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RESEARCH ARTICLE

# Causes of Death in the Kasekela Chimpanzees of Gombe National Park, Tanzania

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Understanding the rates and causes of mortality in wild chimpanzee populations has important implications for a variety of fields, including wildlife conservation and human evolution. Because chimpanzees are long-lived, accurate mortality data requires very long-term studies. Here, we analyze 47 years of data on the Kasekela community in Gombe National Park. Community size fluctuated between 38 and 60, containing 60 individuals in 2006. From records on 220 chimpanzees and 130 deaths, we found that the most important cause of mortality in the Kasekela community was illness (58% of deaths with known cause), followed by intraspecific aggression (20% of deaths with known cause). Previous studies at other sites also found that illness was the primary cause of mortality and that some epidemic disease could be traced to humans. As at other study sites, most deaths due to illness occurred during epidemics, and the most common category of disease was respiratory. Intraspecific lethal aggression occurred within the community, including the killing of infants by both males and females, and among adult males during the course of dominance-related aggression. Aggression between communities resulted in the deaths of at least five adult males and two adult females in the Kasekela and Kahama communities. The frequency of intercommunity violence appears to vary considerably among sites and over time. Intercommunity lethal aggression involving the Kasekela community was observed most frequently during two periods. Other less common causes of death included injury, loss of mother, maternal disability, and poaching. Am. J. Primatol. 70:766–777, 2008. 

**Key words: cause of death; Gombe; chimpanzee**

## INTRODUCTION

Understanding the rates and causes of mortality in wild chimpanzee populations has important implications for a variety of fields, including wildlife conservation [Pusey et al., 2007] and human evolution [Hill et al., 2001, 2007; Kennedy, 2005]. Conservation is perhaps the most pressing concern, because chimpanzee populations across Africa are in decline [Oates, 2006]. Mortality patterns in natural chimpanzee populations can serve as a baseline when trying to conserve threatened populations. Only a few studies have analyzed the relative importance of different mortality factors, and the mortality data from two long-term studies of chimpanzees yielded contrasting results [Taï: Boesch & Boesch-Achermann, 2000; Mahale: Nishida et al., 2003], particularly in the relative importance of diseases, intraspecific aggression, predation and poaching on mortality. Here we update Goodall's [1983, 1986] analyses of the demographic record for chimpanzees of Gombe National Park in Tanzania to explore the relative importance of different causes of death. This record of demographic changes provides a valuable resource for investigating trends in the causes of death in chimpanzees, and comparisons with the Mahale and Taï records can provide further details of the heterogeneity of demographic trends in different chimpanzee populations.

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Chimpanzees live in permanent social groups, called communities, in which individuals spend time alone or in parties of varying size and composition. Males are more social than females, and individual females vary in sociability [Goodall, 1986; Nishida, 1968; Wrangham et al., 1992; but see Lehmann & Boesch, 2005]. At most sites, virtually all female chimpanzees emigrate from their natal community to another at adolescence, but at Gombe many females remain in their natal community [Pusey et al., 1997]. This fission–fusion social system presents challenges in determining demographic changes in the population, since absences from the observed parties for extended periods are common for many individuals. The tropical climate and presence of scavengers mean that a body must be found very soon after death if any evidence for the cause of death is to be recovered, and Gombe's remote location has made it difficult to save and transport samples that are collected. Other research sites share most or all of these challenges. Thus, the cause of death for many chimpanzees inevitably remains uncertain. However, recent advances in preservation methods and diagnostic tools may help identify causes of death in cases where tissue samples are rescued [Leendertz et al., 2006].

## METHODS

This article uses information on chimpanzees that were members of the Kasekela community in the central area of Gombe National Park for at least a portion of their lives between 1960 and 2006. Gombe National Park is a small ($35\,km^2$) park located on the western border of Tanzania, and is home to three communities of chimpanzees. Goodall and colleagues have studied the Kasekela community since 1960 [Goodall, 1986]. Two other communities reside in the park: the Mitumba community on the northern border of the park, for which habituation was begun in the 1980s [Pusey et al., 2007] and the Kalande community in the south of the park, for which formal monitoring began in 1999 [Greengrass, 2000; Pusey et al., 2007]. In addition, the short-lived Kahama community split from the Kasekela community in the 1970s [Goodall, 1986]. All research complied with regulations put forth by Tanzania National Parks, the Institutional Animal Care and Use Committee of the University of Minnesota, and regulations of the many other institutions involved in research at Gombe over the past 47 years.

Multiple data sources were utilized to produce a detailed demographic record for each chimpanzee including data from all-day follows and chimpanzee visits to an artificial provisioning area from 1963 to 2000 [Goodall, 1983]. In all data sources, the presence of all chimpanzees was recorded, as well as notes on behaviors and any noticeable health concerns or injuries to any individual. In addition, a number of other sources of information were available during subsets of the study. A variety of different types of health records have been collected over time [see Lonsdorf et al., 2006], and tissue samples were collected from eight Kasekela chimpanzee remains. Researchers also conducted searches for ill, injured, or missing chimpanzees throughout the study, which yielded 47 bodies of missing Kasekela chimpanzees.

### Categorization of Causes of Death

We assumed that all adult males, most juvenile males, and females under age 10 died if they disappeared. Given that most female transfer occurs between the ages of 10 and 14, we also assumed that most females over the age of 14 that disappeared died. However, older immigrants (and occasionally their dependent offspring of both sexes) appeared sporadically throughout the study in Kasekela [Goodall, 1986]. Thus, we did not assume that all older females who disappeared had died and considered them as potential emigrants. There were 27 chimpanzees in this ''lost-to-follow-up'' category, which included eight adolescent females, ages 10–14 (Bumble, California, Conoco, Female X, Jenny, Sally, Tita, Wunda, and her dependent brother Wolfi); ten older females, some with dependent offspring (seven total) who disappeared with them (Caramel, Dominie, Honey Bee, Harmony, Joanne with Jimi, Jessica with Jay and Lita, Vodka with Quantro, Kidevu, Mandy with Midge and Mantis, Wanda with Romany); and the eight-year-old female Starling who was observed only rarely and may have been old enough to emigrate before disappearing. Four of the older females and their dependents disappeared when the study community split, presumably to become members of the splinter community Kahama, while other disappearances were spread out over time.

For individuals who were not ''lost-to-follow-up,'' we used the following criteria for classifying deaths by type:

*Illness*: The chimpanzees were observed ill before their disappearance or confirmed death. This differs from Nishida et al. [2003] in that if dead infants were observed without injuries, we did not assume they died from illness without having observed symptoms. We classified illnesses as *epidemics* if 20% or more of the population was observed with the same symptoms during a short period (up to 3 months), and more than one chimpanzee died from those symptoms. The median number of chimpanzees to die from illness in an entire year is only one (mean = 1.2). We assumed chimpanzees that were healthy and regularly observed before the epidemic, but were not seen after the epidemic, had died from the epidemic.

*Intraspecific aggression*: Attacks on the chimpanzees were observed, or the chimpanzees were observed with injuries consistent with chimpanzee attack (such as deep bites to limbs and groin area,

defensive wounds and bitten fingers) or (for two infants) mother were observed with injuries consistent with chimpanzee attack when they were first seen without their infants.

*Injury*: Owing to factors other than chimpanzee violence. The chimpanzees were observed with severe injuries before or (in one case) after death, and either the source of those injuries were known or (in four cases) the cause of the injuries were unknown and could not be ascribed to intraspecific aggression.

*Orphan*: The chimpanzees were too young to survive alone (under age three) and disappeared soon after thier mothers did; any dependent offspring who showed signs of grief [as described by Goodall, 1986] and decline in health after the death of their mothers, followed by the offsprings' disappearance or observed death.

*Poaching*: The chimpanzee was observed with an injury (decapitation) that could only be ascribed to human violence.

*Maternal disability*: Infants died because of their mothers' inability to care for them due to her illness, injury, or in one case lack of skill.

*Unknown*: Forty-two chimpanzees (33% of deaths) died or disappeared and were presumed to have died, but there was no direct evidence that allowed us to classify their deaths. Indirect evidence suggests a cause of death in some of these cases, and we describe those cases under each cause of death.

We chose not to classify animals as dying of senescence to investigate specific causes of death for all ages. This differs from Nishida et al. [2003], who assumed chimpanzees died from senescence if they disappeared over the age of 40.

## RESULTS

We compiled a detailed demographic record of all chimpanzees known to be a member of the Kasekela community for some portion of their lives. In the years 1960–2006, the Kasekela community fluctuated in number from 38 to 60, and it contained 60 individuals in 2006. Over this period the community included 220 individuals, of whom 130 died, 63 were still alive on 31 December 2006 (60 still living in Kasekela, three in Mitumba) and 27 were classified lost-to-follow-up. One hundred and twenty-nine were born during the study, and we estimated ages for the remaining 91 (33 of whom were immigrant females and their offspring) by comparing their appearance with that of known-aged individuals [Goodall, 1986]. Because of visible developmental differences at early ages, age estimates are more certain (within one to two years of the true age) for chimpanzees under 15 when first seen, and may be less certain for chimpanzees that were older when first seen. Therefore, only 14% of the study chimpanzees have a confidence interval greater than two to four years around their age estimates.

### Mortality

Overall, we were able to assign a cause to 86 deaths, leaving 44 unknown. Fifty deaths were due to illness, 17 due to intraspecific aggression, seven died as orphans, six due to injury, and four due to maternal disability. In addition, one individual was poached and one was born prematurely. These patterns differ somewhat for males and females (Table I); most notably, males died from intraspecific aggression at a higher rate than females, and of the seven chimpanzees that died as orphans, five were female, one was male, and one was unsexed. There was also some difference in the proportion of deaths with unknown cause; 25% of male deaths, but 40% of female deaths remained unclassified.

### Illness

Illness is the most important cause of death in the Kasekela chimpanzees, making up 58% of deaths with known cause. Illness was an important cause of death at all ages and for both sexes, but impacted some age–sex classes more than others (Fig. 1). In particular, males under age five died of illness at twice the rate of females, and a greater proportion of

**TABLE I. Causes of Death for Males and Females**

| Cause of death | Number of male deaths | Number of female deaths | Percent of male deaths | Percent of female deaths |
|---|---|---|---|---|
| Illness | 30 (+2) | 20 (+4) | 59% (63%) | 61% (67%) |
| Intraspecific aggression | 12 (+8) | 5 (+2) | 24% (39%) | 15% (21%) |
| Injury | 4 | 2 | 8% | 6% |
| Orphaning | 1 | 5 | 2% | 15% |
| Maternal disability | 3 | 1 | 6% | 3% |
| Poaching | 1 | 0 | 2% | – |
| Unknown | 17 | 21 | 25% | 40% |

For each cause of death, number of deaths is listed for males and females, followed by percent of all deaths with a known cause. Under unknown, percentage refers to percent unknown out of all deaths. For illnesses, the number of dependent offspring dying as a result of their mother's illness is in parentheses; for intraspecific aggression, the number of suspected victims is in parentheses. Percentages in parentheses include indirect victims of illness, and suspected victims of intraspecific aggression. Not listed were eight deaths of chimpanzees for which sex was unknown.

females ages 20–30 died of illness. To investigate this further, we categorized illnesses by type, and whether each illness was epidemic in form. We divided illnesses into the following categories: respiratory (both epidemic and nonepidemic in form), ''polio,'' mange, wasting, and a category that includes other causes of death from illness or those for which symptoms were not described. Many chimpanzees dying of illness did so during an epidemic (50%; see Fig. 2). A summary table of the five major epidemics and observed and estimated percentages of morbidity and mortality for each can be found in Table II. These numbers update previous reports by Wallis and Lee [1999] and Lonsdorf et al. [2006].

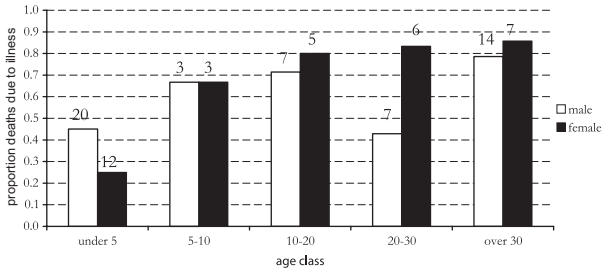


Fig. 1. Proportion of deaths due to illness in each age–sex class out of all deaths with a known cause. Numbers over columns indicate the total number of deaths in each age–sex class with a known cause of death.

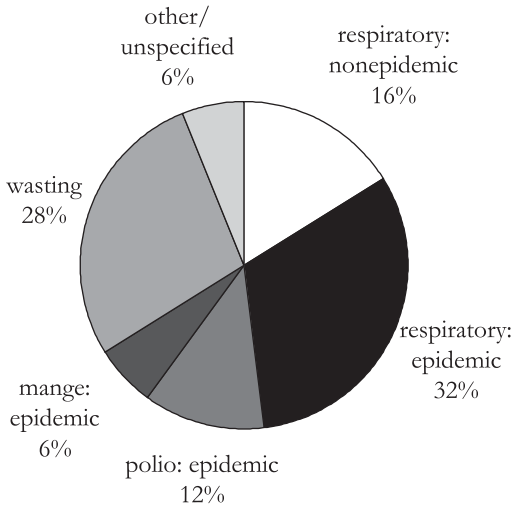


Fig. 2. Relative importance of each type of illness for the 50 chimpanzees that died of illness.

*Respiratory illness*

Respiratory diseases caused the most mortality due to illness, totaling 24 deaths (48% of mortality due to illness; Fig. 2). Males and females died in nearly equal numbers from this type of illness in each age class, with one exception: six males, but only three females over the age 30 died of respiratory illness. Two males and two females under five, as well as four males over 30, died of respiratory diseases that were not epidemic in nature. Most chimpanzees that died from a respiratory illness did so during three epidemics, described below and in Table II. For each epidemic, we noted the number of individuals that were observed with symptoms, as well as the number that died. In addition, we report the estimated morbidity for each epidemic, which takes into account that some of the individuals that were assumed to have died during an epidemic were never seen ill. The percentage of chimpanzees observed ill is almost certainly an underestimate of the total number infected, since many chimpanzees in every epidemic were not observed for long portions of the epidemic period.

*1968*: All four victims of this epidemic died during January (three females ages 13, 15, 27, and one male age 27). In addition, the infants, Cindy and Sorema, died as orphans after their mothers died.

*1987*: This epidemic lasted from April until June. Mortality was greater at older ages (Fig. 3a), and deaths were almost evenly split between males and females. In addition to the chimpanzees that died directly from the illness, the infant Ariadne died as an orphan after her mother died, and Gremlin's unnamed infant died while his mother was seriously ill.

*2000*: This epidemic occurred in February and killed two males ages 10.5 and 12. Samples were taken from humans and ill chimpanzees, and *Streptococcus pneumoniae* and *S. pyogenes* were found in both species [Mlengeya, 2000].

**TABLE II. For Each Epidemic, the Total Population Count, the Number Observed Ill, the Number Assumed Ill and the Number Attributed as Dead is Listed. Percentages of Each Metric Follow**

| Year | Type | Total pop | # observed ill | # assumed ill (morbidity) | # died (mortality) | Percent of morbidity observed | Percent of morbidity estimate | Percent of mortality |
|---|---|---|---|---|---|---|---|---|
| 1966 | Polio | 60 | 12 | 12 | 6 | 20 | 20 | 10 |
| 1968 | Respiratory | 52 | 31 | 33 | 4 | 60 | 63 | 8 |
| 1987 | Respiratory | 52 | 13 | 21 | 9 | 25 | 40 | 17 |
| 1997 | Mange | 47 | 19 | 19 | 3 | 40 | 40 | 6 |
| 2000 | Respiratory | 48 | 35 | 36 | 2 | 73 | 75 | 4 |

The estimated morbidity measures come from the fact that some animals were classified as dying from an epidemic without ever being observed ill.

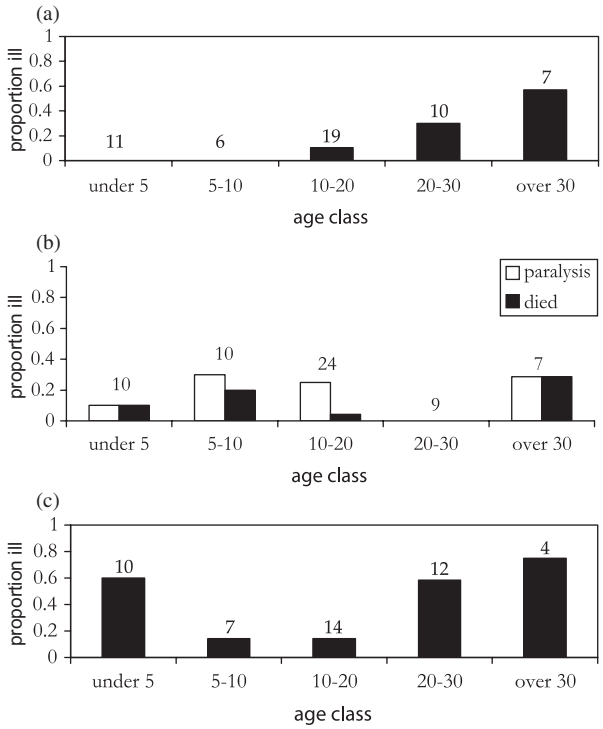


Fig. 3. Proportion of chimpanzees in each age class that exhibited symptoms or died in three epidemics: (a) the 1987 respiratory epidemic, (b) the 1966 polio epidemic, and (c) the 1997 mange epidemic. Numbers over columns indicate the number of susceptible individuals in each age class.

*Polio*

An epidemic illness assumed to be polio occurred in 1966 [Goodall, 1986]. While no definitive diagnosis of the pathogen was made, researchers observed paralysis in 18% of the study population, 73% of whom were male, and 8% of the population died (six, all male). This epidemic affected individuals ages 5–20 years most frequently, with high mortality in the age class five to ten (two of three with observed symptoms). However, polio was fatal in all victims with observed symptoms under age five or over 30 (Fig. 3b). Given that in humans less than 1% of polio cases result in paralysis and greater than 90% of infections are asymptomatic or present a nonspecific fever [Benenson, 1995], infection rate was likely much greater than the rate indicated by observed paralysis.

*Mange*

This illness occurred during one epidemic in 1997. It was characterized by visible symptoms including hair loss and flaky, itchy skin in infected areas. In addition, some individuals showed noticeable weight loss and general lethargy. Mites were collected from one of the victims and laboratory analysis revealed sarcoptic mange (*Sarcoptes scabiei*). Molecular analyses suggested that these mites were more closely related to those infecting nonhuman animals than those infecting humans [Walton et al., 2004; S. F. Walton, personal communication]. Chimpanzees were most susceptible either at very young ages or older ages; 60% or more of individuals under age five or over 20 were seen with symptoms (Fig. 3c), and all three individuals who died were infants. Bald chimpanzees were also observed in the Kalande community to the south of Kasekela, so it is likely that the epidemic was more widespread than just the study community.

*Wasting and other illnesses*

Wasting disease, which we defined as noticeable weight loss and weakness before death, caused 28% (14 cases) of mortality due to illness. The wasting disease category is likely a conglomerate of enteric diseases, parasitic infections, or perhaps cancer or the ''AIDS-like disease'' observed at Mahale [AIDS-like disease is the term used by Nishida et al., 2003]. Four individuals (Melissa, Passion, Pallas, Lolita) had severe diarrhea, often combined with behavior suggesting intestinal cramps, and postmortem or end-of-life fecal samples indicated that four others (Groucho, Michaelmas, Goblin, Atlas) suffered from very high intestinal parasite loads. These parasites included the nematodes of *Strongyloides* sp. and *Oesophagostomum* sp. Two individuals (Worzle and Gilka) had spreading sores on hands that likely contributed to their wasting and entered death. Three other individuals (Nova, Mo, Beethoven) also wasted away without clear evidence of gastrointestinal illness. The final individual classified as dying of a wasting illness was Flo, whose wasting was likely secondary to senescence. We were unable to classify the illnesses of three chimpanzees due to lack of definitive symptoms in the long-term record.

## Intraspecific Aggression

Intraspecific aggression accounted for at least 17 deaths. Overall, it is an important cause of death for both sexes under age five, and is the greatest cause of death in males ages 20–30 (see Fig. 4). At Gombe, lethal intraspecific aggression occurred within the study community as well as between communities, and was conducted by both males and females within the community.

*Within-community aggression*

Within-community lethal aggression against infants occurred at least seven times, and was suspected in an additional four cases. Aggression toward infants committed by females included a series of infanticides by the mother–adult daughter pair, Passion and Pom, who killed at least four infants under age ten weeks: two males and two females [Goodall, 1977]. Goodall [1977] suggested that three additional infants might have been

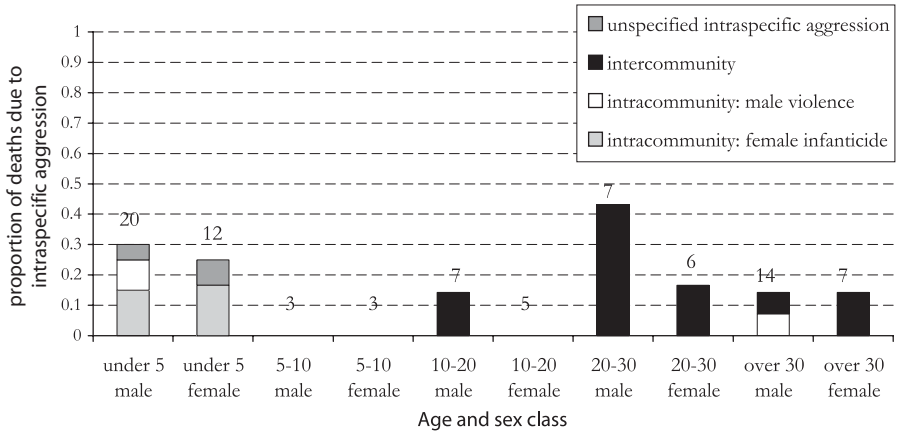


Fig. 4. Proportion of deaths in each age–sex class due to intraspecific aggression, broken into four categories out of all deaths with a known cause. Numbers over columns indicate the total number of deaths in each age–sex class with a known cause of death.

victims of infanticide by females as well. Researchers also observed two unsuccessful infanticide attempts on very young infants by another high-ranking mother–adult daughter pair (Fifi and Fanni) [Pusey et al., 1997, In press]. Within-community aggression by males caused infant death at least twice during the study period. The 1.5-year-old male Kenitum was injured during an attack on his mother and later died of those wounds, while the 3.7-year-old Tofiki was deliberately killed by the adult male Freud [Murray et al., 2007]. In addition, the five-year-old male Michaelmas suffered a near-fatal injury during an attack on his mother [Goodall, 1986]. In two instances, we could not ascribe the aggression to either males or females. One female (Kipara) appeared without her 10-week-old son, Kobe, and with injuries consistent with fending off an intraspecific attack [Pusey et al., In press]. A final case of infant death likely resulted from within-community aggression directed at a recently orphaned two-year-old male, who was found severely injured immediately after chimpanzee screams were heard.

Aggression between adult males from the same community occasionally had lethal consequences. The 41-year-old Huxley died from a wound inflicted by a male community member. The 25-year-old alpha male Goblin sustained a scrotal wound in a fight with his successor that ended his tenure as alpha, and the infection might have killed him without treatment [Goodall, 1992]. Soon after recovering from these wounds, Goblin suffered an unusually severe gang attack by six males, receiving wounds, which again might have proven fatal without antibiotic treatment [Goodall, 1992].

## Between-community aggression

While intraspecific aggression had the greatest impact on infants when occurring within a community, violence observed between communities impacted largely adults, particularly males (Fig. 4). This became clear in the late 1970s when the smaller Kahama community split off from the Kasekela community, and the Kasekela males killed at least six members of the Kahama community, five adult males and one adult female [Goodall, 1986].

Intercommunity aggression may have a greater impact on males in the population, given the number of deaths of unknown cause. Goodall [1986] suggests that the two Kahama males who disappeared and three Kasekela males ages 17–35 (Sherry, Humphrey, Faben) died as a result of intercommunity attacks. Altogether, 6 of the 12 males who died ages 20–30 from both the Kahama and Kasekela communities were either known or suspected to have been victims of intercommunity aggression, as well as two of the males ages 10–20 and two over age 30.

Among females in the population, two adult females, Madam Bee and Patti, were known to be killed during intercommunity aggression. Madam Bee was a 27-year-old Kahama female who was killed by Kasekela chimpanzees. The other female, 44-year-old Patti was a Kasekela community member who was fatally attacked by Mitumba chimpanzees while on consort in the Mitumba area north of Kasekela [Gombe Stream Research Centre, unpublished data]. Five additional females over age 30 disappeared, cause of death unknown, so it is possible that the actual number of female deaths due to intercommunity violence could be much higher.

Infants in the study population may also have suffered from intercommunity aggression. Two mothers (Nope and Passion) who lived near the edges of the community at a time when the range was contracting returned to the group with injuries consistent with fending off an attack by chimpanzees; in Nope's case, her 1.3-year-old infant Hepziba had disappeared, a presumed victim of an intercommunity attack, while Passion's infant son Pax sustained severe injuries of his own [Goodall, 1986].

Two other females Sparrow and Dove, who lived toward the edge of the range, lost their infants during the same period. With no evidence to the contrary, the deaths of these infants were categorized as unknown, but it is possible that they too fell victim to intercommunity violence [Williams et al., 2002].

### Other Causes of Death

Kasekela chimpanzees died from a number of other causes at lower rates, as detailed below.

*Poaching*

Only one Kasekela chimpanzee was known to have been killed by humans. The four-year-old male Getty's decapitated body was found [Goodall, 1990].

*Premature birth*

Researchers observed the body of one infant that was born prematurely.

*Orphans*

Seven dependent offspring died soon after their mothers' deaths; older orphans suffered a decline in health before their own death or disappearance. Of the seven orphans to die, five were female (three under age three, one age 3.2, and Kristal age 5.9), one was male (Flint, age 8.6), and the sex of one orphan was unknown (presumed sibling of the adolescent immigrant Jenny, age 1.5). All chimpanzees under the age of three who died as a result of their mother's death were female, but ten orphans of both sexes ages 2.75–6 survived their mothers by at least one year. One of these was Merlin, who was emaciated 1.5 years after his mother's death when he died of polio; had he not succumbed to polio, he might still have died because he was orphaned [Goodall, 1986]. A final orphan was Shangaa, who was orphaned at age two, but he was killed by chimpanzees shortly after his mother died so was not characterized as dying as a result of being orphaned. With the exception of Flint, orphans over age six did not exhibit a decline in health after their mother's death.

*Mother's disability*

We classified four infants as having died due to their mother's illness, injury, or inexperience. Goodall [1986] described the maladaptive maternal behavior that led to the death of Patti's first infant. This behavior appeared to be due to inexperience, since Patti successfully raised a number of offspring later in her life. Three mothers, Gremlin, Flo and Sparrow, were very ill when their infants died, but the infants were never recorded with symptoms. Thus, we classified those infants as dying as a result of their mother's infirmity.

Mother's disability may have been a contributing factor for the three females who sustained some paralysis due to polio. All four infants known to have been killed by the females Passion and Pom had mothers with paralysis, and six of the remaining eight infants born to these three females died before the age of two [Goodall, 1986].

*Injury*

Of the six chimpanzees categorized as dying of injury, two were injured in falls that were observed and four were observed with injuries but the cause was not known. Of those four, Jane was a three-month-old infant with a compound fracture of her arm. The second was the 10.7-year-old male Mel, whose freshly killed body was observed with injuries consistent with intraspecific violence, but researchers were close by and had not heard the vocalizations such an attack would entail. The third was the 41-year-old male Evered, who died after a wound to his scrotum became infected, but the source of that wound was not known. This wound was similar to one the adult male Goblin sustained during dominance-related aggression, hence we suggest that intraspecific aggression may have been the source of Evered's wound as well. The last was the 16-year-old female Sherehe, who was observed unable to move for the two days before her death, and postmortem exam revealed no signs of illness or injuries except possibly a ruptured gall bladder. Behavior before death and the healthy fat reserves observed in the postmortem exam indicate that she was in good general health before death.

## DISCUSSION

We were able to classify the cause of death for 67% (86 deaths) of the Kasekela chimpanzees, as compared with 56% (116 deaths) at Mahale and 45% (53 deaths) at Taï. As at the other sites, illness was the most important cause of death for Kasekela chimpanzees. The second most common cause of death varied among sites: intraspecific aggression (20%; 17 cases) in Kasekela, senescence (24%) at Mahale, and predation (41%) at Taï.

### Illness

Illnesses killed 58% of chimpanzees in Kasekela with a known cause of death, compared with 48% at Mahale [Nishida et al., 2003] and 41% at Taï [Boesch & Boesch-Achermann, 2000]. The most frequent fatal illnesses in Kasekela were respiratory, which were associated with 48% of all mortality due to illness. Mahale chimpanzees also experienced fatalities associated with respiratory illnesses, accounting for 20% of all victims of illness as of 1999 [Nishida et al., 2003]. However, a recent respiratory outbreak at Mahale claimed the lives of at least 3 and perhaps

as many as 12 chimpanzees [Hanamura et al., 2008], so the impact of respiratory diseases at Mahale may be increased in future analyses. For Taï, no chimpanzee had died from a respiratory illness by 1999 [Boesch & Boesch-Achermann, 2000], but three major outbreaks of respiratory illness occurred at Taï between 1999 and 2006 [Chi et al., 2007; Köndgen et al., 2008]. In addition, the community of chimpanzees studied at Bossou in Guinea has experienced two outbreaks of respiratory illness since research began in 1976 [Tatyana Humle, personal communication; Matsuzawa, 2006].

Epidemics caused 29% of all deaths with known cause in the Kasekela community; if deaths of dependent offspring are included, this increases to 34% of all deaths with assigned cause. Many of the epidemics were respiratory in nature (Table II). Other epidemics at Gombe included the ''polio'' and mange epidemics. Epidemic disease has proven to be a critical cause of death in other ape populations as well, including respiratory disease in the chimpanzee populations listed above, Ebola in Taï chimpanzees [Formenty et al., 1999] and lowland gorillas [Bermejo et al., 2006; Walsh et al., 2003], anthrax in Taï chimpanzees [Leendertz et al., 2004], and an ''AIDS-like'' disease in Mahale [Nishida et al., 2003]. Epidemics in Kasekela killed 4–17% of the susceptible population; this compares with respiratory epidemics at Taï [Köndgen et al., 2008], Mahale [Hanamura et al., 2008], and in the Mitumba community in Gombe [Pysey et al., 2008] that killed 3% to at least 30% of the community members, and the worst Ebola epidemic at Taï, which killed 31% of the population [Boesch & Boesch-Achermann, 2000].

Each epidemic had different effects on the ability of the population to replace its members, or defend its territory, depending on the age and sex of its victims. Respiratory epidemics in Kasekela killed predominantly individuals in their reproductive prime, impacting both reproduction and territorial defense. Indeed, it took the Kasekela community at least 15 years to recover its numbers after the 1987 respiratory epidemic. In contrast, the polio epidemic affected mostly males, which could have had more of an impact on the capacity of the community to defend its territory than on reproduction. Finally, the mange epidemic had a relatively small impact on the viability of the population since just three infants died.

The importance of epidemic disease as a cause of death in apes leads to concern over whether any of these epidemics had human origins. Recent work at Taï confirms that respiratory disease transfers from humans to chimpanzees [Köndgen et al., 2008]. Given the impact of respiratory disease in many sites, this leads to serious concern that researchers may pass such diseases onto their subjects. Out of three respiratory epidemics in the Kasekela community, we were able to obtain and test pathogen samples only for the most recent. Both humans and ill chimpanzees were infected with the same *Streptococcus* species at this time, but molecular analyses on specific clones of the bacteria such as done by Chi et al. [2007] and Köndgen et al. [2008] were not done. Thus, we were unable to determine with certainty whether this epidemic was transmitted from humans. However, it is possible that some or all of Kasekela's respiratory epidemics came from humans, either researchers or the surrounding population. As for nonrespiratory epidemics, the presence of polio in humans living nearby supports the theory that the 1966 polio epidemic in Kasekela was human-derived, while molecular analyses of the mile infecting chimpanzees in 1997 indicated that the epidemic was not directly of human origin, but could have originated from domestic animals in neighboring villages [Walton et al., 2004].

Knowing that human diseases can be transmitted to chimpanzees [Köndgen et al., 2008], we should make every effort to reduce the risks of disease transmission when possible. Published guidelines for the prevention of disease transmission do currently exist [Homsy, 1999] and are now being updated by the IUCN Primate Specialist Group Section on Great Apes [Liz Williamson, personal communication]. Park staff and researchers at Gombe instituted protocols to limit human to chimpanzee disease transmission in 2002 that include quarantine periods for researchers and limited periods for tourists with chimpanzees in the field, as well as reduction of the human population living in the park. In addition, provisioning with bananas was suspended, measures to reduce contact between animals and human belongings in the park were instituted, and a chimpanzee health-monitoring program is in place [Lonsdorf et al., 2006; Travis et al., 2008].

## Intraspecific Aggression

Intraspecific aggression was the second most important cause of death in the Kasekela chimpanzees, accounting for 20% of mortality with a known cause. Mahale experienced a similar level of lethal intraspecific aggression (16%). In contrast, Boesch and Boesch-Achermann [2000] observed only one infanticide victim at Taï, although lethal intraspecific aggression has been observed at this site more recently [Boesch et al., 2008]. Other sites have observed varying levels of lethal intraspecific aggression [Wilson & Wrangham, 2003]. Thus, the frequency of intraspecific killing varies considerably among different chimpanzee populations [Wrangham et al., 2006].

Intraspecific aggression observed in the Kasekela community falls into two main categories, within and between communities. Lethal aggression within communities breaks down further to attacks on infants by females or males, and male attacks on other adult males.

*Within-community aggression*

All observed lethal attacks on infants by females were restricted to infants under age ten weeks, and at least 31% of mortality in Kasekela of infants of that age was due to intraspecific aggression. If suspected cases are included that percentage increases to 50%. Infanticide conducted solely by females has also been observed at Budongo [Townsend et al., 2007], and an adult female joined with an adult male to kill the infant of a peripheral adult female in the Kanyawara community, Kibale National Park [Arcadi & Wrangham, 1999]. In addition, females were observed eating an infant chimpanzee at Taï, but researchers did not witness the killing [Boesch & Boesch-Achermann, 2000].

Kasekela males killed infants from within their own community at least twice, but only one of those attacks appeared to be deliberate infanticide [Murray et al., 2007]. This is in contrast to Mahale, where within-community infanticide by males has been a significant cause of death [Nishida et al., 2003]. Many of the infanticide victims at Mahale were offspring of females who joined M-group after the K-group community disappeared [Hamai et al., 1992].

Dominance-related aggression led to at least one death as well as one injury that was nearly fatal among adult Kasekela males. Within-community aggression directed at adult males has been lethal in the Mitumba community at Gombe [Gombe Stream Research Centre, unpublished data], as well as in Budongo [Fawcett & Muhumuza, 2000], Ngogo [Watts, 2004], and Mahale [Nishida et al., 2003]. A possible victim of that type of attack in Kasekela was the adolescent male Mel, whose body was discovered in the center of the community range with injuries that could have been a result of either chimpanzee aggression or a leopard attack.

*Between-community aggression*

Our data may not reflect the true impact of this cause of death since the presence of researchers might have inhibited attacks on Kasekela chimpanzees by nonhabituated members of neighboring communities. Hence the identity and fate of a victim of aggression were only known when both aggressors and victim were habituated. While adult males in this study died as a result of observed between-community aggression at a higher rate than adult females, older Kasekela females disappeared with no known cause of death at a much higher rate than males of the same age. We know that Kasekela males often severely attacked older females from a neighboring community [Goodall, 1986; Williams et al., 2004]. Thus, older Kasekela females may have been killed by less-habituated communities, but these attacks were not observed.

Lethal intercommunity aggression has been observed at other sites, including the killing of adults at both the Kanyawara and Ngogo study communities in Kibale, and infants at Mahale, Ngogo, and Budongo [Wilson & Wrangham, 2003].

In addition to varying among sites, the level of intercommunity violence may also vary over time, depending on the relative dominance of neighboring communities. Observers at Gombe witnessed a spike in intercommunity lethal aggression when the Kasekela community exterminated the splinter-community of Kahama in the 1970s, and are currently observing another spike in intercommunity aggression that began in the 1990s as Kasekela once again became the aggressor toward its neighbors [Wilson et al., 2004].

Humans may affect intercommunity dominance, and hence rates of intraspecific aggression, in at least two ways at Gombe. First, habitat loss outside the park may increase competition for available space within the park. Second, the decline in the number of adult males in the park's two edge communities–thought to be at least partly the result of people killing chimpanzees–has weakened these communities and made them more vulnerable to the larger Kasekela community [Pusey et al., 2007]. The importance of such edge effects points to size of habitat as an essential variable. Tanzania National Parks and the Jane Goodall Institute are currently working with local communities to reduce illegal killing of chimpanzees, and to restore habitat around Gombe, connecting the park with other pockets of forest in the region [Pusey et al., 2007; TANAPA, 2005].

## Poaching

Hunting by people constitutes one of the greatest threats to chimpanzees across Africa [Kormos et al., 2003]. However, the presence of researchers in long-term study sites likely reduces the threat of poaching. Among the three study sites for which long-term demographic data have been reported (Taï, Mahale and Gombe), poaching was a significant source of mortality only at Taï [17% of deaths with a known cause; Boesch & Boesch-Achermann, 2000]. In contrast to the low impact of poaching on the Kasekela community, Gombe's edge communities appear to be experiencing greater mortality and subsequent decline in numbers from poaching [Pusey et al., 2007]. Snares set for other animals and deliberate killing of chimpanzees take their toll at other sites [Wilson et al., 2007; Wrangham & Mugume, 2000; Wrangham et al., 2000].

## Predation

Despite the presence at Gombe of predators large enough to kill chimpanzees [Wilson et al., 2004], we have no definitive evidence of any chimpanzees being killed by predators at this site. One chimpanzee died from wounds that may have been inflicted by either other chimpanzees or a

leopard, but we were unable to determine the source. This is in contrast to both Mahale and Taï, which each had one period of predation, apparently due to a single predator preying on chimpanzees [leopards: Boesch & Boesch-Achermann, 2000; lions: Nishida et al., 2003]. At Taï, this caused 41% of all mortality with a known cause. Thus, predation by animals other than humans may be an important cause of death periodically or locally, but does not appear to be a widespread, constant threat in chimpanzees studied so far.

### Old Age

While we did not classify chimpanzees as dying of senescence, we examine their causes of death separately for comparison purposes. Only eight individuals lived longer than 40 years at Gombe, accounting for 5.4% of mortality, and senescence appeared to be the primary cause of death in only one individual (Flo), who was estimated to be 53 at death. This was compared with 24% of mortality at Mahale; clearly Mahale chimpanzees survived to this older age class at a much higher rate than Kasekela chimpanzees, despite higher mortality of Mahale infants [Hill et al., 2001; Nishida et al., 2003]. Survivorship of Kasekela chimpanzees is higher than that for Mahale chimpanzees until age 27, when Kasekela survivorship begins to decline at a much higher rate [Hill et al., 2001; Nishida et al., 2003]. Of the 17 Kasekela individuals that died aged 25–30, 18–35% died from intercommunity aggression and 24% from respiratory epidemic disease, so a combination of intercommunity aggression and respiratory epidemics took a serious toll in this age class.

### Other Causes of Death

Eighteen (21%) Kasekela chimpanzees died at low rates from four final causes of death: loss of mother, injury, mother's disability, and premature birth. Nishida et al. [2003] and Boesch and Boesch-Achermann [2000] ascribed a much smaller proportion of deaths to minor causes, including four Mahale infants that died after losing their mother, and one Taï infant that died from injuries after a fall.

## CONCLUSION

Our data demonstrate the importance of disease, especially epidemic disease, as a cause of death among protected chimpanzee populations. In addition, we found that intraspecific aggression is a significant cause of death for the Kasekela community at Gombe, as at Mahale [Nishida et al., 2003] and as suggested by the number of observations of lethal intraspecific aggression in sites in Uganda [Wilson & Wrangham, 2003]. However, our data also reveal distinct variability in comparisons with previous demographic studies at Mahale [Nishida et al., 2003] and Taï [Boesch & Boesch-Achermann, 2000], suggesting that many causes of death vary in importance in different populations. While we were unable to definitively tie any Kasekela epidemics to humans, the growing body of evidence for human-to-ape transmission of disease makes the prevention of such disease transfer of paramount importance for all ape populations that are in contact with humans. While poaching is variable across the communities that live in protected areas compared here, it is a far more significant cause of death in chimpanzees living in unprotected areas. When comparing historic demographic trends throughout the Gombe communities, the fact that the Kasekela community has been able to recover from disease losses and has now surpassed its size when first observed, while the edge communities have almost certainly dwindled, suggests that the protection from poaching and habitat loss the research community has enjoyed may have outweighed any deaths due to disease that researchers may have unknowingly introduced [Pusey et al., 2008; see also Köndgen et al., 2008]. We hope that the data we have presented here will contribute to a greater understanding of causes of death and methods to prevent mortality in wild chimpanzees.

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