



DIGITAL ACCESS TO SCHOLARSHIP AT HARVARD

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

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

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." <i>Nature</i> 513 (7518) (September 17): 414–417.
Published Version	doi:10.1038/nature13727
Accessed	April 17, 2018 5:09:31 PM EDT
Citable 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, as set forth at http://nrs.harvard.edu/urn-3:HUL.InstRepos:dash.current.terms-of-use#LAA

(Article begins on next page)

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

26 killers tend to increase their fitness through increased access to territory, food, mates or other
27 benefits.^{1-5,10-17} Kin selection¹⁸ and evolutionary game theory¹⁹ yield a set of specific
28 predictions for how benefits and costs should vary with the context, age, sex, and genetic
29 relatedness of the attackers and targets. Lethal aggression occurs within a diverse set of
30 circumstances, but is expected to be most commonly committed by males; directed towards
31 males; directed towards non-kin, particularly members of other groups; and committed when
32 overwhelming numerical superiority reduces the costs of killing. Previous studies have
33 developed and tested these specific hypotheses^{2,5,11-17}; the present study represents the first
34 effort to test multiple hypotheses simultaneously with a comprehensive dataset. To do so, we
35 assembled data from communities of eastern (N=12) and western (N=6) chimpanzees²⁴
36 studied over 426 years (median = 21 years; range: 4—53) and from 4 bonobo communities
37 studied for 92 years (median = 21; range: 9—39; Figure E1). We rated each case of killing as
38 observed, inferred, or suspected (see Online Methods; Tables E1-E4). To be conservative, we
39 limited our analyses to those rated “observed” and “inferred” unless otherwise noted. We
40 examined contrasting predictions relating to overall patterns of killings (Table 1) and
41 variation among communities (Table 2).

42

43 Bonobos are consistently found to be less violent than chimpanzees,^{2,23} and lower rates of
44 killing are reported for western than eastern chimpanzees.^{2,11} The human impact hypothesis
45 could in theory ascribe these variations to different levels of disturbance. In contrast, in
46 behavioral ecology, distinct populations are expected to respond to prevailing ecological
47 circumstances through biological evolution and/or phenotypic flexibility. For bonobos and
48 western chimpanzees, ecological factors apparently allow relatively high gregariousness,
49 which reduces the risk of experiencing a lethal attack.^{2,11} Our dataset covers all major studies
50 of both species of *Pan*, which include sites with and without a history of provisioning, and

51 with high and low levels of human *disturbance*, a rating estimated independently by each
52 site's director(s) (Online Methods; Figures E1a, E2a).

53

54 We documented killings by chimpanzees in 15 of 18 communities (58 observed, 41 inferred,
55 and 53 suspected cases; Tables E1-E4) (Figure 1). For bonobos, we documented only a single
56 (suspected) case, which occurred at Lomako, a never-provisioned site with a low disturbance
57 rating. No killings were recorded at other bonobo sites, including one with a history of
58 provisioning and a high disturbance rating (Wamba). Controlling for years of observation,
59 chimpanzees had a higher rate of killing than bonobos; this difference was statistically
60 significant for eastern but not western chimpanzees (Poisson regression: N=22 communities;
61 estimated coefficients±SE for chimpanzees compared to bonobos: $\beta_0 = -4.5 \pm 1.0$;
62 $\beta_{east} = 3.4 \pm 1.0$, $z = 3.3$, $P = 0.0008$; $\beta_{west} = 0.65 \pm 1.2$, $z = 0.56$, $P = 0.57$; overall effect of clade:
63 $\chi^2 = 80.8$, $df = 2$, $P < 0.0001$). This difference persisted when “suspected” cases were included
64 (Table E5a.).

65

66 To investigate which factors best explained variation in killing rates among chimpanzee
67 communities, we used an information theoretic approach,²⁵ controlling for years of
68 observation. We considered three variables for the human impact hypothesis: *provisioned*
69 (whether the community had been artificially fed); *area* (size of protected area, with smaller
70 areas assumed to experience more impacts); and *disturbance*. We also considered three
71 variables for the adaptive strategies hypothesis: *clade* (eastern and western chimpanzees may
72 have different histories of selection for violence); *males* (number of adult males, which may
73 influence rates of killing via intensity of reproductive competition and/or coalitional fighting
74 power), and *density* (number of individuals per km², which may affect frequency of
75 intercommunity encounter and/or intensity of resource competition). We consider *density* to

76 reflect natural food abundance. For example, at Ngogo (4.5 chimpanzees/km²), vegetation
77 sampling revealed high forest productivity²⁶ and chimpanzees have high C-peptide levels,²⁷
78 indicating high energy balance; whereas at Fongoli (0.37 chimpanzees/km²), chimpanzees
79 range widely across a dry savanna with sparse food.²⁸ *Density* was unrelated to *disturbance*
80 (general linear model, $F_{1,16}=1.4$, $P=0.26$).

81

82 Of the 16 models we considered (Table 3), four of the five models in the resulting 95%
83 confidence set included combinations of the adaptive variables; the fifth model included the
84 three human impact variables. The best model included only *males* and *density*, and was
85 supported 6.8 times more strongly than the human impact model (evidence ratio = $w_i/w_j =$
86 $0.40/0.059=6.8$). Considering model-averaged parameter estimates,²⁵ increases in *males* and
87 *density* increased the number of killings; for all other parameter estimates, the 95% CI
88 included zero (Table 3; Figure 2). Excluding one community (Ngogo) that had both an
89 unusually high killing rate and unusually many males resulted in similar values for model-
90 averaged parameters, but only the estimate for *density* excluded zero from the 95% CI (Table
91 E5b; $N = 17$).

92

93 Opposite to predictions from the human impact hypothesis (Table 2), *provisioned* and
94 *disturbance* both had negative effects; the estimates for these parameters included zero in the
95 95% CI (Table 3; Figure E2b). The highest rate of killing occurred at a relatively undisturbed
96 and never-provisioned site (Ngogo); chimpanzees at the least disturbed site (Goualougo)
97 were suspected of one killing and inferred to have suffered an intercommunity killing; and no
98 killings occurred at the site most intensely modified by humans (Bossou).

99

100 As a test of confidence, we investigated the effects of including “suspected” cases and data
101 from bonobos. Including “suspected” cases changed *western* and *provisioned* from negative
102 to positive (Table E5b). Nonetheless, even with these suspected cases, none of the
103 estimates for human impact variables excludes zero from the 95% CI. Including bonobo
104 data widened the confidence intervals for *density* (Table E5b), likely because two
105 bonobo communities had high densities (Figure E1a). With either suspected cases or
106 bonobo data added, only for *males* did the 95% CI exclude zero (Table E5b). Thus, while
107 demographic variables explain variation in rates of killing better than human impact
108 variables, the confidence intervals are sensitive to including suspected cases or data
109 from another species (bonobos).

110

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

115

116 Increasing human impacts have been proposed to cause increasing numbers of killings in
117 recent years.⁸ However, controlling for changes in the number of communities observed per
118 year (*communities*), the rate of killing has not changed over time (*year*). Using an
119 information theoretic approach²⁵ to compare three different models (*year*; *communities*; and
120 *year + communities*), the best model contained only *communities*; considering model-
121 averaged parameters, the 95% CI excluded zero for *communities*, but not *year* (Poisson
122 regression: N=52 years; model-averaged parameters and 95% CI: $\beta_0=10$ (-38—58); $\beta_{year}= -$
123 0.0058 (-0.022—0.010); $\beta_{communities} = 0.18$ (0.10—0.26); Table E5c).

124

125 Killings involved a median of five male attackers (range: 0—19) and no females (range: 0—
126 6). Considering all cases for which the number of attackers was observed (N=58) or could be
127 inferred (N=6), males constituted 92% of participants in attacks (338/366). Controlling for
128 observation time and community composition, males were much more likely to participate in
129 killings than females (negative binomial mixed model: N = 36 observations (fixed effects:
130 *sex* with 2 levels; random effects: *community* with 18 levels); $\beta_0 = -6.9 \pm 0.98$; $\beta_{males} = 2.6 \pm 0.59$,
131 $z = 4.42$, $P < 0.0001$). Females sometimes joined males in attacking grown individuals (N=3),
132 but when acting without males, females killed only young infants (N=8).

133

134 Controlling for observation time and community composition, males and infants had the
135 highest probability of being killed (Table E6). Notably, during infanticides, attackers
136 sometimes removed infants from mothers under circumstances in which they appeared
137 capable of killing the mother as well, but did not do so.

138

139 Most victims were members of different communities from the attackers (N = 62 of 99 cases;
140 63%) and thus not likely to be close kin.²⁹ This difference is particularly striking given that
141 chimpanzees could potentially attack members of their own community on a daily basis, but
142 rarely encounter members of other communities (e.g., 1.9% of follow days at Kanyawara³⁰).

143

144 Intercommunity killings mainly involved parties with many males (median = 9 males, range:
145 2—28, N=36 cases with known numbers of attackers) attacking isolated or greatly
146 outnumbered males or, more often, mothers with infants (median = 0 males, range: 0—3,
147 N=30; median = 1 female, range: 0—5, N=31). For 30 cases in which the number of adult
148 and adolescent males and females on each side were known, attackers outnumbered

149 defenders by a median factor of 8 (range: 1—32; Table E7). Most intercommunity killings
150 thus occurred when attackers overwhelmingly outnumbered victims.
151
152 Several robust patterns emerge from these data. Killing was most common in eastern
153 chimpanzees and least common among bonobos. Among chimpanzees, killings increased
154 with more males and higher population density, whereas none of the three human impact
155 variables had an obvious effect. Male chimpanzees killed more often than females, and killed
156 mainly male victims; attackers most frequently killed unweaned infants; victims were mainly
157 members of other communities (and thus unlikely to be close kin); and intercommunity
158 killings typically occurred when attackers had an overwhelming numerical advantage. The
159 most important predictors of violence were thus variables related to adaptive strategies:
160 species; age-sex class of attackers and victims; community membership; numerical
161 asymmetries; and demography. We conclude that patterns of lethal aggression *Pan* show little
162 correlation with human impacts, but are instead better explained by the adaptive hypothesis
163 that killing is a means to eliminate rivals when the costs of killing are low.

164

165 **Acknowledgements**

166

167 This study was funded by National Science Foundation grants BCS-0648481 and LTREB-
168 1052693. Numerous additional sources of funding have supported the long-term studies that
169 contributed data to this study. We thank James H. Jones for statistical advice; Lilian Pintea
170 for Figure E1b; Iddi Lipende and Ruth Lawrence for providing details on recent cases at
171 Gombe and Kanyantale; Sylvia Amsler for helping to calculate the range of the Kanyantale
172 community, and the many field assistants who collected data.

173

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

184

185 **References**

186

- 187 1. Goodall, J. *The Chimpanzees of Gombe: Patterns of Behavior*. (Belknap Press, 1986).
- 188 2. Wrangham, R. W. The evolution of coalitionary killing. *Yearbook of Physical Anthropology*
189 **42**, 1-30 (1999).
- 190 3. Wilson, M. L. & Wrangham, R. W. Intergroup relations in chimpanzees. *Annual Review of*
191 *Anthropology* **32**, 363-392 (2003).
- 192 4. Boesch, C. *The Real Chimpanzee: Sex Strategies in the Forest*. (Cambridge University Press,
193 2009).
- 194 5. Mitani, J. C., Watts, D. P. & Amstler, S. J. Lethal intergroup aggression leads to territorial
195 expansion in wild chimpanzees. *Current Biology* **20**, R507-R508 (2010).
- 196 6. Power, M. *The Egalitarians—Human and Chimpanzee: An Anthropological View of Social*
197 *Organization*. (Cambridge University Press, 1991).
- 198 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
<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			

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

281 **Methods**

282

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

291

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

301

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

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

317

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

326

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

331 reserve in which community resided); *provisioned* (whether the community had a history of
332 being regularly provisioned with food by researchers) and *disturbance* (sum of five four-
333 point ratings, based on³¹). Each model consisted of a Poisson regression with the total count
334 of observed/inferred killings committed by each community as the dependent variable, and
335 $\log(\text{years of study})$ as an offset. We recognize that *years of study* is a rather coarse-grained
336 measure of observation time, but finer grained measures such as total number of observation
337 hours were not available for all communities. We selected models to distinguish between the
338 predictor variables most closely associated with the adaptive strategies hypothesis (*clade*,
339 *males*, and *density*) and the human impact hypothesis (*protected area*, *provisioned* and
340 *disturbance*), including the null model, models with each variable by itself, combinations of
341 up to three variables associated with each hypothesis, and the full model. We limited the
342 number of variables per model to avoid over-fitting, and limited the number of models tested
343 to reduce the risk of finding spurious correlations. We corrected for overdispersion and small
344 sample size using QAICc, ranked models according to QAICc score (lowest=best), and used
345 results from all models to calculate model-averaged estimates of parameters.²³

346

347 To test for sex differences in participation in lethal aggression, we conducted a GLMM with
348 negative binomial error structure using the glmmADMB package.³⁴ For the dependent
349 variable, we used the number of *participations* in killings by each sex for each community.
350 We defined *participation* as the active involvement of an individual during a lethal attack
351 (e.g., making or attempting to make direct aggressive contact with the victim). For each case
352 for which the attackers were observed directly, or could be inferred with confidence, we
353 counted the number of attackers of each sex. For each community, we summed the number of
354 attackers across all cases to obtain the number of times individuals of each sex participated in
355 attacks. Independent variables consisted the fixed effect *sex* (2 levels: *male* and *female*) and

356 the random effect *community* (18 levels). To control for community composition, we used
357 $\log(\text{chimp-years})$ for each sex in each community as an offset. *Chimp-years* was defined for
358 each age-sex class as *years of study* multiplied by the mean number of individuals of that
359 age-sex class present in the victim's community.

360

361 To test for patterns in the age-sex class of victims, we conducted a GLMM with Poisson error
362 structure using the lme4 (1.0-5) package.³⁵ To control for possible sex differences in
363 motivation for killing, we excluded from analysis the 8 cases that were known to have been
364 committed solely by females. For the dependent variable, we used the number of observed
365 and inferred victims of each age-sex class for each community. Independent variables with
366 fixed effects were *sex* (2 levels) and *age-class* (four levels, as categorized above
367 (Demographic Data)) and the random effect *community* (26 levels: 18 habituated
368 communities and 8 unhabituated communities (victims of intercommunity killings by study
369 communities). Because one community (Kahama) had zero adolescent males, and the number
370 of infants and juveniles were not specified for another (Kalinzu), the total number of age-sex
371 class and community combinations in our analysis (N=203) was less than would be if all age-
372 sex classes were represented for each community ((2 sexes)x(4 age classes)x(26
373 communities)=208). To control for the composition of the different communities, we used
374 $\log(\text{chimp-years})$ as an offset. For unhabituated communities, for which demographic
375 information was not available, we defined *chimp-years* as the number of years of observation
376 of the focal community (the community being observed when the killing occurred),
377 multiplied by the median number of individuals of that age-sex class present in the median
378 chimpanzee community. Because the range size and membership of unhabituated
379 communities was not known, we assigned victims to no more than one unhabituated
380 community per study community; this undoubtedly underestimates the total number of

381 communities involved, but should not affect the goal of this analysis, which was to estimate
382 the effect of age and sex class on the risk of being killed, given the proportion of each age-
383 sex class in the population. For chimp-years for victims of unknown sex, we used the mean
384 number of males and females present for that age class. To keep type I error rate at the
385 nominal level of 5% we included random slopes of each level of the fixed effects *sex* and
386 *age-class* within the random effect *community*.^{36,37}

387

388 Additional citations for Online Methods

389

- 390 31. Bishop, N., Hrdy, S. B., Teas, J. & Moore, J. Measures of human influence in habitats of
391 South Asian monkeys. *International Journal of Primatology* **2**, 153-167 (1981).
- 392 32. R: A language and environment for statistical computing v. 3.0.2 (R Foundation for
393 Statistical Computing, Vienna, Austria, 2013).
- 394 33. Field, A. *Discovering Statistics Using SPSS*. (Sage Publications, 2005).
- 395 34. Bolker, B., Skaug, H., Magnusson, A. & Nielsen, A. *Getting started with the glmmADMB*
396 *package*, <<http://glmmadmb.r-forge.r-project.org/glmmADMB.html>> (2012).
- 397 35. Bates, D., Maechler, M., Bolker, B. & Walker, S. *lme4: Linear mixed-effects models using*
398 *Eigen and S4. R package version 1.0-5*, <[http://www.inside-r.org/packages/lme4/versions/1-](http://www.inside-r.org/packages/lme4/versions/1-0-5)
399 [0-5](http://www.inside-r.org/packages/lme4/versions/1-0-5)> (2013).
- 400 36. Schielzeth, H. & Forstmeier, W. Conclusions beyond support: overconfident estimates in
401 mixed models. *Behavioral Ecology* **20**, 416-420 (2009).
- 402 37. Barr, D. J., Levy, R., Scheepers, C. & Tily, H. J. Random effects structure for confirmatory
403 hypothesis testing: Keep it maximal. *Journal of Memory and Language* **68**, 255–278 (2013).

404

405 **Extended Data**

406

407 **Figure E1. Summary data and location of study sites. a,** Summary data for each
408 community. *Clade*: bonobos (B), eastern chimpanzees (E), western chimpanzees (W);
409 *Community*: mean total size of the community; *Males*: mean number of males ≥ 12 years old;
410 *Females*: mean number of females ≥ 12 years old; *Home range*: mean size of the
411 community's home range (km²); *Density*=(community)/(home range); *Area*: size of protected
412 area inhabited by the community; *Provisioned*: whether community was regularly
413 provisioned with food; *Disturbance*: sum of the disturbance rating scores. **b,** Location of
414 chimpanzee (circles; N=10) and bonobo (squares; N=3) study sites in Africa.

415

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

423

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

426

427 **Table E2: Intercommunity infanticides**

428

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

430

431 **Table E4: Intracommunity infanticides**

432

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

434 **a**, Species-level comparison of rates of killing between bonobos and chimpanzees. Using

435 only observed and inferred cases (Row 1) results in a complete separation problem (and thus

436 undefined 95% CIs); which is resolved when including either the one suspected case for

437 bonobos (Row 2) or all suspected cases for both species (Row 3). **b**, Community-level

438 comparisons of factors affecting rates of killing focusing either within chimpanzees (Rows 1-

439 3) or including bonobos (Row 4). For comparison, the model-averaged parameter estimates

440 from Table 3 (observed and inferred cases only) are presented in Row 1. Rows 2-4 show the

441 effects of including suspected cases, excluding the unusually large Ngogo community, and

442 adding bonobos, respectively. For the analysis presented in Row 4, the suspected case for

443 bonobos has been included to prevent a complete separation problem. **c**, Summary statistics

444 showing that, controlling for the number of communities under observation, the number of

445 killings observed per year has not increased.

446

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

448 of being killed. Poisson regression; N=203 combinations of *sex*, *age class* and *community*;

449 fixed effects: *sex* with two levels (*male*, *female*); *age class* with four levels (*infant*, *juvenile*,

450 *adolescent*, *adult*); random effects: 26 levels of *community*, including 8 unhabituated

451 communities; log-likelihood = -123. The effect of different age classes is in comparison with

452 *adolescent*; the effect of male is in comparison with *female*. We confirmed the statistical

453 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



