Primates (2006) 47: 14–26
DOI 10.1007/s10329-005-0140-1

ORIGINAL ARTICLE

**Richard W. Wrangham · Michael L. Wilson**
**Martin N. Muller**

# Comparative rates of violence in chimpanzees and humans

Received: 20 July 2004 / Accepted: 22 January 2005 / Published online: 20 August 2005


**Abstract** This paper tests the proposal that chimpanzees (*Pan troglodytes*) and humans have similar rates of death from intraspecific aggression, whereas chimpanzees have higher rates of non-lethal physical attack (Boehm 1999, Hierarchy in the forest: the evolution of egalitarian behavior. Harvard University Press). First, we assembled data on lethal aggression from long-term studies of nine communities of chimpanzees living in five populations. We calculated rates of death from intraspecific aggression both within and between communities. Variation among communities in mortality rates from aggression was high, and rates of death from intercommunity and intracommunity aggression were not correlated. Estimates for average rates of lethal violence for chimpanzees proved to be similar to average rates for subsistence societies of hunter–gatherers and farmers. Second, we compared rates of non-lethal physical aggression for two populations of chimpanzees and one population of recently settled hunter–gatherers. Chimpanzees had rates of aggression between two and three orders of magnitude higher than humans. These preliminary data support Boehm's hypothesis.

R.W. Wrangham (✉)
Department of Anthropology, Harvard University,
Peabody Museum, 11 Divinity Avenue,
Cambridge, MA, 02138, USA
E-mail: wrangham@fas.harvard.edu
Tel.: +1-617-4955948
Fax: +1-617-4968041

M.L. Wilson
Department of Ecology, Evolution and Behavior,
University of Minnesota, St. Paul, MN, USA

M.L. Wilson
Gombe Stream Research Centre,
The Jane Goodall Insitute,
Kigoma, Tanzania

M.N. Muller
Department of Anthropology, Boston University,
Boston, MA, USA

**Keywords** Chimpanzee · Human · Lethal aggression · Mortality rate · Physical attack

## Introduction

Knauft (1991, 1994) and Boehm (1999) claimed that humans and chimpanzees (*Pan troglodytes*) have similarly high rates of lethal aggression ("homicide"), but that humans "exhibit a relatively low level of lesser conflict" (Boehm 1999, p.227). Such claims are important because they imply different social dynamics in chimpanzees and humans. For example, Boehm (1999) proposed that group selection is required to explain what appears to be a relatively low level of non-lethal conflict within human communities. We agree that the apparent differences between human and chimpanzee patterns of violence provoke important questions. Therefore, because relevant quantitative data have not previously been assembled, we conduct here a preliminary analysis designed to compare chimpanzee and human rates of aggression.

First, we consider lethal aggression. Among chimpanzees, fatalities occur in both intercommunity and intracommunity encounters. Intercommunity interactions are harder to observe. They were first documented in Gombe and Mahale (both in Tanzania: Goodall et al. 1979; Nishida 1979). In subsequent decades, intercommunity relationships have been described in more detail both from Gombe and Mahale (Nishida et al. 1985; Williams et al. 2002a, b) and from two further populations in Taï (Ivory Coast: Boesch and Boesch-Achermann 2000; Herbinger et al. 2001) and Kibale (Uganda: Watts and Mitani 2001; Wilson et al. 2001; Watts et al. 2005). Elsewhere, chimpanzee behavior has yielded few or no descriptions of intercommunity interactions even in sites with a decade or more of observation. In one case, this is because the study community has been isolated by a long distance from the nearest other chimpanzees (Bossou, Guinea:

Sugiyama 1989). In others, chimpanzees have apparently not been frequently observed outside their core areas, so there has been little opportunity for reporting on intercommunity encounters (e.g., Kalinzu, Uganda: Furuichi et al. 2001; Budongo, Uganda: Newton-Fisher 2003). Thus, current accounts of chimpanzee intercommunity relationships come mainly from four populations (Gombe, Mahale, Kibale and Taï), all of which also provide information on intracommunity aggression.

Here, we use data from these populations to assess rates of fatality. We also include data from the Sonso community at Budongo, because although intercommunity interactions have not been described from Sonso, both demographic and home-range data are available (Reynolds 1998; Newton-Fisher 2003). We compare our results with rates of death recorded in human intergroup interactions as summarized by Keeley (1996) and others.

Second, we examine non-lethal violence. Boehm (1999) conducted an extensive review that showed that, in general, physical fights rarely occur within hunter–gatherer communities. However, few data on rates of non-lethal physical aggression appear to be available for comparing chimpanzees and humans. In an attempt to quantify Boehm's claim in relation to chimpanzees, we use data collected by Burbank (1992) on the number of physical fights occurring among a group of recently settled Australian aborigines. Burbank was impressed at the apparently high frequency of physical aggression in her study. Her data therefore offer a rare opportunity for a quantitative comparison with chimpanzee physical aggression.

## Methods

Data on chimpanzee fatalities were extracted from the literature, including figures from a previous compilation (Wilson and Wrangham 2003), amplified by information from the Gombe Stream Research Centre and Anne Pusey (personal communication). Individual cases are presented in Appendices 1, 2, 3 and 4 and summarized in Appendices 5, 6, 7 and 8.

To calculate death rates, we assembled data on community composition and the length of time over which survival and mortality were monitored. First, Appendix 9 shows average age–sex class composition of study communities. The number of years from which the data were compiled is as low as a single year (for Budongo and Ngogo). Although this lack of precision is not ideal, we consider these estimates adequate for current purposes because, in early years, the study composition was not precisely known. In all cases where community composition has been reported to change markedly we have incorporated the variation (e.g., Mahale *K*-group). When calculating death rates, we excluded the one case that took place before long-term study began (a Budongo infanticide in 1967).

Second, we estimated the number of years up to and including 2004 during which study communities were sufficiently well observed to allow fatal aggression to be recorded or inferred. These estimates are given in Appendix 10. Communities were sometimes well known demographically at a time when observers did not visit their territorial boundaries. During such periods observers would be unlikely to record intercommunity aggression, and we therefore exclude those periods from estimates of death rates from intercommunity aggression. We have accordingly tried to estimate the duration of these periods (the number of years when intergroup aggression could easily occur without being detected) based on the literature from each site. Our estimates, which are necessarily subjective, are generally conservative. For example, although the Kasekela community is judged to have been well known since 1966 (Williams et al. 2002b), observers rarely visited the territorial borders until 1970. Nevertheless, we estimated the data period as starting in 1966. Similarly, because the Sonso community has been demographically characterized and observed daily since 1994, we estimated the Sonso data period as 8 years (1995–2002). Yet the Sonso territorial borders still appear to be largely unknown, so it is possible that intercommunity aggression has gone unobserved.

Detailed data on rates of non-lethal aggression by wild chimpanzees are surprisingly rare, given the behavior's conspicuous expression and decades of observation. Although agonistic interactions have been studied at most of the long-term sites (e.g., Gombe: Bygott 1974; Goodall 1986; Mahale: Nishida and Hosaka 1996; Kibale: Muller 2002; Taï: Wittig and Boesch 2003; Budongo: Newton-Fisher 2004), clear-cut rates of aggression are rarely presented in a form that permits intersite comparison. For example, Newton-Fisher (2004) presents rates of "agonistic behavior" derived from supplants, stationary threats, displays, chases and attacks. Muller (2002) presents rates for displays, chases and attacks, but excludes supplants and stationary threats. In some studies it is not clear which subset of agonistic behaviors has been included in rate calculations. Finally, as not all studies of aggression are designed to estimate rates, ad libitum observations are frequently grouped with focal data, making it difficult to extract rates from the literature.

In order to identify chimpanzee data comparable to our human sample, we focused on rates of actual physical aggression. Following Goodall (1986), an "attack" was defined as contact aggression, including hits, kicks or slaps delivered in passing (level 1), more extended episodes of pounding, dragging and biting (level 2), and similar incidents lasting more than 30 s or leading to serious injury (level 3). Systematic data on attack rates are available from 1 year at Kanyawara (1998) and 3 years at Gombe: 1970 (Bygott 1974), 1976 and 1978 (Goodall 1986).

Kanyawara data are from behavioral observations conducted by MNM over 12 months in 1998. Forty-minute group focals were used to generate rates of aggression for individual chimpanzees; this was equivalent to all-occurrence sampling (see Muller and Wrangham 2004 for details). Data are presented for 11 adult males and 10 adult females for whom at least 25 observation hours were recorded (male median: 145 h, female median: 70 h). Rates (Tables 7 and 8) are means of individual male rates. The Gombe data (Goodall 1986) are from six adult males and six adult females in 1976, and seven adult males and seven adult females in 1978, all with more than 100 observation hours. Both Gombe and Kanyawara rates exclude observations made when individuals were traveling alone or solely with dependent offspring. All rates are for attacks given, not received.

For humans, we calculated aggression rates recorded by Burbank (1992), who studied Australian Aborigines in Arnhem Land. Burbank recorded 793 cases of physical aggression among about 600 people, during 34 months of fieldwork over a 12-year period. By cross checking information obtained from 46 women and 9 men, she believed that her data was as good as any crime database in the USA. We restricted our calculation initially to the cases of physical aggression (whether armed or unarmed) listed in her Table 2, i.e., 103 cases for men and 100 for women. These numbers are probably over-estimates since they include cases where the same incident included both armed and unarmed fighting, according to Burbank's comment on p.272 that 145 (18.1%) of her 793 arguments were "related". However, as a conservative measure, we have assumed they were independent. Cases of aggression excluded by Burbank in this compilation included juvenile delinquency, punishment of children, sorcery, vandalism and sexual coercion. The only one of these categories comparable with chimpanzee data is sexual coercion, which Burbank reported as "perhaps four or five cases, past and present, that might be defined as" (sexual coercion) (p.272). Thus, some of these four to five cases apparently occurred before Burbank's fieldwork. Nevertheless, we included five additional cases of aggression for male, and five for female (i.e., five rapes), in order to obtain a maximal estimate of the rate of aggression.

Thus, the total cases of aggression were 108 (men) and 105 (women). The number of adults (individuals of 15 years and older) averaged 156 men and 159 women, according to censuses in 1981 and 1988. We assumed a 12-h active day, even though fights could occur at any time, and an average 30 days per month for 34 months. These assumptions produced rates of 0.0566 episodes of physical aggression per 1,000 h for men and 0.0539 per 1,000 h for women.

We present data on killing rates as number of deaths per 100,000 per year, following standard practice in human compilations.

Statistical tests are two-tailed.

## Results

### Lethal aggression in chimpanzees

Chimpanzee data on lethal aggression are taken from nine social communities in five populations observed with good demographic data for a total of 158 data-years (Appendix 10). The median duration of good observation per community was 18 data-years, with a median 46.3 individuals in the community (mean 53.6: Appendices 9 and 10). During the 158 data-years, intercommunity attacks appeared responsible for 49 deaths (direct evidence, 33 deaths; suspected, 16 deaths). This total of 49 observed and suspected kills included 27 members of study communities (24 adult or adolescent, 3 infants or juveniles) and 22 members of unhabituated communities (8 adult or adolescent and 14 infants or juveniles) (Appendices 1, 2, 5 and 6). In the same period, attacks within communities were reported to have killed 26 individuals (direct evidence, 19 deaths; suspected, 7 deaths). Victims of intracommunity aggression included five adults or adolescents, and 21 infants or juveniles (Appendices 3, 4, 7 and 8).

First, death rates of study chimpanzees from intercommunity aggression are summarized in Table 1. The total sample included 8,828 "chimpanzee-years" of observation (1,970 adult and adolescent male, 3,596 adult and adolescent female, 3,262 infant and juvenile). Pooling all mortality data and observation years across sites yields an overall range of estimated mortality rates from intercommunity aggression of between 125 and 306 deaths per 100,000 individuals per year (Table 1). Pooling data, however, may allow outliers to have an undue influence on the final figure. Considering each population as an independent sample, the median mortality rate from intercommunity aggression is 69 to 287 deaths per 100,000 per year (Table 5). Overall, adult and adolescent males experienced a higher death rate than infants and juveniles. However, some deaths of infants that occurred from unknown causes could have been due to intercommunity killing.

Table 1 shows that there was substantial variation among communities in estimated mortality rates from intercommunity violence. Three communities experienced no observed, inferred or suspected intercommunity killings. Two of these were reported to kill members of neighboring communities, however, i.e., Budongo (Sonso) and Kibale (Ngogo) (Table 2). This suggests that within populations, differences in rates of violent death among communities come not only from measurement error, but also from variation among communities in their intergroup relationships. In support of this idea, across study communities the correlation between the rate of violent death and the rate of killing in intercommunity encounters was not significant (Tables 1 and 2: $r = 0.44$, $n = 9$, n.s.).

Second, death rates from intracommunity aggression are presented in Table 3. Again, there was substantial

**Table 1** Mortality rates from intercommunity aggression by chimpanzees (*Pan troglodytes*) directed at members of study communities

| Site | Community | Adult + adolescent males | Adult + adolescent females | Infants and juveniles | All | No. of data years |
|---|---|---|---|---|---|---|
| Budongo | Sonso | 0 | 0 | 0 | 0 | 10 |
| Gombe | Kahama | 20,833 (29,167) | 7,143 | 0 | 12,000 (16,000) | 5 |
| Gombe | Kasekela | 0 (1,179) | 0 | 0 | 0 (222) | 39 |
| Gombe | Mitumba | 2,344 | 0 | 1,389 | 1,008 | 9 |
| Kibale | Kanyawara | 562 (2,250) | 0 | 0 | 162 (648) | 14 |
| Kibale | Ngogo | 0 | 0 | 0 | 0 | 8 |
| Mahale | *K*-group | 0 (11,513) | 0 | 801 | 243 (1,946) | 16 |
| Mahale | *M*-group | 0 | 0 | 111 | 37 | 34 |
| Taï | Northern | 0 | 0 | 0 | 0 | 23 |
| Total | | 355 (1,167) | 28 | 92 | 125 (306) | 158 |

Cells show number of deaths per 100,000 per year, based on "observed plus inferred" fatalities caused by intercommunity aggression. Figures in parentheses show rates using "observed plus inferred plus suspected" killings. Calculations are made using data in Appendices 1, 2, 5, 6, 9 and 10, based only on deaths of chimpanzees in the study communities. The "Total" row shows mortality rates based on the summed deaths and summed individual-study-years across all communities

**Table 2** Rates of intercommunity killing by chimpanzees in study communities

| Site | Community | Adult + adolescent males | Adult + adolescent females | Infants and juveniles | Total victims |
|---|---|---|---|---|---|
| Budongo | Sonso | 0 | 0 | 1.67 | 1.67 |
| Gombe | Kahama | 0 | 4.76 | 0 | 4.76 |
| Gombe | Kasekela | 2.06 | 0.29 | 1.77 | 4.76 |
| Gombe | Mitumba | 0 | 0 | 0 | 0 |
| Kibale | Kanyawara | 0.71 | 0 | 0 | 0.71 |
| Kibale | Ngogo | 2.60 | 0 | 3.13 | 5.73 |
| Mahale | *K*-group | 0 | 0 | 1.64 | 1.64 |
| Mahale | *M*-group | 0 | 0 | 0.69 | 0.69 |
| Taï | Northern | 0 | 0 | 0 | 0 |
| Total | | 0.97 | 0.15 | 1.26 | 2.38 |

Cells show number of individuals killed per 100 adult-male years. Number of victims comes from Appendices 1 and 2. Number of adult-male years is from Appendices 9 and 10

variation among communities, and the correlation between rates of death from intracommunity and intercommunity violence was not significant ($r = -0.33$ to $-0.43$, $n = 9$, n.s.). Table 3 shows that infants and juveniles were the most frequent victims, followed by adult and adolescent males.

The effects of both intercommunity and intracommunity violence are summed in Table 4 and Fig. 1. The only age–sex class that experienced little violence-related mortality was adult and adolescent females, and all communities experienced violent deaths in at least one age–sex class. Overall mortality rates were similar when calculated by pooling all data (see "Total" in Table 4) or as medians across the nine study communities. Adult and adolescent males were killed at rates similar to, but marginally higher than, infants and juveniles (365–609 deaths per 100,000 per year for males vs 476–521 deaths per 100,000 per year for infants and juveniles). Inclusion

**Table 3** Annual mortality rates from intracommunity aggression in chimpanzees

| Site | Community | Adult + adolescent males | Adult + adolescent females | Infants and juveniles | Total victims |
|---|---|---|---|---|---|
| Budongo | Sonso | 625 | 0 | 0 | 200 |
| Gombe | Kahama | 0 | 0 | 0 | 0 |
| Gombe | Kasekela | 0 | 0 | 368 (1,403) | 277 (644) |
| Gombe | Mitumba | 2,344 | 0 | 1,389 | 1,008 |
| Kibale | Kanyawara | 0 | 0 | 476 | 162 |
| Kibale | Ngogo | 320 | 0 | 0 | 87 |
| Mahale | *K*-group | 0 | 0 | 0 | 0 |
| Mahale | *M*-group | 365 | 0 | 663 (774) | 298 (335) |
| Taï | Northern | 0 | 0 | 169 | 71 |
| Total | | 254 | 0 | 429 (644) | 215 (294) |

Cells show number of deaths per 100,000 per year, based on "observed plus inferred" fatalities caused by intercommunity aggression. Figures in parentheses show rates using "observed plus inferred plus suspected" killings. Calculations are made using data in Appendices 3, 4, 7, 8, 9 and 10, based only on deaths of chimpanzees in the study communities. The "Total" row shows mortality rates based on the summed deaths and summed individual-study-years across all communities

**Table 4** Total estimated mortality rates from aggression in chimpanzees, between and within communities

| Site | Community | Adult + adolescent males | Adult + adolescent females | Infants and juveniles | Total victims |
|---|---|---|---|---|---|
| Budongo | Sonso | 625 | 0 | 0 | 200 |
| Gombe | Kahama | 20,833 (29,167) | 7,143 | 0 | 12,000 (16,000) |
| Gombe | Kasekela | 0 (977) | 0 | 638 (1,403) | 277 (831) |
| Gombe | Mitumba | 4,688 | 0 | 2,778 | 2,017 |
| Kibale | Kanyawara | 562 (2,250) | 0 | 476 | 324 (810) |
| Kibale | Ngogo | 321 | 0 | 0 | 87 |
| Mahale | *K*-group | 0 (9,511) | 0 | 801 | 243 (1,946) |
| Mahale | *M*-group | 365 | 0 | 774 (885) | 335 (372) |
| Taï | Northern | 0 | 0 | 169 | 71 |
| Total | | 609 (1,421) | 28 | 521 (736) | 340 (600) |
| Median | | 365 (977) | 0 | 476 | 277 (810) |

Cells show number of deaths per 100,000 per year, based on ''observed plus inferred'' fatalities caused by intercommunity aggression. Figures in parentheses show rates using ''observed plus inferred plus suspected'' killings. Data are summed from Tables 1 and 3. The ''Total'' row shows mortality rates based on the summed deaths and summed individual-study-years across all communities. ''Median'' is the median across nine communities

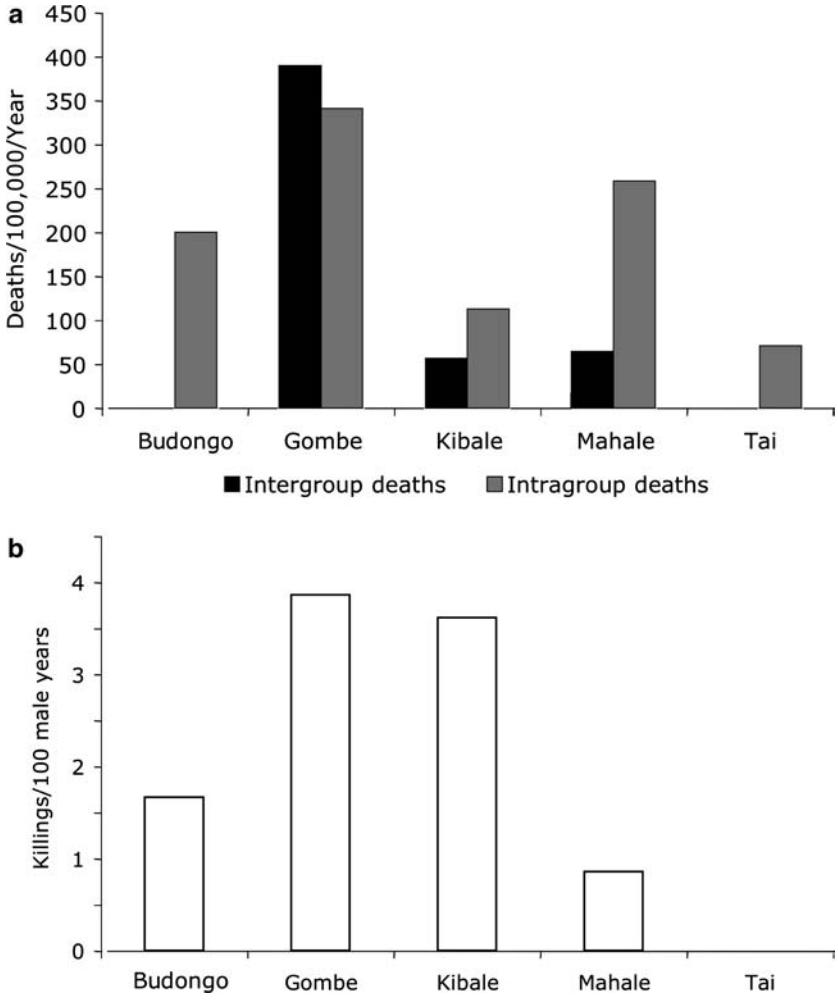


**Fig. 1** Rates of inter- and intracommunity killing in five major long-term chimpanzee study sites. **a** *Bars* show the number of deaths per 100,000 individuals per year caused by attacks from members of other communities (*black*) and by members of the victim's own community (*grey*) for each population. Because different communities at the same study site do not necessarily represent independent samples, a single rate was calculated for each population, based on the total number of killings observed or inferred and the total observation time and mean population size for each community. **b** *Bars* indicate the rate at which study communities were observed to commit intercommunity killings, expressed in killings per 100 years observation per adult male

of suspected cases suggests that males were killed at rates about twice those of infants and juveniles (977–1,421 per 100,000 per year for males vs 476–736 deaths per 100,000 per year for infants and juveniles).

The sex difference in susceptibility to violent death among adults and adolescents appears to be mirrored among infants and juveniles. Thus, Appendices 2 and 4 show that for infanticides where the death of the infant was recorded, there were five male and two female victims in intercommunity aggression, versus 13 male and 3 female victims in intracommunity aggression. This difference (18 male, 5 female) is significantly different from

a 50:50 ratio, which is the approximate sex ratio at birth ($P < 0.01$, $\chi^2 = 7.3$, 1 *df*).

## Lethal aggression in humans

Data on human mortality rates from intergroup aggression (war) came principally from a compilation by Keeley (1996), supplemented by other data that we found with the help of Doug Jones. We focused on independent subsistence societies, coding separately for hunter–gatherers and farmers. Results are shown in Table 6. For hunter–gatherers median annual mortality from intergroup aggression was 164 deaths per 100,000 (mean 249, SD 273, $n = 12$). For farmers, median annual mortality from intergroup aggression was 595 deaths per 100,000, (mean 580, SD 313, $n = 20$). This sample conforms to the conclusion that subsistence farmers have higher rates of mortality from warfare (Mann–Whitney $U = 43.5$, $n = 12$, 20, $P < 0.01$).

We have not compiled death rates from intragroup aggression in human subsistence societies. In subsistence societies they are generally reported to be low compared to rates of death from warfare (e.g., Heider 1997), though of course there is much variation.

**Table 5** Summary of mortality rates among chimpanzees from aggression, with data pooled within each population

| Population | Intergroup deaths/100,000 individuals/year | Intergroup killing/100 male years | Intragroup deaths/100,000 individuals/year | Total deaths/100,00 individuals/year |
|---|---|---|---|---|
| Budongo | 0 | 1.85 | 271 | 271 |
| Gombe | 417 (782) | 4.76 | 261 (626) | 678 (1408) |
| Kibale | 72 (287) | 3.03 | 144 | 216 (287) |
| Mahale | 69 (310) | 0.90 | 275 (310) | 344 (620) |
| Taï | 0 | 0.00 | 78 | 78 |
| Median | 69 (287) | 1.85 | 261 (271) | 271 (287) |

Calculated as in prior tables by combining data from different communities on ''observed plus inferred'' killings. Figures in parentheses show rates using ''observed plus inferred plus suspected'' killings. ''Median'' is the median across five populations

**Table 6** Annual mortality rates in human subsistence societies from intergroup aggression

| Group | Region | Hunter/farmer | Deaths/100,000/year | References |
|---|---|---|---|---|
| Semai | Malaysia | H | 0 | Keeley (1996) |
| Andamanese 30 years | India | H | 20 | Keeley (1996) |
| Dobe !Kung | South Africa | H | 42 | Lee (1979) |
| Canadian Eskimo | Canada | H | 100 | Graburn (1969) |
| Gidjingali | Australia | H | 148 | Hiatt (1965) |
| Tiwi 1893–1903 | Australia | H | 160 | Keeley (1996) |
| Yaghan | Tierra del Fuego | H | 169 | Cooper (1917) |
| Yurok | California | H | 240 | Keeley (1996) |
| Casiguran Agta | Philippines | H | 326 | Headland (1989) |
| Murngin | Australia | H | 330 | Keeley (1996) |
| Modoc | California–Oregon | H | 450 | Keeley (1996) |
| Piegan | North America | H | 1,000 | Keeley (1996) |
| Boko Dani | New Guinea | F | 140 | Keeley (1996) |
| Gebusi | New Guinea | F | 200 | Keeley (1996) |
| Mohave 1840s | Western America | F | 230 | Keeley (1996) |
| Yanomama | Venezuela | F | 290 | Keeley (1996) |
| Tauade | New Guinea | F | 320 | Keeley (1996) |
| Mae Enga | New Guinea | F | 320 | Keeley (1996) |
| Auyana | New Guinea | F | 420 | Keeley (1996) |
| Manga 1949–1956 | New Guinea | F | 460 | Keeley (1996) |
| Dugum Dani 1961 | New Guinea | F | 480 | Keeley (1996) |
| Mtetwa | South Africa | F | 590 | Keeley (1996) |
| Kalinga | Philippines | F | 600 | Keeley (1996) |
| Kunimaipa | New Guinea | F | 621 | Hallpike (1977) |
| Tauna Awa | New Guinea | F | 624 | Hayano (1974) |
| Buin | New Guinea | F | 710 | Keeley (1996) |
| Telefolmin 1939–1950 | New Guinea | F | 740 | Keeley (1996) |
| Chippewa 1825–1832 | North America | F | 750 | Keeley (1996) |
| Hewa | New Guinea | F | 778 | Steadman (1971) |
| Fiji 1860s | Fiji | F | 870 | Keeley (1996) |
| Dani-S. Grand Valley | New Guinea | F | 1,000 | Keeley (1996) |
| Kato 1840s | California | F | 1,450 | Keeley (1996) |
| | Median ($n = 12$) | Hunter | 164 | |
| | Median ($n = 20$) | Farmer | 595 | |

Annual death rates from intergroup aggression. See especially Table 6.1 in Keeley (1996)

## Lethal aggression: humans and chimpanzees compared

Comparison of Tables 4, 5 and 6 shows that according to current data, the average conservatively estimated risk of violent death for chimpanzees (271 per 100,000 per year, Table 5) falls in the same order of magnitude as the median values for rates of death from warfare among subsistence-society hunters and farmers (164 and 595 per 100,000 per year, respectively). Thus, among chimpanzees the risk of death from violence appears roughly similar to the risk experienced by humans living in subsistence societies (see Fig. 2).

Violent mortality among chimpanzees was distributed approximately equally among two major classes: adult/adolescent males and infants (Table 4). Among humans, by contrast, war mortality appears generally to be highest in adult males. For example in seven subsistence farming societies with data compiled by Keeley (1996: Table 6.2) the median percentage of deaths due to warfare was 28.5% for males (range 8.3–59.0) versus 6.1% for females (range 2.3–27.0). Considering only adult males, therefore, rates of mortality may be higher for humans (Fig. 2).

## Non-lethal physical aggression in chimpanzees and humans

Rates of physical attack among wild chimpanzees have been tallied for Gombe (Bygott 1974; Goodall 1986) and Kanyawara. Four samples derived from more than 4,000 observation hours for adult males and 3,200 h for adult females yielded median rates of 2,301 attacks per 100,000 h (males), and 911 attacks per 100,000 h (females) (Tables 7 and 8), with relatively little variation in attack rates among samples. Males in both populations engaged in contact aggression more frequently than females (Kanyawara, Mann–Whitney *U*-test: $Z = -2.21$, $n = 11, 10$, $P < 0.05$). Adult males at Kanyawara directed aggression toward male and female victims at equivalent rates (Wilcoxon signed ranks test: $W = -3.5$, $n = 11$, $P$ n.s.). A captive study with 19 chimpanzees and 701 "high-level" aggressive acts (including chasing as well as physical contact) found a similarly high rate to the wild (3,213 attacks per 100,000 h, Noë et al. 1980).

We have found few comparable data on rates of physical aggression among humans in subsistence societies. However, when Burbank (1992) studied aboriginal women in Australia, she found that they experienced an unusually high rate of physical aggression, and she therefore recorded it systematically. In this open-air society of recently settled hunter–gatherers, overt physical and verbal aggression occurred regularly and was accepted as a legitimate form of social action, though it was always a cause of gossip and discussion. Among 315 adults it led to over 300 lifetime wounds from hitting with or without weapons. Women were often involved and were injured more than men.

Tables 7 and 8 summarize our estimates of the rate of physical aggression from Burbank's data. They show a mean rate of six attacks per 100,000 h (males) and five attacks per 100,000 h (females). This means that chimpanzee attacks occurred at a median rate that was 384 times higher for males (2,301/6) and 182 times higher for females (911/5) than among the Arnhem Land people.

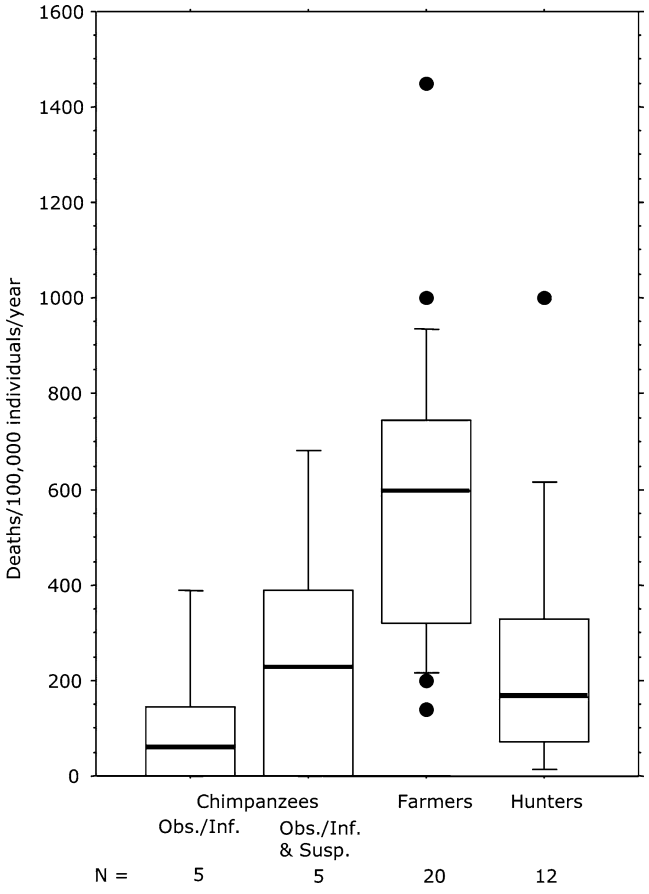


**Fig. 2** *Box* plots illustrating the death rate from intergroup aggression for chimpanzees and humans in subsistence societies. *Boxes* enclose the 25th, 50th and 75th percentile of each data set. The 50th percentile (median) is indicated by a *thick horizontal line*. *Whiskers* indicate the 10th and 90th percentiles, and *dots* indicate more extreme outliers. The number of populations for each data set (*N*) is given below the graph. Two estimates are shown for chimpanzees: one based strictly on observed or inferred cases, and one that also includes suspected cases. Human data are shown for subsistence farmers and hunter–gatherers

## Discussion

Our aim was to test Boehm's hypothesis (Boehm 1999) that rates of lethal aggression tend to be similar in chimpanzees and humans, whereas rates of non-lethal aggression are higher in chimpanzees than in humans. This hypothesis has not been addressed quantitatively before. Our data are subject to considerable variance (e.g., rates of lethal aggression in different communities of chimpanzees or humans), and small sample size (e.g., only one sample of rates of non-lethal physical aggression among humans). Nevertheless, it is clear that within the limits of the data, Boehm's hypothesis is strongly supported.

**Table 7** Rates of physical attack in adult male chimpanzees and humans

| Species | Community | When | Attacks per 100,000 h |
|---|---|---|---|
| Chimpanzee | Kibale–Kanyawara | 1998 | 2,670 |
| Chimpanzee | Gombe–Kasekela | 1978 | 1,464 |
| Chimpanzee | Gombe–Kasekela | 1976 | 1,931 |
| Chimpanzee | Gombe–Kasekela | 1970 | 3,030 |
| Chimpanzee | Median | | 2,301 |
| Human | Arnhem Land–Mangrove | 1977–1988 | 6 |

Chimpanzee data are from Muller (2002). Human data are calculated from Burbank (1992). For definitions and calculations, see Methods. Attacks were cases of aggression involving non-lethal physical contact

**Table 8** Rates of physical attack in adult female chimpanzees and humans

| Species | Site | When | Attacks per 100,000 h |
|---|---|---|---|
| Chimpanzee | Kibale–Kanyawara | 1998 | 620 |
| Chimpanzee | Gombe–Kasekela | 1978 | 911 |
| Chimpanzee | Gombe–Kasekela | 1976 | 1,003 |
| Chimpanzee | Median | | 911 |
| Human | Arnhem Land–Mangrove | 1977–1988 | 5 |

Data as in Table 7

First, we calculated rates of lethal aggression for nine communities of wild chimpanzees in five populations, and compared them with data from human warfare. The average rates of violent death among chimpanzees were clearly in the same order of magnitude as the average for humans. Similarly, the range of variation over approximately four decades of sampling was similar to the range of variation in mortality rates among human cultures. Thus, current data indicate that chimpanzees and humans living in subsistence societies have similarly high rates of death from intraspecific violence. This has not always been appreciated. For example, Kelly (2000, p.175) inferred that compared to nomadic hunter–gatherers, chimpanzees have high rates of mortality from intercommunity aggression. Evidence of demographically similar kill rates from violence does not mean that chimpanzee and human lethal aggression is similar in other ways, of course. Further analysis may show that even if the rates of mortality are similar, the patterns of homicide could differ importantly. For example, hypotheses suggested by our analysis include: chimpanzees may have relatively high rates of death from intracommunity violence compared to humans; chimpanzees may experience higher rates of infant mortality from violent death, and chimpanzees may have lower rates of violent death among adult females. Many such ideas remain to be tested.

Second, we compared rates of non-lethal physical aggression between two communities of wild chimpanzees and a single community of humans, i.e., a population of recently settled Australian aboriginal hunter–gatherers (Burbank 1992). Our comparison is limited by having only one human and two chimpanzee populations. We justify this comparison by the fact that preliminary data are useful, that the data from the two chimpanzee populations are similar, that the differences between chimpanzees and humans are large enough to be strongly suggestive, and that Burbank (1992) believed that the people she was studying had relatively high rates of aggression. Given Burbank's impression, it is striking that our calculations found the Australian aboriginals to experience rates of physical aggression that were 182–384 times lower than the median for chimpanzees.

Furthermore, our estimate of chimpanzee aggression is highly conservative. Restricting our analysis to incidents of actual contact aggression excluded other high-level aggressive acts, such as chases. Most chases would probably have resulted in contact aggression, had the aggressor been able to catch the victim. Combining chases and contact aggression in the Kanyawara sample increases the adult male mean dramatically—from 2,670 to 9,248 incidents per 100,000 h.

Many ethnographic accounts support the conclusion that foraging populations exhibit low rates of non-lethal physical aggression, as Boehm (1999) showed. For example, Marshall (1998) spent seventeen and a half months with two bands of Nyae Nyae !Kung that averaged 60–75 people. She personally saw "only four flare-ups of discord and heard about three others which occurred in neighboring bands during that period" (Marshall 1998, p.71). Nevertheless, physical violence can occur among foragers. Turnbull (1965, p.287) reported that among Mbuti pygmies, "a certain amount of wife-beating is considered good, and the wife is expected to fight back." Cultural variation means that quantitative data are desirable, and that our conclusions must be preliminary.

Finally, there are several important problems to solve with regard to estimating rates of violent death among chimpanzees with increased confidence. For example, it seems likely that our category of "Observed + Inferred" underestimates the number of cases of lethal violence, because when chimpanzees in a study community disappear for unknown reasons, violence is a reasonable explanation. An improved way to assign such cases to "Suspected" or "Unlikely" would be helpful.

It is currently unclear how important observer effects are. The presence of observers might partially protect study chimpanzees from aggression by unhabituated neighbors. For example, in January 2004, an adult male Kanyawara chimpanzee who was being attacked by a group of males from a neighboring community escaped after his attackers fled on seeing a human observer (D. Muhangyi, personal communication).

Improved data quality will allow more confidence in assessing rates. Thus we included data from Budongo, even though the territorial borders appear not to be known for the Sonso community.

As we have tried to make clear, therefore, the relatively small sample size and great variation among sites

renders imprecise any estimate of violence-related mortality rates for chimpanzees as a species. Nonetheless, three key findings emerge.

First, despite a widespread emphasis on intercommunity killing in chimpanzees, when all age–sex classes are considered together, it becomes clear that in most populations, study communities lost more members to violent attacks from within their community, rather than from foreign chimpanzees. Most victims of intragroup killings, however, were infants, whereas many victims of intergroup killings were adults.

Second, overall the study communities appeared to inflict somewhat more killing than they themselves suffered. This was not always the case. Thus, Nishida et al. (1985) found that males in the habituated *K*-group dwindled in number, apparently as a result of attacks from the poorly habituated *M*-group. Nevertheless, study communities lost members to intergroup aggression in three of five populations, but were reported to kill members of other communities in four of five populations. If substantiated, such an effect could be due to study communities being (on average) larger than non-study communities, and hence less vulnerable to attack. In addition, it could result from study communities benefiting from the protective effects of researchers, who may inadvertently frighten away unhabituated neighbors during intergroup encounters.

Third, Gombe stands out with its high level of intergroup violence, both suffered and committed by study communities. (Mortality from intragroup violence, however, was comparable to other sites). Many of the intergroup deaths at Gombe occurred during the much discussed extermination of the Kahama community by Kasekela males in the 1970s. However, intergroup violence continues to occur at Gombe, and is now known to occur at other sites. As data continue to accumulate from Gombe and other sites, Gombe may turn out to be less exceptional.

**Acknowledgements** RWW thanks Toshisada Nishida for his invitation to share the celebration of his retirement, for his hospitality in Mahale in 1971, and for his inspiration over four decades. Doug Jones assisted in finding homicide data. We are grateful to Chris Boehm, Polly Weissner and two anonymous reviewers for comments, and to Sylvia Amsler, Tofiki Mikidadi, Carson Murray, Hogan Sherrow and David Watts for access to unpublished data. RWW thanks the National Science Foundation for funds (proposal 0416125).

## Appendix 1

Intercommunity killings, adults and adolescents, up to 2004

| Site | Date | Victim (sex) | Sex | Aggressors' community | Victim's community | Evidence | References | Certain/suspected |
|---|---|---|---|---|---|---|---|---|
| Gombe | 1974 | Godi | M | Kasekela | Kahama | Attack observed | 3 | Certain |
| Gombe | 1974 | Dé | M | Kasekela | Kahama | Attack observed | 3 | Certain |
| Gombe | 1975 | Goliath | M | Kasekela | Kahama | Attack observed | 3 | Certain |
| Gombe | 1975 | Madam Bee | F | Kasekela | Kahama | Attack observed | 3 | Certain |
| Gombe | 1977 | Sniff | M | Kasekela | Kahama | Attack observed | 3 | Certain |
| Gombe | 1998 | Unknown | M | Kasekela | Kalande | Attack observed | 5 | Certain |
| Gombe | 1972 | Unknown | F | Kahama? | Kalande? | Body found | 1 | Certain |
| Gombe | 1977 | Charlie | M | Kasekela | Kahama | Body found | 3 | Certain |
| Gombe | 2002 | Rusambo | M | Kasekela | Mitumba | Body found | 5 | Certain |
| Gombe | 1973 | Hugh | M | Kasekela? | Kahama | Disappeared | 3 | Suspected |
| Gombe | 1975 | Faben | M | Unknown | Kasekela | Disappeared | 3 | Suspected |
| Gombe | 1977 | Willy Wally | M | Kasekela? | Kahama | Disappeared | 3 | Suspected |
| Gombe | 1979 | Sherry | M | Unknown | Kasekela | Disappeared | 3, 7 | Suspected |
| Gombe | 1981 | Humphrey | M | Unknown | Kasekela | Disappeared | 3 | Suspected |
| Gombe | 1982 | Figan | M | Unknown | Kasekela | Disappeared | 3 | Suspected |
| Kibale | 2002 | Unknown | M | Ngogo | Unknown | Attack observed | 6 | Certain |
| Kibale | 2002 | Unknown | M | Ngogo | Unknown | Attack observed | 6 | Certain |
| Kibale | 2002 | Unknown | M | Ngogo | Unknown | Attack observed | 6 | Certain |
| Kibale | 2004 | Unknown | M | Ngogo | Unknown | Attack observed | 9 | Certain |
| Kibale | 2004 | Unknown | M | Ngogo | Unknown | Attack observed | 10 | Certain |
| Kibale | 1992 | Ruwenzori | M | Rurama | Kanyawara | Body found | 4 | Certain |
| Kibale | 1998 | Unknown | M | Kanyawara | Sebitole | Body found | 4 | Certain |
| Kibale | 1994 | Julian | M | Unknown | Kanyawara | Disappeared | 8 | Suspected |
| Kibale | 1998 | Badfoot | M | Unknown | Kanyawara | Disappeared | 8 | Suspected |
| Kibale | 2001 | Light Brown | M | Unknown | Kanyawara | Disappeared | 8 | Suspected |
| Mahale | 1970 | Kaguba | M | *M*-group? | *K*-Group | Disappeared | 2 | Suspected |
| Mahale | 1975 | Kasanga | M | *M*-group? | *K*-Group | Disappeared | 2 | Suspected |
| Mahale | 1975 | Kajabala | M | *M*-group? | *K*-Group | Disappeared | 2 | Suspected |
| Mahale | 1978 | Kasonta | M | *M*-group? | *K*-Group | Disappeared | 2 | Suspected |
| Mahale | 1979 | Sobongo | M | *M*-group? | *K*-Group | Disappeared | 2 | Suspected |
| Mahale | 1982 | Kamemanfu | M | *M*-group? | *K*-Group | Disappeared | 2 | Suspected |
| Mahale | 1982 | Masisa | M | *M*-group? | *K*-Group | Disappeared | 2 | Suspected |

References: 1, Wrangham (1975); 2, Nishida and Kawanaka (1985); 3, Goodall (1986); 4, Wrangham (1999); 5, Wilson et al. (submitted); 6, Watts and Mitani (personal communication); 7, Jane Goodall Institute's Center for Primate Studies; 8, Kibale Chimpanzee Project records; 9, Muller (personal observation), Watts et al. (2005); 10, Watts et al. (2005)

## Appendix 2

Intercommunity infanticides up to 2002

| Site | Date | Infant's sex | Aggressors' community | Victim's community | Evidence | References |
|---|---|---|---|---|---|---|
| Budongo | 1991 | M | Sonso | N15 | Attack observed | 5 |
| Budongo | 1991 | Unknown | Sonso | N15 | Body seen | 5 |
| Gombe | 1971 | Unknown | Kasekela | Unknown | Attack observed | 1 |
| Gombe | 1975 | F | Kasekela | Unknown | Attack observed | 2 |
| Gombe | 1975 | M | Kasekela | Unknown | Body seen | 2 |
| Gombe | 1979 | Unknown | Kasekela | Unknown | Attack observed | 4 |
| Gombe | 1993 | F | Kasekela | Mitumba | Attack observed | 8 |
| Gombe | 1998 | Unknown | Kasekela | Kalande | Attack observed | 8 |
| Kibale | 1995 | Unknown | Ngogo | Eastern | Attack observed | 6 |
| Kibale | 1995 | Unknown | Ngogo | Eastern | Attack observed | 6 |
| Kibale | 2001 | Unknown | Ngogo | Northern | Attack observed | 7 |
| Kibale | 2001 | Unknown | Ngogo | Northern | Body seen | 7 |
| Kibale | 2004 | M | Ngogo | ? | Attack observed | 10 |
| Kibale | 2004 | Unknown | Ngogo | ? | Attack observed | 10 |
| Mahale | 1970 | M | *K*-group | *M*-group | Body seen | 3 |
| Mahale | 1971 | M | *M*-group | *K*-group | Body seen | 3 |
| Mahale | 2001 | M | *M*-group | Unknown | Attack observed | 9 |

References: 1, Bygott (1972); 2, Goodall (1977); 3, Nishida (1979); 4, Goodall (1986); 5, Newton-Fisher (1999); 6, Watts and Mitani (2000); 7, Watts et al. (2002); 8, Wilson et al. (2004); 9, Kutsukake and Matsusaka (2002); 10, Hogan Sherrow and Sylvia Amsler (personal communication)

## Appendix 3

Intracommunity killings, adults and adolescents, up to 2002

| Site | Date | Victim | Sex | Community | Evidence | References | Certain/suspected |
|---|---|---|---|---|---|---|---|
| Mahale | 1995 | Ntologi | M | *M*-group | Attack observed | 1 | Certain |
| Mahale | 1996 | Jilba | M | *M*-group | Body found | 2 | Certain |
| Budongo | 1998 | Zesta | M | Sonso | Attack observed | 3 | Certain |
| Kibale | 2002 | Grapelli | M | Ngogo | Attack observed | 4 | Certain |
| Gombe | 2004 | Vincent | M | Mitumba | Attack observed | 5 | Certain |

References: 1, Nishida (1996); 2, Wrangham (1999); 3, Fawcett and Muhumuza (2000); 4, Watts (2004); 5, Tofiki Mikidadi (personal communication)

## Appendix 4

Intracommunity infanticides up to 2004

| Site | Date | Victim | Sex | Community | Evidence | Attackers | References |
|---|---|---|---|---|---|---|---|
| Budongo | 1967 | Unknown | ? | Sonso? | Body found | | 1 |
| Gombe | 1975 | Otta | F | Kasekela | Observed | Females | 2 |
| Gombe | 1976 | Orion | M | Kasekela | Observed | Females | 2 |
| Gombe | 1976 | Genie | F | Kasekela | Observed | Females | 2 |
| Gombe | 2004 | Tofiki | M | Kasekela | Observed | Male | 5 |
| Gombe | 1976 | MLB2 | M | Kasekela | Body found | Unknown | 2 |
| Gombe | 1994 | Rafiki's | ? | Mitumba | Body found | | 3 |
| Gombe | 1976 | Banda | F | Kasekela | Suspected | Unknown | 2 |
| Gombe | 1974 | Gandalf | M | Kasekela | Suspected | Unknown | 2 |
| Gombe | 1975 | Patti's | unk | Kasekela | Suspected | | 4 |
| Gombe | 1976 | Little Bee's | unk | Kasekela | Suspected | | 4 |
| Gombe | 1991 | Kenitum | M | Kasekela | Suspected | | 6 |

Appendix 4 (Contd.)

| Site | Date | Victim | Sex | Community | Evidence | Attackers | References |
|---|---|---|---|---|---|---|---|
| Gombe | 2004 | Kobe | M | Kasekela | Suspected | | 5 |
| Kibale | 1994 | Temba | M | Kanyawara | Observed | Male, female | 7 |
| Mahale | 1983 | Watendele's | M | *M*-group | Observed | Males | 8 |
| Mahale | 1985 | TMs | M | *M*-group | Observed | Male | 9 |
| Mahale | 1989 | Mirinda's | M | *M*-group | Observed | Males | 10 |
| Mahale | 1977 | Humbe (Ndilo's) | M | *M*-group | Body found | Male? | 11 |
| Mahale | 1983 | Chausiku's | M | *M*-group | Body found | Male? | 12 |
| Mahale | 1990 | Betty's | M | *M*-group | Observed | Male | 10 |
| Mahale | 1979 | Wakasunga's | M | *M*-group | Suspected | Unknown | 13 |
| Taï | ? | ? | ? | Northern | Body found | | 14 |

References: 1, Suzuki (1971) (occurred before long-term study and hence not used in calculation of death rates); 2, Goodall (1986), Jane Goodall Institute CPS; 3, Anne Pusey (personal communication); 4, Goodall (1986, p.284) (''Three other mothers, etc.''); 5, Carson Murray (personal communication); 6, JGI-CPS unpublished data (observers thought that victim was hurt during an attack on his mother); 7, Arcadi and Wrangham (1999); 8, Takahata (1985); 9, K. Masui unpublished observation (1986), cited in Hamai et al. (1992); 10, Hamai et al. (1992); 11, Norikoshi (1982); 12, Nishida and Kawanaka (1985); 13, Kawanaka (1981); 14, Boesch and Boesch-Achermann (2000, p 33) (infant found being eaten by females, and young mother without infant seen in border region)

## Appendix 5

Number of known, inferred or suspected adult or adolescent victims of intercommunity aggression at long-term study sites up to 2002

| Site | Attack observed | Body found | Disappearance | Total |
|---|---|---|---|---|
| Budongo | 0 | 0 | 0 | 0 |
| Gombe | 6 | 3 | 6 | 15 |
| Kibale | 5 | 2 | 3 | 10 |
| Mahale | 0 | 0 | 7 | 7 |
| Taï | 0 | 0 | 0 | 0 |
| Total | 11 | 5 | 16 | 32 |

Data are from Appendix 1. ''Disappearance'' means that an individual disappeared without suffering from ill health or old age

## Appendix 6

Number of known or inferred victims of intercommunity infanticide at long-term study sites up to 2002

| | Attack observed | Body found | Total |
|---|---|---|---|
| Budongo | 1 | 1 | 2 |
| Gombe | 5 | 1 | 6 |
| Kibale | 5 | 1 | 6 |
| Mahale | 1 | 2 | 3 |
| Taï | 0 | 0 | 0 |
| Total | 12 | 5 | 17 |

Data are from Appendix 2. Although observers sometimes consider infants that disappeared to have been possible victims of infanticide, no attempt is made to list them because infants often die from other causes also

## Appendix 7

Number of known, inferred or suspected adult or adolescent victims of intracommunity aggression at long-term study sites up to 2002

| | Attack observed | Body found | Total |
|---|---|---|---|
| Budongo | 1 | 0 | 1 |
| Gombe | 1 | 0 | 1 |
| Kibale | 1 | 0 | 1 |
| Mahale | 1 | 1 | 2 |
| Taï | 0 | 0 | 0 |
| Total | 4 | 1 | 5 |

Data are from Appendix 3

## Appendix 8

Number of known or inferred victims of intracommunity infanticide at long-term study sites up to 2004

| | Attack observed | Body found | Suspected | Total |
|---|---|---|---|---|
| Budongo | 0 | 1 | 0 | 1 |
| Gombe | 3 | 2 | 6 | 11 |
| Kibale | 1 | 0 | 0 | 1 |
| Mahale | 4 | 2 | 1 | 7 |
| Taï | 0 | 1 | 0 | 1 |
| Total | 8 | 6 | 7 | 21 |

Data are from Appendix 4

## Appendix 9

Average community composition for study communities

| Site | Community | Years | A–M | A–F | Adol–M | Adol–F | IJ | Total | References |
|---|---|---|---|---|---|---|---|---|---|
| Budongo | Sonso | 1996 | 12.0 | 11.0 | 4.0 | 6.0 | 17.0 | 50.0 | 1 |
| Gombe | Kahama | 1973–1977 | 4.2 | 1.8 | 0.6 | 1.0 | 2.4 | 10.0 | 2 |
| Gombe | Kasekela | 1966–1998 | 8.7 | 12.2 | 1.8 | 3.5 | 20.1 | 46.3 | 2 |
| Gombe | Mitumba | 1996–2002 | 3.1 | 7.4 | 1.6 | 1.9 | 8.0 | 22.0 | 2 |
| Kibale | Kanyawara | 1988–2000 | 10.0 | 13.2 | 2.7 | 3.2 | 15.0 | 44.1 | 3 |
| Kibale | Ngogo | 1999 | 24.0 | 47.0 | 15.0 | 9.0 | 49.0 | 144.0 | 4 |
| Mahale | *K*-group | 1966–1983 | 3.8 | 10.7 | 0.8 | 2.6 | 7.8 | 25.7 | 5 |
| Mahale | *M*-group | 1980–1999 | 8.5 | 28.6 | 7.6 | 7.7 | 26.6 | 79.0 | 6 |
| Taï | Northern | 1982–1996 | 6.7 | 21.5 | 3.0 | 4.2 | 25.8 | 61.2 | 7 |

References: 1, Reynolds (1998), Newton-Fisher (2002); 2, Jane Goodall Institute's Center for Primate Studies (unpublished); 3, Kibale Chimpanzee Project (unpublished); 4, Watts et al. (2002); 5, Nishida et al. (1985); 6, Nishida et al. (2003); 7, Boesch and Boesch-Achermann (2000)

## Appendix 10

Duration of study periods relevant to observation of lethal aggression

| Site | Community | Study begin | Study end | No. of study years | No. of years poorly known | No. of dData years |
|---|---|---|---|---|---|---|
| Budongo | Sonso | 1991 | 2004 | 14 | 4 | 10 |
| Gombe | Kahama | 1973 | 1977 | 5 | 0 | 5 |
| Gombe | Kasekela | 1960 | 2004 | 45 | 6 | 39 |
| Gombe | Mitumba | 1994 | 2004 | 11 | 2 | 9 |
| Kibale | Kanyawara | 1987 | 2004 | 18 | 4 | 14 |
| Kibale | Ngogo | 1994 | 2004 | 11 | 3 | 8 |
| Mahale | *K*-group | 1966 | 1983 | 18 | 2 | 16 |
| Mahale | *M*-group | 1968 | 2004 | 37 | 3 | 35 |
| Taï | Northern | 1979 | 2004 | 26 | 3 | 23 |
| Total | | | | 185 | 27 | 158 |

"Study end", ongoing studies are considered through 2004; "# Study years", number of years when community was demographically well-known; "# Years poorly known", period when demography uncertain, and/or observers rarely visited territorial boundaries and did not observe contacts with neighboring communities; "No. of dData years", estimated number of years when intercommunity aggression could be observed

## References


Arcadi AC, Wrangham RW (1999) Infanticide in chimpanzees: review of cases and a new within-group observation from the Kanyawara study group in Kibale National Park. Primates 40:337–351

Boehm C (1999) Hierarchy in the forest: the evolution of egalitarian behavior. Harvard University Press, Cambridge, MA

Boesch C, Boesch-Achermann H (2000) The chimpanzees of the Taï Forest: behavioral ecology and evolution. Oxford University Press, Oxford

Burbank VK (1992) Sex, gender, and difference: dimensions of aggression in an Australian Aboriginal community. Hum Nat 3:251–277

Bygott JD (1972) Cannibalism among wild chimpanzees. Nature 238:410–411

Bygott JD (1974) Agonistic behavior and dominance in wild chimpanzees. Ph.D. dissertation, Cambridge University

Cooper JM (1917) Analytical and critical biography of the tribes of Tierra del Fuego. Smithsonian Institute, Bureau of American Ethnology, Bulletin 63, US Government Printing Office, Washington DC

Fawcett K, Muhumuza G (2000) Death of a wild chimpanzee community member: possible outcome of intense sexual competition. Am J Primatol 51:243–247

Furuichi T, Hashimoto C, Tashiro Y (2001) Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: examination of fallback foods. Int J Primatol 22:929–945

Goodall J (1977) Infant-killing and cannibalism in free-living chimpanzees. Folia Primatol 22:259–282

Goodall J (1986) The chimpanzees of Gombe: patterns of behavior. Harvard University Press, Cambridge, Mass.

Goodall J, Bandora A, Bergmann E, Busse C, Matama H, Mpongo E, Pierce A, Riss D (1979) Intercommunity interactions in the chimpanzee population of the Gombe National Park. In: Hamburg DA, McCown ER (eds) The great apes. Benjamin/Cummings, Menlo Park, Calif., pp 13–54

Graburn N (1969) Eskimos without igloos. Little-Brown, New York

Hallpike CR (1977) Bloodshed and vengeance in the Papuan mountains: the generation of conflict in Tauade society. Clarendon Press, Oxford

Hamai M, Nishida T, Takasaki H, Turner LA (1992) New records of within-group infanticide in wild chimpanzees. Primates 33:151–162

Hayano DM (1974) Marriage, alliance and warfare: a view from the New Guinea highlands. Am Ethnol 1:281–293

Headland TN (1989) Population decline in a Philipine Negrito hunter–gatherer society. Am J Hum Biol 1:59–72

Heider KG (1997) Grand Valley Dani: peaceful warriors. Holt, Rinehart, Winston, New York

Herbinger I, Boesch C, Rothe H (2001) Territory characteristics among three neighboring chimpanzee communities in the Tai National Park, Ivory Coast. Int J Primatol 22:143–167
Hiatt LR (1965) Kinship and conflict: a study of an aboriginal community in northern Arnhemland. Australian National University, Canberra
Kawanaka K (1981) Infanticide and cannibalism in chimpanzees, with special reference to the newly observed case in the Mahale Mountains. Afr Study Monogr 1:69–99
Keeley LH (1996) War before civilization. Oxford University Press, New York
Kelly RC (2000) Warless societies and the origins of war. University of Michigan Press, Ann Arbor, Mich.
Knauft BM (1991) Violence and sociality in human evolution. Curr Anthropol 32:391–428
Knauft BM (1994) Reply to Erdal and Whiten. Curr Anthropol 35:181–182
Kutsukake N, Matsusaka T (2002) Incident of intense aggression by chimpanzees against an infant from another group in Mahale Mountains National Park, Tanzania. Am J Primatol 58:175–180
Lee RB (1979) The !Kung San: men, women and work in a foraging society. Cambridge University Press, Cambridge
Marshall L (1998) Sharing, talking, and giving: relief of social tensions among the !Kung. In: Gowdy JM (ed) Limited wants, unlimited means: a reader on hunter–gatherer economics and the environment. Island Press, Washington DC, pp 65–85
Muller MN (2002) Agonistic relations among Kanyawara chimpanzees. In: Boesch C, Hohmann G, Marchant L (eds) Behavioural diversity in chimpanzees and Bonobos. Cambridge University Press, Cambridge, pp 112–124
Muller MN, Wrangham RW (2004) Dominance, aggression and testosterone in wild chimpanzees: a test of the challenge hypothesis. Anim Behav 67:113–123
Newton-Fisher NE (1999) Infant killers of Budongo. Folia Primatol 70:167–169
Newton-Fisher NE (2002) Relationships of male chimpanzees in the Budongo Forest, Uganda. In: Boesch C, Hohman G, Marchant LF (eds) Behavioural diversity in Chimpanzees and Bonobos. Cambridge University Press, Cambridge, pp 124–137
Newton-Fisher NE (2003) The home range of the Sonso community of chimpanzees from the Budongo Forest, Uganda. Afr J Ecol 41:150–156
Newton-Fisher NE (2004) Hierarchy and social status in Budongo chimpanzees. Primates 45:81–87
Nishida T (1979) The social structure of chimpanzees of the Mahale Mountains. In: Hamburg DA, McCown ER (eds) The Great Apes. Benjamin/Cummings, Menlo Park, Calif., pp 73–121
Nishida T (1996) The death of Ntologi, the unparalleled leader of M Group. Pan Africa News 3: http://jinrui.zool.kyoto-u.sac.jp/PAN/3(1)/nt.death.html
Nishida T, Kawanaka K (1985) Within-group cannibalism by adult male chimpanzees. Primates 26:274–285
Nishida T, Hosaka K (1996) Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In: McGrew W, Marchant LF, Nishida T (eds) Great Ape Societies. Cambridge University Press, Cambridge, pp 114–134
Nishida T, Haraiwa-Hasegawa M, Takahata Y (1985) Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania. Z Tierpsychol 67:284–301
Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Turner L, Uehara S, Zamma K (2003) Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. Am J Primatol 59:99–121
Noë R, de Waal FBM, van Hooff JARAM (1980) Types of dominance in a chimpanzee colony. Folia Primatol 34:90–110
Norikoshi K (1982) One observed case of cannibalism among wild chimpanzees of the Mahale Mountains. Primates 23:66–74
Reynolds V (1998) Demography of chimpanzees *Pan troglodytes schweinfurthii* in Budongo Forest, Uganda. Afr Primates 3:25–28
Steadman LB (1971) Neighbors and killers: residence and dominance among the Hewa of New Guinea. Ph.D. dissertation, Australian National University
Sugiyama Y (1989) Population dynamics of chimpanzees at Bossou, Guinea. In: Heltne PG, Marquardt LA (eds) Understanding chimpanzees. Harvard University Press, Cambridge, Mass., pp 134–145
Suzuki A (1971) Carnivory and cannibalism observed in forest-living chimpanzees. J Anthropol Soc Nippon 74:30–48
Takahata Y (1985) Adult male chimpanzees kill and eat a newborn infant: newly observed intragroup infanticide and cannibalism in Mahale National Park, Tanzania. Folia Primatol 44:161–170
Turnbull C (1965) Wayward servants: the two worlds of the African pygmies. Greenwood Press, Westport, Conn.
Watts DP (2004) Intracommunity coalitionary killing of an adult male chimpanzee at Ngogo, Kibale National Park, Uganda. Int J Primatol 25:507–521
Watts DP, Mitani JC (2000) Infanticide and cannibalism by male chimpanzees at Ngogo, Kibale National Park, Uganda. Primates 41:357–365
Watts DP, Mitani JC (2001) Boundary patrols and intergroup encounters in wild chimpanzees. Behaviour 138:299–327
Watts DP, Mitani JC, Sherrow HM (2002) New cases of intercommunity infanticide by male chimpanzees at Ngogo, Kibale National Park, Uganda. Primates 43:263–270
Watts DP, Muller MN, Mbabazi G, Mitani JC (2005) Lethal intergroup aggression by chimpanzees in the Kibale National Park, Uganda. Am J Primatol (in press)
Williams JM, Liu H-Y, Pusey AE (2002a) Costs and benefits of grouping in female chimpanzees at Gombe. In: Boesch C, Hohmann G, Marchant LF (eds) Behavioral diversity in Pan. Cambridge University Press, Cambridge, pp 192–203
Williams JM, Pusey AE, Carlis JV, Farm BP, Goodall J (2002b) Female competition and male territorial behavior influence female chimpanzees' ranging patterns. Anim Behav 63:347–360
Wilson ML, Wrangham RW (2003) Intergroup relations in chimpanzees. Annu Rev Anthropol 32:363–392
Wilson ML, Hauser MD, Wrangham RW (2001) Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? Anim Behav 61:1203–1216
Wilson ML, Wallauer W, Pusey AE (2004) New cases of intergroup violence among chimpanzees in Gombe National Park, Tanzania. Int J Primatol 25:523–549
Wittig R, Boesch C (2003) "Decision-making" in conflicts of wild chimpanzees (*Pan troglodytes*): an extension of the Relational Model. Behav Ecol Sociobiol 54:491–504
Wrangham RW (1975) The behavioural ecology of chimpanzees in Gombe National Park, Tanzania. Ph.D. dissertation, University of Cambridge
Wrangham RW (1999) Evolution of coalitionary killing. Yearb Phys Anthropol 42:1–39