



Lethal Aggression in Pan Is Better Explained by Adaptive Strategies Than Human Impacts

Citation

Wilson, Michael L., Christophe Boesch, Barbara Fruth, Takeshi Furuichi, Ian C. Gilby, Chie Hashimoto, Catherine L. Hobaiter, et al. 2014. "Lethal Aggression in Pan Is Better Explained by Adaptive Strategies Than Human Impacts." *Nature* 513 (7518) (September 17): 414–417.

Published version

<https://doi.org/10.1038/nature13727>

Link

<http://nrs.harvard.edu/urn-3:HUL.InstRepos:13041029>

Terms of use

This article was downloaded from Harvard University's DASH repository, and is made available under the terms and conditions applicable to Other Posted Material (LAA), as set forth at

<https://harvardwiki.atlassian.net/wiki/external/NGY5NDE4ZjgzNTc5NDQzMGIzZWZhMGFIOWI2M2EwYTg>

Accessibility

<https://accessibility.huit.harvard.edu/digital-accessibility-policy>

Share Your Story

The Harvard community has made this article openly available.
Please share how this access benefits you. [Submit a story](#)

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

Michael L. Wilson^{1,2}, Christophe Boesch³, Barbara Fruth^{4,5}, Takeshi Furuichi⁶, Ian C. Gilby^{7,8}, Chie Hashimoto⁶, Catherine Hobaiter⁹, Gottfried Hohmann³, Noriko Itoh¹⁰, Kathelijne Koops¹¹, Julia N. Lloyd¹², Tetsuro Matsuzawa^{6,13}, John C. Mitani¹⁴, Deus C. Mjungu¹⁵, David Morgan¹⁶, Martin N. Muller¹⁷, Roger Mundry¹⁸, Michio Nakamura¹⁰, Jill Pruetz¹⁹, Anne E. Pusey⁷, Julia Riedel³, Crickette Sanz²⁰, Anne M. Schel²¹, Nicole Simmons¹², Michel Waller²², David P. Watts²³, Frances White²², Roman M. Wittig³, Klaus Zuberbühler^{9,24}, and Richard W. Wrangham²⁵

1. Department of Anthropology, University of Minnesota, 395 Humphrey Center, 301 19th Ave S., Minneapolis, Minnesota 55455, USA

2. Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, St. Paul, Minnesota 55108, USA

3. Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany

4. Division of Neurobiology, Ludwig-Maximilians Universitaet Muenchen, Germany

5. Centre for Research and Conservation, Royal Zoological Society of Antwerp, Belgium

6. Primate Research Institute, Kyoto University, 41-2 Kanrin, Inuyama, Aichi 484-8506, Japan

7. Department of Evolutionary Anthropology, Duke University, 104 Biological Sciences Building, Box 90383, Durham, North Carolina 27708-0680, USA

8. School of Human Evolution and Social Change, Arizona State University, PO Box 872402, Tempe, Arizona 85287-2402

9. School of Psychology and Neuroscience, University of St. Andrews, Westburn Lane, St. Andrews, Fife, Scotland, KY16 9JP, United Kingdom
10. Wildlife Research Center, Kyoto University, 2-24 Tanaka-Sekiden-Cho, Sakyo, Kyoto, Japan
11. Division of Biological Anthropology, Department of Archaeology & Anthropology, University of Cambridge, Henry Wellcome Building, Fitzwilliam Street, Cambridge CB2 1QH, United Kingdom
12. Zoology Department, Makerere University, P.O.Box 7062, Kampala, Uganda
13. Japan Monkey Center, 26 Kanrin, Inuyama, Aichi 484-0081, Japan
14. Department of Anthropology, University of Michigan, 101 West Hall, 1085 S. University Ave. Ann Arbor, Michigan 48109, USA
15. Gombe Stream Research Centre, the Jane Goodall Institute – Tanzania, P.O. Box 1182, Kigoma, Tanzania
16. The Lester E. Fisher Center for the Study and Conservation of Apes, Lincoln Park Zoo, Chicago, Illinois 60614, USA
17. Department of Anthropology, MSC01-1040, Anthropology 1, University of New Mexico, Albuquerque, New Mexico 87131
18. Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany
19. Department of Anthropology, Iowa State University, 324 Curtiss, Ames, Iowa 50011, USA
20. Department of Anthropology, Washington University in St. Louis, Campus Mailbox 1114, One Brookings Drive, St. Louis, Missouri 63130
21. University of York, Department of Psychology, Heslington, York, YO10 5DD, United Kingdom

22. Department of Anthropology, University of Oregon, Eugene, Oregon 97403, USA
23. Department of Anthropology, Yale University, 10 Sachem Street, New Haven, Connecticut 06511, USA
24. Université de Neuchâtel, Institut de Biologie, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland
25. Department of Human Evolutionary Biology, Harvard University, 11 Divinity Avenue Cambridge, Massachusetts 02138

Corresponding author:

Michael L. Wilson

University of Minnesota

Department of Anthropology

395 Humphrey Center, 301 19th Ave S

Minneapolis, MN 55455

Telephone: 612-625-1376

email: wilso198@umn.edu

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 resources such as food or mates.¹⁻⁵ Alternatively, it could be a
6 non-adaptive result of human impacts, such as habitat change or food provisioning.⁶⁻⁹
7 To discriminate between these hypotheses we compiled information from 18
8 chimpanzee communities and 4 bonobo communities studied over five decades. 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 were the most frequent attackers (92% of participants) and victims (73%); most
12 killings (66%) involved intercommunity attacks; and attackers greatly outnumbered
13 their victims (median 8:1 ratio). Variation in killing rates was unrelated to measures of
14 human impacts. Our results are compatible with previously proposed adaptive
15 explanations for killing by chimpanzees whereas the human impact hypothesis is not
16 supported.

17
18 Substantial variation exists in rates of killing across chimpanzee study sites.^{2-5,10-12} The
19 human impact and adaptive strategies hypotheses both seek to explain this variation, but have
20 contrasting predictions, which we test here (Tables 1, 2). The human impact hypothesis states
21 that killing is an incidental outcome of aggression, exacerbated by human activities such as
22 deforestation, introducing diseases, hunting or providing food. Accordingly, lethal aggression
23 should be high where human disturbance is high.⁸

24
25 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.^{1-5,10-17} Kin selection¹⁸ and evolutionary game theory¹⁹ 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^{2,5,11-17}; the present study represents the first effort to test multiple hypotheses simultaneously with a comprehensive dataset. To do so, we assembled data from communities of eastern (N=12) and western (N=6) chimpanzees²⁴ studied over 426 years (median = 21 years; range: 4—53) and from 4 bonobo communities studied for 92 years (median = 21; range: 9—39; Figure E1). We rated each case of killing as observed, inferred, or suspected (see Online Methods; Tables E1-E4). 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,^{2,23} and lower rates of killing are reported for western than eastern chimpanzees.^{2,11} The human impact hypothesis could in theory ascribe these variations to different levels of disturbance. In contrast, in behavioral ecology, distinct populations are expected to respond to prevailing ecological circumstances through biological evolution and/or phenotypic flexibility. For bonobos and western chimpanzees, ecological factors apparently allow relatively high gregariousness, which reduces the risk of experiencing a lethal attack.^{2,11} Our dataset 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) (Online Methods; Figures E1a, E2a).

We documented killings by chimpanzees in 15 of 18 communities (58 observed, 41 inferred, and 53 suspected cases; Tables E1-E4) (Figure 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 $\pm$ SE for chimpanzees compared to bonobos: $\beta_0=-4.5\pm1.0$; $\beta_{east}=3.4\pm1.0$, $z=3.3$, $P=0.0008$; $\beta_{west}=0.65\pm1.2$, $z=0.56$, $P=0.57$; overall effect of clade: $\chi^2=80.8$, $df=2$, $P<0.0001$). This difference persisted when “suspected” cases were included (Table E5a.).

To investigate which factors best explained variation in killing rates among chimpanzee communities, we used an information theoretic approach,²⁵ controlling for years of observation. We considered three variables for the human impact hypothesis: *provisioned* (whether the 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 km², 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/km²), vegetation sampling revealed high forest productivity²⁶ and chimpanzees have high C-peptide levels,²⁷ indicating high energy balance; whereas at Fongoli (0.37 chimpanzees/km²), chimpanzees range widely across a dry savanna with sparse food.²⁸ *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,²⁵ increases in *males* and *density* increased the number of killings; for all other parameter estimates, the 95% CI included zero (Table 3; Figure 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% CI (Table E5b; $N = 17$).

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% CI (Table 3; Figure E2b). 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 (Table E5b). Nonetheless, even with these suspected cases, none of the estimates for human impact variables excludes zero from the 95% CI. Including bonobo data widened the confidence intervals for *density* (Table E5b), likely because two bonobo communities had high densities (Figure E1a). With either suspected cases or bonobo data added, only for *males* did the 95% CI exclude zero (Table E5b). Thus, while 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.⁸ 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 approach²⁵ to compare three different models (*year*; *communities*; and *year + communities*), the best model contained only *communities*; considering model-averaged parameters, the 95% CI excluded zero for *communities*, but not *year* (Poisson regression: N=52 years; model-averaged parameters and 95% CI: $\beta_0=10$ (-38—58); $\beta_{year}=-0.0058$ (-0.022—0.010); $\beta_{communities}=0.18$ (0.10—0.26); Table E5c).

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 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); $\beta_0 = -6.9 \pm 0.98$; $\beta_{males} = 2.6 \pm 0.59$, $z = 4.42$, $P < 0.0001$). 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 (Table E6). 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.²⁹ 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 (e.g., 1.9% of follow days at Kanyawara³⁰).

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; Table E7). 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 *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.

Acknowledgements

This study was funded by National Science Foundation grants BCS-0648481 and LTREB-1052693. Numerous additional sources of funding have supported the long-term studies that contributed data to this study. We thank James H. Jones for statistical advice; Lilian Pintea for Figure E1b; Iddi Lipende and Ruth Lawrence for providing details on recent cases at Gombe and Kanyantale; Sylvia Amsler for helping to calculate the range of the Kanyantale community, and the many field assistants who collected data.

Author Contributions. All authors contributed to the acquisition, analysis and interpretation of the data; MLW, RWW, and JCM initiated and conceived the study; MLW and RM performed statistical analyses; CB, BF, TF, CH, CLH, GH, NI, KK, JNL, TM, JCM, DCM, DM, MNM, MN, JP, AEP, CS, NS, DPW, FW, KZ, MLW, RW, and RWW conducted and supervised fieldwork; CB, TF, ICG, CH, CLH, GH, JNL, TM, JCM, DCM, DM, MNM, MN, JP, JR, CS, AMS, NS, MLW, MW, DPW, FW, RWW and KZ provided demographic and ranging data; CB, TF, CH, GH, JNL, TM, JCM, MN, JP, AEP, NS, FW, MLW, RWW, and KZ provided data on site characteristics and human disturbance ratings; MLW coordinated the contributions of all authors; MLW wrote the paper with JCM, DPW, RWW and input from all authors.

References

1. Goodall, J. *The Chimpanzees of Gombe: Patterns of Behavior*. (Belknap Press, 1986).
2. Wrangham, R. W. The evolution of coalitionary killing. *Yearbook of Physical Anthropology* **42**, 1-30 (1999).
3. Wilson, M. L. & Wrangham, R. W. Intergroup relations in chimpanzees. *Annual Review of Anthropology* **32**, 363-392 (2003).
4. Boesch, C. *The Real Chimpanzee: Sex Strategies in the Forest*. (Cambridge University Press, 2009).
5. Mitani, J. C., Watts, D. P. & Amsler, S. J. Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology* **20**, R507-R508 (2010).
6. Power, M. *The Egalitarians—Human and Chimpanzee: An Anthropological View of Social Organization*. (Cambridge University Press, 1991).
7. Sussman, R. W. in *War, Peace, and Human Nature: The Convergence of Evolutionary and*

- 199 *Cultural Views* (ed Douglas P. Fry) Ch. 6, 97-111 (Oxford University Press, 2013).
- 200 8. Ferguson, R. B. in *Origins of Altruism and Cooperation* (eds R. W. Sussman & C. R.
- 201 Cloninger) 249-270 (2011).
- 202 9. Bartlett, T. Q., Sussman, R. W. & Cheverud, J. M. Infant killing in primates: a review of
- 203 observed cases with specific reference to the sexual selection hypothesis. *American*
- 204 *Anthropologist* **95**, 958-990 (1993).
- 205 10. Mitani, J. C. 2009. Cooperation and competition in chimpanzees: current understanding and
- 206 future challenges. *Evolutionary Anthropology* 18:215-227.
- 207 11. Boesch, C. *et al.* Intergroup conflicts among chimpanzees in Tai National Park: Lethal
- 208 violence and the female perspective. *American Journal of Primatology* **70**, 519-532 (2008).
- 209 12. Wrangham, R. W., Wilson, M. L. & Muller, M. N. Comparative rates of violence in
- 210 chimpanzees and humans. *Primates* **47**, 14-26 (2006).
- 211 13. Williams, J. M., Oehlert, G., Carlis, J. & Pusey, A. E. Why do male chimpanzees defend a
- 212 group range? Reassessing male territoriality. *Animal Behaviour* **68**, 523-532 (2004).
- 213 14. Mitani, J. C. Demographic influences on the behavior of chimpanzees. *Primates* **47**, 6-13
- 214 (2006).
- 215 15. Fawcett, K. & Muhumuza, G. Death of a wild chimpanzee community member: possible
- 216 outcome of intense sexual competition. *American Journal of Primatology* **51**, 243-247
- 217 (2000).
- 218 16. Watts, D. P. Intracommunity coalitionary killing of an adult male chimpanzee at Ngogo,
- 219 Kibale National Park, Uganda. *International Journal of Primatology* **25**, 507-521 (2004).
- 220 17. Pusey, A. E. *et al.* Severe aggression among female chimpanzees at Gombe National Park,
- 221 Tanzania. *International Journal of Primatology* **29**, 949-973 (2008).
- 222 18. Hamilton, W. D. The genetical evolution of social behavior. I, II. *Journal of Theoretical*
- 223 *Biology* **7**, 1-52 (1964).

- 224 19. Maynard Smith, J. (1974). "The theory of games and the evolution of animal conflicts."
225 Journal of Theoretical Biology **47**(1): 209-221.
- 226 20. Enquist, M. & Leimar, O. The evolution of fatal fighting. *Animal Behaviour* **39**, 1-9 (1990).
- 227 21. Pusey, A. E., G. W. Oehlert, J. M. Williams and J. Goodall (2005). "The influence of
228 ecological and social factors on body mass of wild chimpanzees." International Journal of
229 Primatology **26**: 3-31.
- 230 22. Hrdy, S. B. Infanticide among animals: A review, classification, and examination of the
231 implications for the reproductive strategies of females. *Ethology and Sociobiology* **1**, 13-40
232 (1979).
- 233 23. Boesch, C., Hohmann, G. & Marchant, L. F. *Behavioral Diversity in Chimpanzees and*
234 *Bonobos*. (Cambridge University Press, 2002).
- 235 24. Prado-Martinez, J. *et al.* Great ape genetic diversity and population history. *Nature* **499**, 471-
236 475, doi:10.1038/nature12228
- 237 25. Burnham, K. P. & Anderson, D. R. *Model Selection and Multimodel Inference: A Practical*
238 *Information-Theoretic Approach*. Second Edition edn, xxvi, 488 (Springer, 2002).
- 239 26. Potts, K. B., Watts, D. P. & Wrangham, R. W. Comparative Feeding Ecology of Two
240 Communities of Chimpanzees (*Pan troglodytes*) in Kibale National Park, Uganda.
241 *International Journal of Primatology* **32**, 669-690, doi:10.1007/s10764-011-9494-y (2011).
- 242 27. Emery Thompson, M., Muller, M. N., Wrangham, R. W., Lwanga, J. S. & Potts, K. B.
243 Urinary C-peptide tracks seasonal and individual variation in energy balance in wild
244 chimpanzees. *Hormones and Behavior* **55**, 299-305, doi:10.1016/j.yhbeh.2008.11.005 (2009).
- 245 28. Sponheimer, M. *et al.* Do "savanna" chimpanzees consume C-4 resources? *Journal of Human*
246 *Evolution* **51**, 128-133, doi:10.1016/j.jhevol.2006.02.002 (2006).
- 247 29. Inoue, E., Inoue-Murayama, M., Vigilant, L., Takenaka, O. & Nishida, T. Relatedness in wild
248 chimpanzees: Influence of paternity, male philopatry, and demographic factors. *American*

- 249 *Journal of Physical Anthropology* **137**, 256-262, doi:10.1002/ajpa.20865 (2008).
- 250 30. Wilson, M. L., Kahlenberg, S. M., Wells, M. T. & Wrangham, R. W. Ecological and social
- 251 factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Animal*
- 252 *Behaviour* **83**, 277-291 (2012).

253 Figure 1: **Number of victims killed per year by members of study communities.** Bars
254 indicate the annual rate of observed (black), inferred (grey), and suspected (white) killings by
255 each community for bonobos (B; N=4), eastern chimpanzees (E; N=12), and western
256 chimpanzees (W; N=6). Communities with a history of provisioning are indicated by (P).
257

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

263 **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

264

265

266 **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	+

267

268 **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
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			

269

270 Parameters include the intercept (*b*); impact of western relative to the eastern *clade* of
271 chimpanzees; mean number of adult males per community (*males*); mean population density
272 per community (*density*); size of protected area in km² (*area*); history of regular provisioning
273 with food (*prov.*); disturbance rating (*dist.*); the number of free parameters (*k*) including the
274 dispersion parameter ($\hat{c}$); the difference in Akaike information criterion (corrected for
275 overdispersion: QAICc) between the *i*th model and the best model (Δ_i); and model weight
276 (w_i). Models are arranged in order from best (lowest Δ QAICc_{*i*}) to worst (highest Δ QAICc_{*i*}).
277 The weight of the model (w_i) is the probability that a given model is the best model in a given
278 set of models. Model-averaged parameter estimates (*MAP*) with upper (97.5%) and lower
279 (2.5%) bounds of the 95% confidence intervals are given in the bottom rows.

280

Methods

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 prior to 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: ≥ 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 from³¹, 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—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* 3.0.2.³² To test for differences in rate of killing between bonobos and the two clades of chimpanzees (eastern and western²⁴), 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.³³ 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 ≥ 12 years old), *density* (mean number of individuals per community/home range (km^2); *area* (size (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 on³¹). 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.²³

To test for sex differences in participation in lethal aggression, we conducted a GLMM with negative binomial error structure using the glmmADMB package.³⁴ 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 (e.g., 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.³⁵ 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 sexes)x(4 age classes)x(26 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*.^{36,37}

Additional citations for Online Methods

31. Bishop, N., Hrdy, S. B., Teas, J. & Moore, J. Measures of human influence in habitats of South Asian monkeys. *International Journal of Primatology* **2**, 153-167 (1981).
32. R: A language and environment for statistical computing v. 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria, 2013).
33. Field, A. *Discovering Statistics Using SPSS*. (Sage Publications, 2005).
34. Bolker, B., Skaug, H., Magnusson, A. & Nielsen, A. *Getting started with the glmmADMB package*, <<http://glmmadmb.r-forge.r-project.org/glmmADMB.html>> (2012).
35. Bates, D., Maechler, M., Bolker, B. & Walker, S. *lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-5*, <<http://www.inside-r.org/packages/lme4/versions/1-0-5>> (2013).
36. Schielzeth, H. & Forstmeier, W. Conclusions beyond support: overconfident estimates in mixed models. *Behavioral Ecology* **20**, 416-420 (2009).
37. Barr, D. J., Levy, R., Scheepers, C. & Tily, H. J. Random effects structure for confirmatory hypothesis testing: Keep it maximal. . *Journal of Memory and Language* **68**, 255–278 (2013).

Extended Data

Figure E1. 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 ≥ 12 years old; *Females*: mean number of females ≥ 12 years old; *Home range*: mean size of the community's home range (km^2); *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.

Figure E2. 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).

Table E1: Intercommunity killings of weaned victims. For Tables E1-E4, *Ref.* (*References*) refers to references in Table E8.

Table E2: Intercommunity infanticides

Table E3: Intracommunity killings of weaned victims

Table E4: Intracommunity infanticides

Table E5: Summary of model averaged parameters using different subsets of the data.

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% CIs); 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.

Table E6. Summary of parameter estimates for test of the effect of age and sex on probability of being killed. 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

454 the random effects: $\chi^2=32.7$, $df=4$, $P<0.0001$) and a reduced model with sex, but not age-
455 class, as a fixed effect ($\chi^2=14.4$, $df=3$, $P=0.002$).

456

457 **Table E7: Number of attackers and defenders on each side for intercommunity killings.**

458

459 **Table E8: References for data in tables E1-E4.**

460



