5%) and lower (2.5%) bounds of the 95% confidence intervals are given in the bottom rows.

Killings involved a median of five male attackers (range: 0–19) and no females (range: 0–6). Considering all cases for which the number of attackers was observed ( $n = 58$ ) or could be inferred ( $n = 6$ ), males



**Figure 2 | Number of killings per year for each community versus number of males and population density.** Rates for each community are indicated by black diamonds (chimpanzees;  $n = 18$ ) and open squares (bonobos;  $n = 4$ ). Black lines indicate simple linear regression for chimpanzee data for illustrative purposes only; statistical tests were done using Poisson regressions. **a**, Number of killings versus number of males. **b**, Number of killings versus population density (individuals per km<sup>2</sup>).

constituted 92% of participants in attacks (338/366). Controlling for observation time and community composition, males were much more likely to participate in killings than females (negative binomial mixed model:  $n = 36$  observations (fixed effects: *sex* with 2 levels; random effects: community with 18 levels);  $\beta_0 = -6.9 \pm 0.98$ ;  $\beta_{\text{males}} = 2.6 \pm 0.59$ ,  $z = 4.42$ ,  $P < 0.0001$ ). Females sometimes joined males in attacking grown individuals ( $n = 3$ ), but when acting without males, females killed only young infants ( $n = 8$ ).

Controlling for observation time and community composition, males and infants had the highest probability of being killed (Extended Data Table 6). Notably, during infanticides, attackers sometimes removed infants from mothers under circumstances in which they appeared capable of killing the mother as well, but did not do so.

Most victims were members of different communities from the attackers ( $n = 62$  of 99 cases; 63%) and thus not likely to be close kin<sup>26</sup>. This difference is particularly striking given that chimpanzees could potentially attack members of their own community on a daily basis, but rarely encounter members of other communities (for example, 1.9% of follow days at Kanyawara<sup>27</sup>).

Intercommunity killings mainly involved parties with many males (median = 9 males, range: 2–28,  $n = 36$  cases with known numbers of attackers) attacking isolated or greatly outnumbered males or, more often, mothers with infants (median = 0 males, range: 0–3,  $n = 30$ ; median = 1 female, range: 0–5,  $n = 31$ ). For 30 cases in which the number of adult and adolescent males and females on each side were known, attackers outnumbered defenders by a median factor of 8 (range: 1–32; Extended Data Table 7). Most intercommunity killings thus occurred when attackers overwhelmingly outnumbered victims.

Several robust patterns emerge from these data. Killing was most common in eastern chimpanzees and least common among bonobos. Among chimpanzees, killings increased with more males and higher population density, whereas none of the three human impact variables had an obvious effect. Male chimpanzees killed more often than females, and killed mainly male victims; attackers most frequently killed unweaned infants; victims were mainly members of other communities (and thus unlikely to be close kin); and intercommunity killings typically occurred when attackers had an overwhelming numerical advantage. The most important predictors of violence were thus variables related to adaptive strategies: species; age–sex class of attackers and victims; community membership; numerical asymmetries; and demography. We conclude that patterns of lethal aggression in *Pan* show little correlation with human impacts, but are instead better explained by the adaptive hypothesis that killing is a means to eliminate rivals when the costs of killing are low.

**Online Content** Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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## METHODS

**Animal subjects.** We report data from non-invasive field studies of wild bonobos (*Pan paniscus*;  $n = 4$  communities) and chimpanzees (*Pan troglodytes*) from eastern ( $n = 12$ ) and western ( $n = 6$ ) populations. We included all populations that were fully habituated and monitored for at least 10 years (one community, Kahama, was monitored as an independent community for less than 10 years (1973–1977), but these chimpanzees had been monitored previously (1960–1972) before the splitting of the Kasekela community). Neither randomization nor blinding of investigators was used, as the study involved collection of long-term data rather than experimental trials. All studies were conducted in compliance with IRB requirements of the respective institutions.

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

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

**Human disturbance scores.** We scored human disturbance as the sum of five separate ratings adapted from<sup>28</sup>, each scored on a 1 to 4 point scale, giving a possible range of 5–20 points: (1) disturbance to habitat; (2) degree of harassment of study animals by people; (3) amount of hunting of study animals; (4) degree of habituation to human observers at beginning of studies; and (5) whether major predators have been eliminated (on the assumption that the elimination of major predators by humans is associated with higher levels of human impact). The different measures of disturbance were not strongly inter-correlated. Of the 10 pairwise comparisons among the 5 measures, the median correlation coefficient for the 22 study communities was 0.24 (range:  $-0.06$  to  $0.78$ ). The two pairs that had a correlation coefficient higher than 0.5 were (home range)(harassment) = 0.78, and (harassment)(predators) = 0.52. Thus, communities with high disturbance to their home range habitat also suffered more harassment by people, and communities with more harassment by people also had fewer natural predators remaining in their habitat. The median variance among the 5 measures was 1.0 (range:  $0.7$ – $1.4$ ). None of these variances differed significantly from the others ( $F$ -tests:  $P > 0.05$ ).

**Statistical tests.** We conducted statistical tests using R 3.0.2 (ref. 29). To test for differences in rates of killing between bonobos and the two clades of chimpanzees (eastern and western<sup>30</sup>), we conducted Poisson regressions with  $\log(\text{years of study})$  as an offset. The fact that bonobos had the same response for all communities (zero observed/inferred killings) resulted in a complete separation problem<sup>30</sup>. We addressed this by doing a series of four Poisson regressions, each time replacing the 0 killings for one of the four bonobo communities with 1 killing to make the data less extreme, and averaging the results. This provides a conservative estimate of the difference in rates of killing between chimpanzees and bonobos.

To investigate which factors best explained the number of killings per chimpanzee community, we examined a set of a priori specified models, based on hypothesized effects of six independent variables: clade; males (mean number of males  $\geq 12$  years old), density (mean number of individuals per community/home range ( $\text{km}^2$ )); area (size ( $\text{km}^2$ ) of national park or reserve in which community resided); provisioned (whether the community had a history of being regularly provisioned with food by researchers) and disturbance (sum of five four-point ratings, based on ref. 28). Each model consisted of a Poisson regression with the total count of observed/inferred killings committed by each community as the dependent variable, and  $\log(\text{years of study})$  as an offset. We recognize that years of study is a rather coarse-grained measure of observation time, but finer grained measures such as total number of observation hours were not available for all communities. We selected models to distinguish between the predictor variables most closely associated with the adaptive strategies hypothesis (clade, males, and density) and the human impact hypothesis (protected area, provisioned and disturbance), including the null model, models with each variable by itself, combinations of up to three variables associated with each hypothesis, and the full model. We limited the number of variables per model to avoid over-fitting, and limited the number of

models tested to reduce the risk of finding spurious correlations. We corrected for overdispersion and small sample size using QAICc, ranked models according to QAICc score (lowest = best), and used results from all models to calculate model-averaged estimates of parameters<sup>21</sup>.

To test for sex differences in participation in lethal aggression, we conducted a GLMM with negative binomial error structure using the *glmmADMB* package<sup>31</sup>. For the dependent variable, we used the number of participations in killings by each sex for each community. We defined participation as the active involvement of an individual during a lethal attack (for example, making or attempting to make direct aggressive contact with the victim). For each case for which the attackers were observed directly, or could be inferred with confidence, we counted the number of attackers of each sex. For each community, we summed the number of attackers across all cases to obtain the number of times individuals of each sex participated in attacks. Independent variables consisted the fixed effect *sex* (2 levels: male and female) and the random effect community (18 levels). To control for community composition, we used  $\log(\text{chimp-years})$  for each sex in each community as an offset. *Chimp-years* was defined for each age–sex class as years of study multiplied by the mean number of individuals of that age–sex class present in the victim's community.

To test for patterns in the age–sex class of victims, we conducted a GLMM with Poisson error structure using the *lme4* (1.0-5) package<sup>32</sup>. To control for possible sex differences in motivation for killing, we excluded from analysis the 8 cases that were known to have been committed solely by females. For the dependent variable, we used the number of observed and inferred victims of each age–sex class for each community. Independent variables with fixed effects were *sex* (2 levels) and age-class (four levels, as categorized above (demographic data)) and the random effect community (26 levels: 18 habituated communities and 8 unhabituated communities) (victims of intercommunity killings by study communities). Because one community (Kahama) had zero adolescent males, and the number of infants and juveniles were not specified for another (Kalinzu), the total number of age–sex class and community combinations in our analysis ( $n = 203$ ) was less than would be if all age–sex classes were represented for each community ( $(2 \text{ sexes}) \times (4 \text{ age classes}) \times (26 \text{ communities}) = 208$ ). To control for the composition of the different communities, we used  $\log(\text{chimp-years})$  as an offset. For unhabituated communities, for which demographic information was not available, we defined *chimp-years* as the number of years of observation of the focal community (the community being observed when the killing occurred), multiplied by the median number of individuals of that age–sex class present in the median chimpanzee community. Because the range size and membership of unhabituated communities was not known, we assigned victims to no more than one unhabituated community per study community; this undoubtedly underestimates the total number of communities involved, but should not affect the goal of this analysis, which was to estimate the effect of age and sex class on the risk of being killed, given the proportion of each age–sex class in the population. For *chimp-years* for victims of unknown sex, we used the mean number of males and females present for that age class. To keep type I error rate at the nominal level of 5% we included random slopes of each level of the fixed effects *sex* and age–class within the random effect community<sup>33,34</sup>.

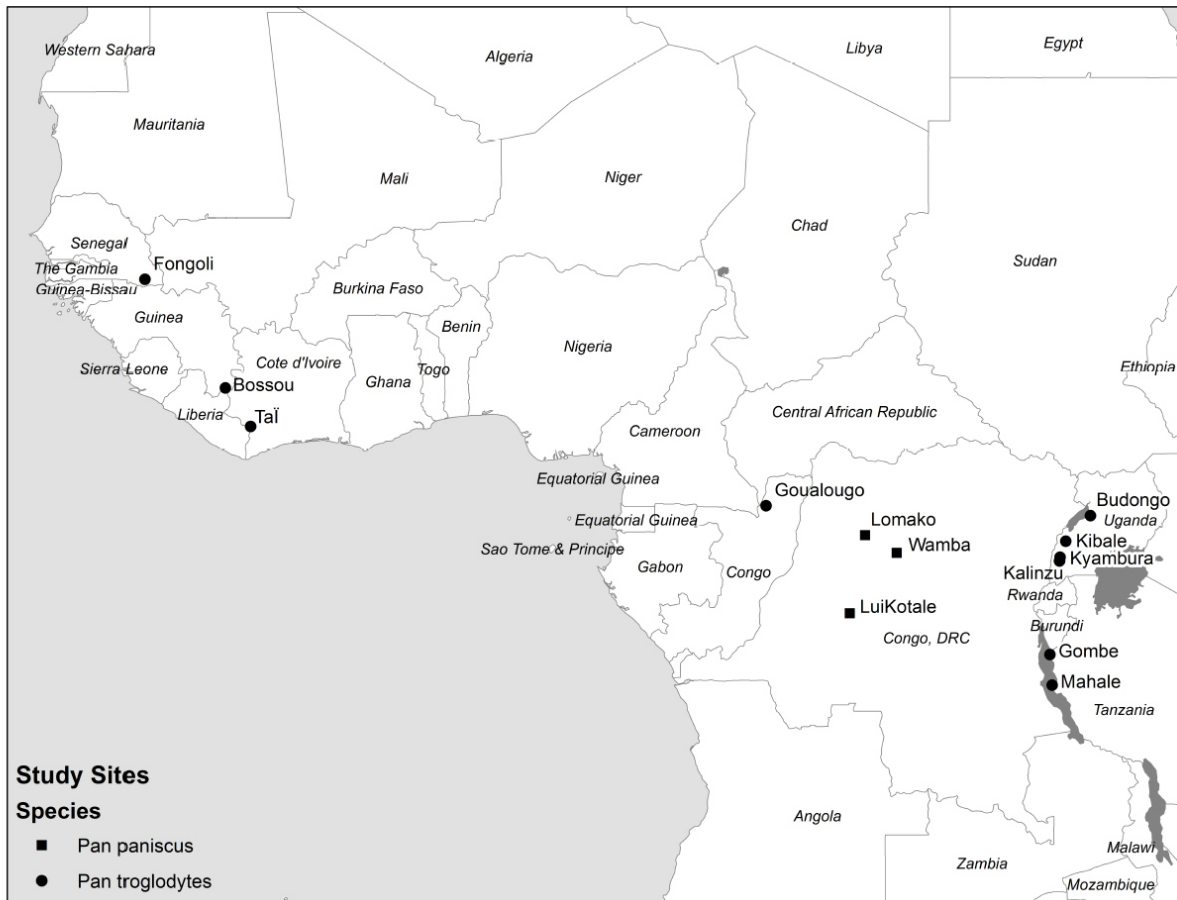
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a.

Clade	Site	Community	Study duration	Years	Community	Males	Females	Home range	Density	Area (km <sup>2</sup> )	Provisioned	Disturbance
E	Gombe	Kasekela	1960-present	53	48.5	11.5	16.9	12.2	4	35	yes	11
E	Gombe	Kahama	1973-1977	4	15.6	4.0	2.6	4.1	3.8	35	yes	10
E	Gombe	Mitumba	1985-present	28	24.6	3.0	8.1	4.6	5.3	35	yes	12
E	Mahale	K-group	1965-1982	17	23.5	4.0	10.1	10.4	2.3	1613	yes	7
E	Mahale	M-group	1965-present	48	70.3	11.7	27.3	17.7	4	1613	yes	8
E	Budongo	Sonso	1990-present	23	62.6	13.5	23.2	6.8	9.2	435	no	12
E	Kalinzu	Kalinzu M-group	1997-present	16	73.0	14.0	20.0	10.5	7	137	no	12
E	Kibale	Kanyawara	1987-present	26	47.7	11.4	16.4	16.5	2.9	766	no	13
E	Kibale	Ngogo	1995-present	18	144.0	37.0	51.0	32.0	4.5	766	no	9
E	Kibale	Kanyantale	1997-present	16	84.0	22.5	25.5	12.0	7	766	no	12.5
E	Kyambura	Kyambura	1994-present	19	18.0	3.0	6.0	4.3	4.2	3.05	no	13.5
E	Goualougo	Moto	1999-present	14	42.0	11.0	14.0	25.0	1.7	4237	no	5
W	Tai	North	1979-present	34	36.4	4.3	13.0	16.8	2.2	5400	no	8
W	Tai	South	1989-present	24	42.5	5.3	14.7	26.5	1.6	5400	no	8
W	Tai	Middle	1989-present	24	6.7	2.0	2.1	12.1	0.6	5400	no	8
W	Tai	East	2000-present	13	43.1	4.9	15.0	30.0	1.4	5400	no	8
W	Bossou	Bossou	1976-present	37	17.0	1.9	6.7	9.0	1.9	0	no	17
W	Fongoli	Fongoli	2001-present	12	31.7	11.8	7.0	86.0	0.37	0	no	14
B	Lomako	Bakumba	1977-1998	21	44.0	8.0	14.0	2.8	15.7	3600	no	6
B	Lomako	Eyengo	1977-1998	21	31.2	5.0	7.0	2.9	10.6	3600	no	6
B	LuiKotale	Bompusa	2002-present	11	32.2	3.8	10.2	25.0	1.3	36000	no	12
B	Wamba	E1	1974-present	39	24.1	6.3	6.6	20.0	1.2	481	yes	16

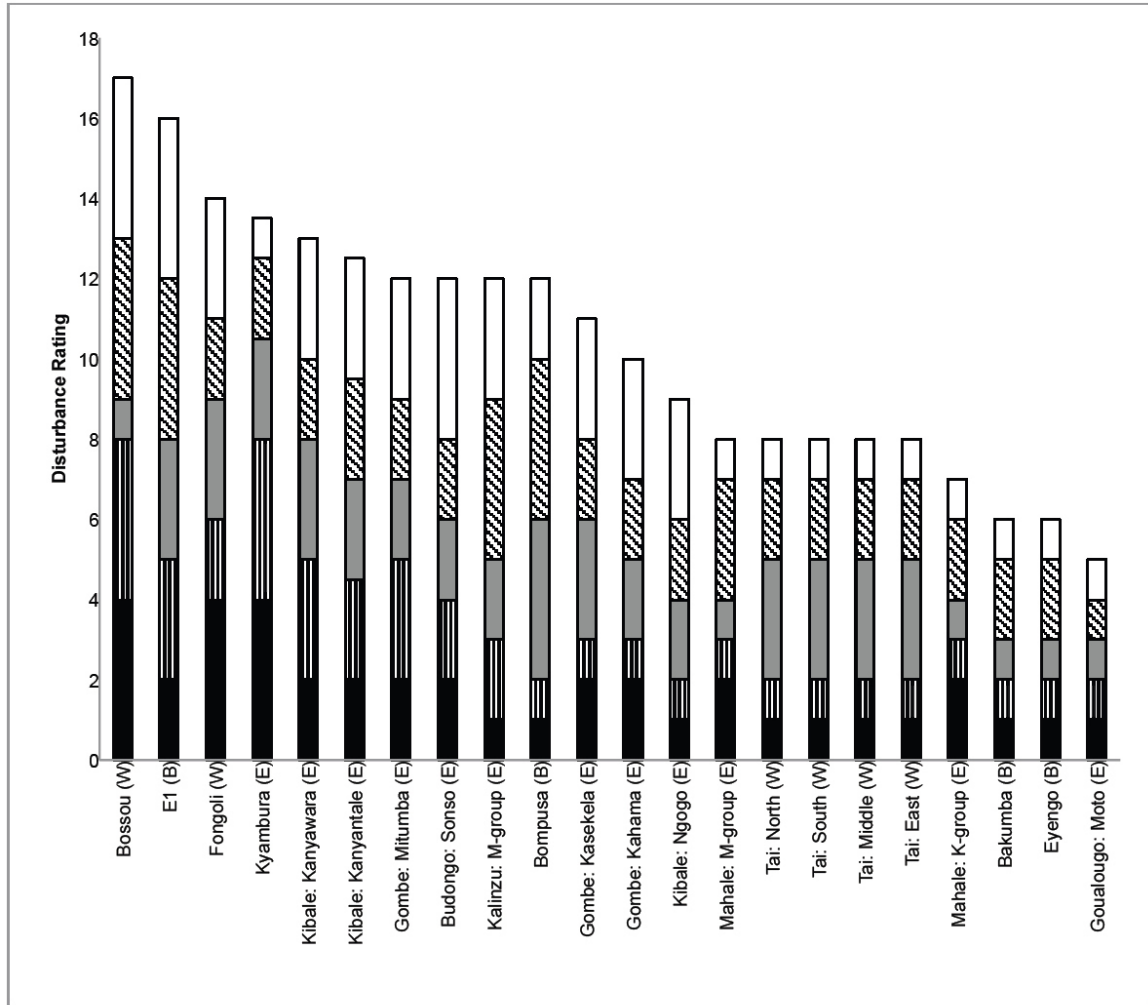
b.



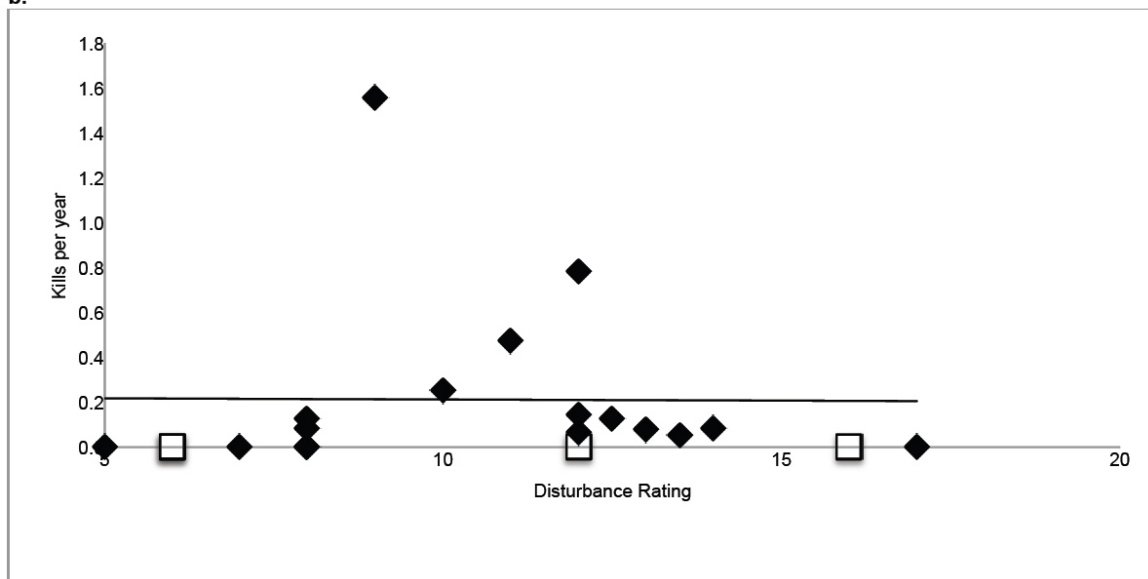
**Extended Data Figure 1 | Summary data and location of study sites.**  
**a.** Summary data for each community. Clade: bonobos (B), eastern chimpanzees (E), western chimpanzees (W); community: mean total size of the community; males: mean number of males  $\geq 12$  years old; females: mean number of females  $\geq 12$  years old; home range: mean size of the community's

home range (km<sup>2</sup>); density = (community)/(home range); area: size of protected area inhabited by the community; provisioned: whether community was regularly provisioned with food; disturbance: sum of the disturbance rating scores. **b.** Location of chimpanzee (circles;  $n = 10$ ) and bonobo (squares;  $n = 3$ ) study sites in Africa.

a.



b.



**Extended Data Figure 2 | Disturbance ratings.** a, Disturbance ratings for each site: disturbance to habitat (black bars); harassment of study animals by people (vertical lines); amount of hunting of study animals (grey); degree of habituation to people at start of study (diagonal hatching); and whether major predators have been eliminated (white). Clade is indicated by letters following

community name: bonobos (B), eastern chimpanzees (E), and western chimpanzees (W). b, Number of killings per year vs. disturbance. Rates for each community are indicated by black diamonds (chimpanzees;  $n = 18$ ) and open squares (bonobos;  $n = 4$ ).



Extended Data Table 1 | Intercommunity killings of weaned victims

Site	Date	Victim	Age (years)	Sex	Aggressor's community	Victim's community	Certainty	Ref.
Gombe	7-Jan-74	Godi	20.5	M	Kasekela	Kahama	Observed	1
Gombe	26-Feb-74	Dé	25.8	M	Kasekela	Kahama	Observed	1
Gombe	7-Feb-75	Goliath	37.6	M	Kasekela	Kahama	Observed	1
Gombe	14-Sep-75	Madam B	30.2	F	Kasekela	Kahama	Observed	1
Gombe	12-Nov-77	Sniff	17.4	M	Kasekela	Kahama	Observed	1
Gombe	14-Aug-98	Unknown	10	M	Kasekela	Kalande	Observed	35
Gombe	19-Sep-05	Patti	44.3	F	Mitumba	Kasekela	Observed	36
Kibale	3-Jun-02	Unknown	Adult	M	Ngogo	North-eastern	Observed	37
Kibale	9-Aug-02	Unknown	6	M	Ngogo	North-eastern	Observed	37
Kibale	23-Nov-02	Unknown	Adult	M	Ngogo	Wantabu	Observed	37
Kibale	1-Aug-04	Unknown	Adult	M	Ngogo	North-eastern	Observed	37
Kibale	22-Nov-04	Unknown	Adult	M	Ngogo	South-western	Observed	*
Kibale	11-Aug-06	Unknown	Adult	M	Ngogo	North-eastern	Observed	5
Kibale	2-Aug-09	Unknown	Adult	F	Ngogo	South-western	Observed	5
Tai	1-Mar-05	Nerone	Adult	M	South	East	Observed	11
Budongo	7-May-11	Zak	8	M	Northwest	Sonso	Inferred	*
Budongo	7-May-11	Zimba	44	F	Northwest	Sonso	Inferred	*
Gombe	12-Aug-73	Unknown	Adult	F	Kahama?	Kalande?	Inferred	38
Gombe	8-Sep-77	Charlie	25.9	M	Kasekela	Kahama	Inferred	1
Gombe	26-Jun-02	Rusambo	12	M	Kasekela	Mitumba	Inferred	35
Kalinzu	2-Feb-13	Unknown	Adult	M	Kalinzu M-group	Unknown	Inferred	*
Kalinzu	13-Sep-03	Nui	Adult	M	Unknown	Kalinzu M-group	Inferred	39
Kibale	25-Aug-98	Unknown	Adult	M	Kanyawara	Sebitole	Inferred	37,40
Kibale	7-May-06	Unknown	Adult	M	Ngogo	North-eastern	Inferred	5
Kibale	19-Mar-11	Unknown	Adult	M	Ngogo	North-eastern	Inferred	*
Kibale	29-Apr-04	Dani	Adult	F	Northeastern	Ngogo	Inferred	*
Kibale	10-Aug-92	Ruwenzori	13.1	M	Rurama	Kanyawara	Inferred	2
Kibale	31-Jul-05	Waller	15	M	West-Southwest	Ngogo	Inferred	*
Kibale	31-Jul-05	Branford	21	M	West-Southwest	Ngogo	Inferred	*
Gombe	21-Jan-98	Prof	26.2	M	Kalande?	Kasekela	Suspected	*
Gombe	7-Dec-72	Hugh	28.4	M	Kasekela?	Kahama	Suspected	1
Gombe	16-Dec-77	Willy Wally	26.5	M	Kasekela?	Kahama	Suspected	1
Gombe	1-Sep-04	Fifi	46.2	F	Mitumba?	Kasekela	Suspected	*
Gombe	6-Sep-75	Faben	28.2	M	Unknown	Kasekela	Suspected	1
Gombe	5-Nov-79	Sherry	18.3	M	Unknown	Kasekela	Suspected	1
Gombe	29-May-81	Humphrey	34.9	M	Unknown	Kasekela	Suspected	1
Gombe	20-Jul-82	Figan	29	M	Unknown	Kasekela	Suspected	1
Kibale	2010	Unknown	Adult	M	Kanyantale	Buraiga	Suspected	*
Kibale	5-Dec-98	Unknown	Adult	M	Ngogo?	Kanyantale?	Suspected	*
Kibale	27-Jul-94	Julian	20.1	M	Unknown	Kanyawara	Suspected	12
Kibale	18-Aug-98	Badfoot	32.1	M	Unknown	Kanyawara	Suspected	12
Kibale	24-Feb-01	Light Brown	32.6	M	Unknown	Kanyawara	Suspected	12
Mahale	1970	Kaguba	Adult	M	M-group?	K-group	Suspected	41
Mahale	1978	Kasonta	Adult	M	M-group?	K-group	Suspected	41
Mahale	Apr-75	Kasanga	Adult	M	M-group?	K-group	Suspected	41
Mahale	Oct-75	Kajabala	Adult	M	M-group?	K-group	Suspected	41
Mahale	Jun-79	Sobongo	Adult	M	M-group?	K-group	Suspected	41
Mahale	Sep-82	Kamemanfu	Adult	M	M-group?	K-group	Suspected	41
Mahale	Dec-82	Masisa	Adult	M	M-group?	K-group	Suspected	41

The reference column (ref.) also includes references 35–41 listed in the Methods or the asterisk symbol in the reference column indicates unpublished data from the following sources: Kibale (22 November 2004) from Alfred Tumusiime and Adolph Magoba; Budongo (7 May 2011) from Budongo Chimpanzee Project; Kalinzu (2 February 2013) from Kathelijne Koops and Chie Hashimoto; Kibale (19 March 2011) from John C. Mitani; Kibale (29 April 2004) from Monica L. Wakefield; Kibale (31 July 2005) from David P. Watts; Gombe (21 January 1998 and 1 September 2004) from Gombe Stream Research Centre; and Kibale (2010 and 5 December 1998) from Julia Lloyd.

Extended Data Table 2 | Intercommunity infanticides

Site	Date	Victim	Age (years)	Sex	Aggressor's community	Victim's community	Certainty	Ref.
Budongo	29-Sep-95	Unknown	Infant	M	Sonso	N15_(Nature Reserve)	Observed	42
Budongo	3-Feb-06	Unknown	0.003	Unknown	Sonso	Unknown	Observed	43
Gombe	Sep-71	Unknown	Infant	Unknown	Kasekela	Unknown	Observed	44
Gombe	2-Nov-75	Unknown	1.75	F	Kasekela	Unknown	Observed	45
Gombe	20-Mar-79	Unknown	2	Unknown	Kasekela	Unknown	Observed	1
Gombe	30-Mar-93	Rejea	0.38	F	Kasekela	Mitumba	Observed	35
Gombe	29-Oct-98	Unknown	1	Unknown	Kasekela	Kalande	Observed	35
Kibale	21-Feb-11	Unknown	Infant	Unknown	Ngogo	Northeastern	Observed	*
Kibale	3-Apr-99	Unknown	Infant	Unknown	Ngogo	Northeastern	Observed	46
Kibale	28-Jun-99	Unknown	Infant	Unknown	Ngogo	Eastern	Observed	46
Kibale	5-Jul-00	Unknown	2	Unknown	Ngogo	Northeastern	Observed	47
Kibale	19-Jul-01	Unknown	Juvenile	Unknown	Ngogo	Northeastern	Observed	5
Kibale	6-Oct-04	Unknown	Infant	Unknown	Ngogo	Southwestern	Observed	48
Kibale	12-Oct-04	Unknown	Infant	Unknown	Ngogo	Wantabu	Observed	48
Kibale	12-Oct-04	Unknown	Infant	Unknown	Ngogo	Wantabu	Observed	48
Kibale	13-Oct-05	Unknown	Infant	Unknown	Ngogo	Southwestern	Observed	5
Kibale	1-Feb-06	Unknown	Infant	Unknown	Ngogo	Northeastern	Observed	*
Kibale	25-Jul-07	Unknown	Infant	Unknown	Ngogo	Northeastern	Observed	5
Kibale	29-Jun-11	Unknown	2	Unknown	Ngogo	Southwestern	Observed	*
Mahale	12-Dec-00	Unknown	2.5	M	M-group	Unknown	Observed	49
Tai	8-Sep-02	Unknown	Infant	M	South	West?	Observed	11
Budongo	2-Feb-95	Unknown	Infant	Unknown	Sonso	N15_(Nature Reserve)	Inferred	42
Budongo	1-Aug-97	Unknown	0.06	Unknown	Sonso	Unknown	Inferred	*
Budongo	22-Jan-00	Unknown	0.08	F	Sonso	Unknown	Inferred	*
Budongo	6-Aug-05	Unknown	Infant	Unknown	Sonso	Unknown	Inferred	*
Budongo	25-Jan-13	Unknown	Infant	Unknown	Sonso	Unknown	Inferred	*
Gombe	30-Sep-75	Unknown	0.75	M	Kasekela	Unknown	Inferred	45
Gombe	13-Aug-05	Andromeda	0.67	F	Kasekela	Mitumba	Inferred	36
Goualougo	16-May-05	Rausch	0.7	M	Unknown	Moto	Inferred	*
Kibale	5-Jul-00	Unknown	2	Unknown	Ngogo	Northeastern	Inferred	47
Kibale	21-Feb-05	Unknown	Infant	Unknown	Ngogo	Southwestern	Inferred	5
Kibale	27-Jul-07	Unknown	2	Unknown	Ngogo	Northeastern	Inferred	5
Kibale	26-Apr-10	Unknown	Infant	Unknown	Ngogo	Northeastern	Inferred	*
Gombe	15-Oct-81	Hepziba	1.3	F	Mitumba?	Kasekela	Suspected	1,36
Gombe	1-Sep-04	Furaha	1.90	F	Mitumba?	Kasekela	Suspected	*
Gombe	31-Jul-81	Dapples	2.8	M	Unknown	Kasekela	Suspected	36
Gombe	30-Jul-82	Barbet	3.9	F	Unknown	Kasekela	Suspected	36
Kibale	15-Sep-14	Unknown	Juvenile	Unknown	Kanyantale	Unknown	Suspected	*
Mahale	25-Apr-74	Shigeo	3	M	K-group	M-group	Suspected	50
Mahale	15-Jan-76	Wanten-dele's infant	1.5	M	M-group	K-group	Suspected	50

The reference column (ref.) also includes references 42–50 listed in the Methods or the asterisk symbol indicates unpublished data from the following sources: Kibale (21 February 2011) from Jim Fenton and Godfrey Mbabazi; Kibale (1 February 2006) from Sylvia J. Amstler and William R. Wallauer; Kibale (29 June 2011) from David P. Watts; Budongo (1 August 1997, 22 January 2000, 6 August 2005 and 25 January 2013) from Budongo Chimpanzee Project; Goualougo (16 May 2005) from David B. Morgan and Crickette M. Sanz; Kibale (26 April 2010) from Melanie Beuerlein, Alfred Tumusiime and Ambrose Twineomujuni; Gombe (1 September 2004) from Gombe Stream Research Centre; and Kibale (15 September 2014) from Julia Lloyd.

Extended Data Table 3 | Intracommunity killings of weaned victims

Site	Date	Victim	Age	Sex	Community	Certainty	References
Kyambura	17-Feb-11	Hatari	21	M	Kyambura	Observed	*
Mahale	2-Oct-11	Pimu	23	M	M-group	Observed	51
Gombe	22-Dec-04	Vincent	28.5	M	Mitumba	Observed	36
Kibale	29-Aug-02	Grapelli	Adult	M	Ngogo	Observed	52
Fongoli	15-Jun-13	Foudouko	25	M	Fongoli	Inferred	*
Gombe	9-Oct-94	Mel	10.7	M	Kasekela	Inferred	36
Gombe	21-Apr-67	Huxley	40.8	M	Kasekela	Inferred	1
Gombe	17-Jan-05	Ebony	8.2	M	Mitumba	Inferred	36
Budongo	4-Nov-98	Zesta	Adult	M	Sonso	Inferred	53
Fongoli	18-24 Mar 2010	Frito	12	M	Fongoli	Suspected	*
Gombe	24-May-10	Kris	28.3	M	Kasekela	Suspected	*
Gombe	4-Mar-93	Evered	40.7	M	Kasekela	Suspected	36
Gombe	10-Nov-13	Frodo	37.4	M	Kasekela	Suspected	*
Mahale	14-Nov-95	Ntologi	40	M	M-group	Suspected	54
Lomako (Bonobo)	28-Oct-97	Volker	Adult	M	Eyengo	Suspected	55
Budongo	15-Jan-08	Lola	21	F	Sonso	Observed	56
Budongo	3-Aug-07	Zana	27	F	Sonso	Inferred	*
Gombe	22-Jan-68	Pooch	12.6	F	Kasekela	Suspected	1

The reference column (ref.) also includes references 51–56 listed in the Methods or the asterisk symbol indicates unpublished data from the following sources: Kyambura (17 February 2011) from Nicole Simmons; Fongoli (15 June 2013 and 18–24 March 2010) from Jill Pruetz; Gombe (24 May 2010 and 10 November 2013) from Gombe Stream Research Centre; and Budongo (3 August 2007) from Budongo Chimpanzee Project.

Extended Data Table 4 | Intracommunity infanticides

Site	Date	Victim	Age	Sex	Community	Certainty	References	Attacker(s)
Gombe	13-Jun-04	Tofiki	3.7	M	Kasekela	Observed	57	Male
Gombe	24-Aug-13	Tarime	0.88	F	Kasekela	Observed	*	Male
Mahale	3-Oct-89	Mirinda's infant	0.5	M	M-group	Observed	58	Males
Mahale	5-Jul-83	Wantendele's infant	0.08	M	M-group	Observed	59	Males
Mahale	16-Jul-85	Tomato's infant	0.8	M	M-group	Observed	58	Males
Mahale	24-Jul-90	Betty's infant	0.4	M	M-group	Observed	58	Males
Kibale	10-Aug-05	Unnamed infant	0.007	Unknown	Ngogo	Observed	*	Males
Kibale	17-Jun-09	Unknown	0.008	Unknown	Ngogo	Observed	*	Males
Budongo	25-Jul-12	Unknown	0.003	F	Sonso	Observed	*	Males
Budongo	30-Jul-13	Kalema's infant	0.01	Unknown	Sonso	Observed	*	Males
Kibale	14-Dec-96	Temba	2.5	M	Kanyawara	Observed	77	Male and female
Gombe	3-Sep-12	Eliza's infant	0.01	F	Kasekela	Observed	*	Males and female
Budongo	13-Aug-09	Juliet's infant	0.02	Unknown	Sonso	Observed	*	Male and females
Gombe	15-Aug-75	Otta	0.08	F	Kasekela	Observed	1,45	Females
Gombe	21-Nov-76	Genie	0.05	F	Kasekela	Observed	45	Females
Gombe	22-Oct-76	Orion	0.2	M	Kasekela	Observed	45	Females
Budongo	9-Nov-12	Janie's infant	0.01	Unknown	Sonso	Observed	*	Females
Gombe	8-Jan-76	Melissa's infant	0.004	M	Kasekela	Inferred	45	Females
Gombe	17-Feb-94	Rafiki's infant	0.1	Unknown	Mitumba	Inferred	61	Females
Budongo	2-Jul-06	Mukwano's Infant	Infant	Unknown	Sonso	Inferred	43	Females
Budongo	12-Mar-04	Unnamed infant	0.02	Unknown	Sonso	Inferred	43	Females
Budongo	6-Sep-13	Oakland's	0.003	M	Sonso	Inferred	*	Females
Tai	Unknown	Unknown	Infant	Unknown	North	Suspected	62	Females
Kibale	2-Mar-99	Unknown	0.5	M	Kanyantale	Inferred	*	Unknown
Gombe	14-Feb-65	Jane	0.2	F	Kasekela	Inferred	36	Unknown
Budongo	17-Feb-13	Kutu's infant	0.01	F	Sonso	Inferred	*	Unknown
Gombe	5-Mar-76	Banda	0.04	F	Kasekela	Suspected	45	Unknown
Gombe	10-Jan-91	Kenitum	1.5	M	Kasekela	Suspected	36	Unknown
Gombe	10-Oct-07	Schweini's infant	0.08	Unknown	Kasekela	Suspected	*	Unknown
Gombe	16-Sep-07	Imani's infant	0.1	M	Kasekela	Suspected	*	Unknown
Gombe	2-Oct-65	Sophie's infant	0.003	Unknown	Kasekela	Suspected	45	Unknown
Gombe	11-Mar-84	Sprout's baby	0.03	Unknown	Kasekela	Suspected	61	Unknown
Gombe	27-Apr-04	Kobe	0.17	M	Kasekela	Suspected	36, 61	Unknown
Mahale	13-Jan-77	Ndilo's infant (Humbe)	0.2	M	M-group	Suspected	63	Unknown
Mahale	14-Jun-79	Wakasunga's infant	0.1	M	M-group	Suspected	64	Unknown
Mahale	1981	WAbaby	0.04	M	M-group	Suspected	58, 65	Unknown
Mahale	15-Dec-83	Chausiku's infant	0.3	M	M-group	Suspected	66	Unknown
Mahale	1988	FAbaby	0.67	M	M-group	Suspected	58, 65	Unknown
Mahale	1989	JNbaby	0.75	M	M-group	Suspected	58, 65	Unknown
Mahale	1987	GMbaby	0.83	F	M-group	Suspected	58, 65	Unknown
Mahale	29-Oct-93	Unknown	0.005	M	M-group?	Suspected	67	Unknown
Kibale	1997	Unknown	Infant	Unknown	Ngogo	Suspected	*	Unknown
Budongo	22-Oct-06	Unknown	0.04	Unknown	Sonso	Suspected	*	Unknown
Budongo	6-Sep-13	Bakata	0.25	M	Sonso	Suspected	*	Unknown
Goulougo	13-May-06	Unknown	0.5	Unknown	Unknown	Suspected	*	Unknown

The reference column (ref.) also includes references 57–67 listed in the Methods or the asterisk symbol indicates unpublished data from the following sources: Gombe (24 August 2013, 3 September 2012, 10 October 2007 and 16 September 2007) from Gombe Stream Research Centre; Kibale (10 August 2005 and 17 June 2009) from David P. Watts; Kibale (17 June 2009) from John C. Mitani; Budongo (25 July 2012, 30 July 2013, 13 August 2009, 9 November 2012, 6 September 2013, 17 February 2013 and 22 October 2006) from Budongo Chimpanzee Project; Kibale (2 March 1999) from Julia Lloyd; Kibale (1997) from Jeremiah S. Lwanga; and Goulougo (13 May 2006) from David B. Morgan and Crickette M. Sanz.

Extended Data Table 5 | Summary of model averaged parameters using different subsets of the data

a.

Row	Dataset	Intercept	Eastern clade	Western Clade
1	All chimpanzee and bonobo groups; inferred and observed cases only	-20 (NA)	19 (NA)	17 (NA)
2	Chimpanzees and bonobos; observed and inferred cases for chimps; 1 suspected case for bonobos	-4.5 (-7.4—-3.0)	3.4 (1.9—6.2)	0.65 (-1.4—3.7)
3	Chimpanzees and bonobos; inferred, observed, and suspected cases	-4.5 (-7.4—-3.0)	3.7 (2.2—6.6)	1.2 (-0.66—4.1)

b.

Row	Dataset	Intercept	Eastern clade	Western Clade	Males	Density	Protected Area	Provisioned	Disturbance
1	Chimpanzees only; inferred and observed cases only	-2.4 (-5.0—0.12)	NA	-0.78 (-1.8—0.25)	0.073 (0.053—0.093)	0.11 (0.00029—-0.22)	-0.00010 (-0.00027—0.000083)	-0.078 (-0.24—0.082)	-0.038 (-0.11—0.033)
2	Chimpanzees only; observed, inferred, and suspected cases	-1.5 (-4.6—1.7)	NA	0.045 (-4.1—4.1)	0.071 (0.027—0.12)	0.19 (-0.048—0.42)	-0.00030 (-0.00077—0.000017)	0.070 (-0.44—1.9)	-0.14 (-0.53—0.25)
3	Chimpanzees only; observed and inferred cases only; excluding Ngogo;	-1.1 (-5.9—3.7)	NA	-0.72 (-1.7—0.30)	0.0070 (-0.0080—0.021)	0.21 (0.079—0.35)	-0.000080 (-0.00023—0.000070)	0.00 (-0.030—0.030)	-0.020 (-0.050—0.020)
4	Chimpanzees and bonobos: observed and inferred cases for chimpanzees; 1 suspected case for bonobos	0.36 (-12—13)	1.5 (-0.28—3.2)	0.59 (-0.81—2.0)	0.042 (0.0049—0.080)	0.025 (-0.019—0.069)	-0.00077 (-0.0016—0.00010)	-0.60 (-1.3—0.10)	-0.29 (-0.61—0.039)

c.

Model number	Intercept	Year	Number of communities under observation	$\Delta_i$	$w_i$
1	-1.2		0.17	0.0	0.72
2	40	-0.02	0.22	1.9	0.28
3	-663	0.34		21.1	0.00
<b>Model averaged parameters</b>	10 (-38—58)	-0.0058 (-0.022—0.010)	0.18 (0.10—0.26)		
<b>Residual deviance</b>	76.9				
<b>df</b>	52				
<b><math>\hat{c}</math></b>	1.48				

a, Species-level comparison of rates of killing between bonobos and chimpanzees. Using only observed and inferred cases (row 1) results in a complete separation problem (and thus undefined 95% confidence intervals); which is resolved when including either the one suspected case for bonobos (row 2) or all suspected cases for both species (row 3). b, Community-level comparisons of factors affecting rates of killing focusing either within chimpanzees (rows 1–3) or including bonobos (row 4). For comparison, the model-averaged parameter estimates from Table 3 (observed and inferred cases only) are presented in row 1. Rows 2–4 show the effects of including suspected cases, excluding the unusually large Ngogo community, and adding bonobos, respectively. For the analysis presented in row 4, the suspected case for bonobos has been included to prevent a complete separation problem. c, Summary statistics showing that, controlling for the number of communities under observation, the number of killings observed per year has not increased.

**Extended Data Table 6 | Summary of parameter estimates for test of the effect of age and sex on probability of being killed**

Parameter	Estimated coefficient $\pm$ SE	z	P
intercept	-8.1 $\pm$ 0.62	-14	<0.0001
infant	1.7 $\pm$ 0.56	3.1	0.003
juvenile	-0.97 $\pm$ 0.88	-1.1	0.27
adult	0.87 $\pm$ 0.54	1.6	0.11
male	1.4 $\pm$ 0.29	4.7	<0.0001

Poisson regression;  $n = 203$  combinations of sex, age class and community; fixed effects: sex with two levels (male, female); age class with four levels (infant, juvenile, adolescent, adult); random effects: 26 levels of community, including 8 unhabituated communities; log-likelihood = -123. The effect of different age classes is in comparison with adolescent; the effect of male is in comparison with female. We confirmed the statistical significance of the fixed effects by comparing the full model with the null model (with just the random effects:  $\chi^2 = 32.7$ ,  $df = 4$ ,  $P < 0.0001$ ) and a reduced model with sex, but not age-class, as a fixed effect ( $\chi^2 = 14.4$ ,  $df = 3$ ,  $P = 0.002$ ).

Extended Data Table 7 | Number of attackers and defenders on each side for intercommunity killings

Date	Victim	Aggressor's community	Victim's community	Males in attacking party	Females in attacking party	Total # attackers	Males in defending party	Females in defending party	Total # defenders	Attackers/Defenders ratio
7-Jan-74	Godi	Kasekela	Kahama	7	1	8	1	0	1	8
26-Feb-74	Dé	Kasekela	Kahama	3	1	4	3	1	4	1
7-Feb-75	Goliath	Kasekela	Kahama	6	0	6	1	0	1	6
14-Sep-75	Madam B	Kasekela	Kahama	5	4	9	0	1	1	9
12-Nov-77	Sniff	Kasekela	Kahama	7	0	7	1	0	1	7
14-Aug-98	Adolescent male	Kasekela	Kalande	4	0	4	1	0	1	4
19-Sep-05	Patti	Mitumba	Kasekela	2	5	7	1	1	2	3.5
3-Jun-02	Adult male	Ngogo	Northeastern	15	0	15	1	2	3	5
9-Aug-02	Juvenile male	Ngogo	Northeastern	18	0	18	Unknown	Unknown	Unknown	Unknown
23-Nov-02	Adult male	Ngogo	Wantabu	19	0	19	1	1	2	9.5
1-Aug-04	Adult male	Ngogo	Northeastern	11	1	12	1	5	6	2
22-Nov-04	Adult male	Ngogo	Southwestern	28	4	32	Unknown	Unknown	Unknown	Unknown
11-Aug-06	Adult male	Ngogo	Northeastern	17	5	22	Unknown	Unknown	Unknown	Unknown
2-Aug-09	Adult female	Ngogo	Southwestern	14	3	17	0	1	1	17
1-Mar-05	Nerone	South	East N15_(Nature Reserve)	6	4	10	1	0	1	10
29-Sep-95	Infant male	Sonso	Reserve)	9	6	15	0	1	1	15.0
3-Feb-06	Infant	Sonso	Unknown	3	6	9	0	1	1	9.0
Sep-71	Infant	Kasekela	Unknown	5	0	5	0	2	2	2.5
2-Nov-75	Infant female	Kasekela	Unknown	7	2	9	Unknown	2	Unknown	Unknown
20-Mar-79	Infant	Kasekela	Unknown	9	2	11	0	2	2	5.5
30-Mar-93	Rejea	Kasekela	Mitumba	11	4	15	0	1	1	15.0
29-Oct-98	Infant	Kasekela	Kalande	5	2	7	1	2	3	2.3
21-Feb-11	Infant	Ngogo	Northeastern	9	3	12	0	1	1	12.0
3-Apr-99	Infant	Ngogo	Northeastern	13	0	13	0	1	1	13.0
28-Jun-99	Infant	Ngogo	Eastern	16	0	16	0	1	1	16.0
5-Jul-00	Infant	Ngogo	Northeastern	10	0	10	3	2	5	2.0
19-Jul-01	Juvenile	Ngogo	Northeastern	8	0	8	Unknown	Unknown	Unknown	Unknown
6-Oct-04	Infant	Ngogo	Southwestern	27	5	32	0	1	1	32.0
12-Oct-04	Infant	Ngogo	Wantabu	28	1	29	0	4	4	7.3
12-Oct-04	Infant	Ngogo	Wantabu	28	0	28	0	4	4	7.0
13-Oct-05	Infant	Ngogo	Southwestern	8	0	8	0	1	1	8.0
1-Feb-06	Infant	Ngogo	Northeastern	9	0	9	Unknown	Unknown	Unknown	Unknown
25-Jul-07	Infant	Ngogo	Northeastern	7	3	10	0	1	1	10.0
29-Jun-11	Infant	Ngogo	Southwestern	15	6	21	0	3	3	7.0
12-Dec-00	Infant male	M-group	Unknown	5	5	10	0	1	1	10.0
8-Sep-02	Infant male	South	West?	5	9	14	0	1	1	14.0