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Original Contribution

A Retrospective Analysis of Factors Correlated to Chimpanzee (*Pan troglodytes schweinfurthii*) Respiratory Health at Gombe National Park, Tanzania

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Abstract: Infectious disease and other health hazards have been hypothesized to pose serious threats to the persistence of wild ape populations. Respiratory disease outbreaks have been shown to be of particular concern for several wild chimpanzee study sites, leading managers, and researchers to hypothesize that diseases originating from and/or spread by humans pose a substantial risk to the long-term survival of chimpanzee populations. The total chimpanzee population in Gombe National Park, Tanzania, has declined from 120–150 in the 1960s to about 100 by the end of 2007, with death associated with observable signs of disease as the leading cause of mortality. We used a historical data set collected from 1979 to 1987 to investigate the baseline rates of respiratory illness in chimpanzees at Gombe National Park, Tanzania, and to analyze the impact of human-related factors (e.g., banana feeding, visits to staff quarters) and non-human-related factors (e.g., sociality, season) on chimpanzee respiratory illness rates. We found that season and banana feeding were the most significant predictors of respiratory health clinical signs during this time period. We discuss these results in the context of management options for the reduction of disease risk and the importance of long-term observational data for conservation.

Keywords: chimpanzees, Gombe National Park, disease, respiratory illness, risk management, conservation

Introduction

There is widespread concern that infectious diseases pose one of the greatest risks to the survival of apes in the wild (Homsy, 1999; Leendertz et al., 2006; Altizer et al., 2007; Chi et al., 2007; Pederson et al., 2007; Köndgen et al., 2008). Although often difficult to diagnose, numerous infections or syndromes have been described in wild great apes; both endemic and epidemic diseases have proven to be a critical cause of morbidity and mortality (Leendertz et al., 2006). Examples include: Ebola virus in chimpanzees in the Taï Forest, Cote D'Ivoire (Formenty et al., 1999) and chimpanzees and gorillas in central Africa (Walsh et al., 2003; Leroy et al., 2004; Bermejo et al., 2006); anthrax in Taï chimpanzees (Leendertz et al., 2004); an "AIDS-like" dis-

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ease in Mahale Mountains National Park, Tanzania (Nishida et al., 2003); as well as the recently confirmed pathogenic SIV infections in Gombe National Park, Tanzania (Keele et al., 2009). Many disease outbreaks are suspected to be the result of close contact with humans (Homsy, 1999; Wallis and Lee, 1999; Ferber, 2000; Barnett et al., 2004; Chi et al., 2007; Goldberg et al., 2007) and as such, the mitigation and/or management of these risks is one of the highest priorities within the ape conservation community. Köndgen et al. (2008) recently showed convincing evidence that respiratory viruses originating from humans (either researchers studying the animals or poachers) were responsible for significant population declines in the Taï chimpanzees. Similarly, Kaur et al. (2008) presented evidence of a human-related metapneumovirus in association with fatal respiratory outbreaks at Mahale in Tanzania. On the other hand, the Köndgen study revealed evidence that humans can have a protective effect since communities without a research presence were subject to heavier poaching. Balancing the relative costs and benefits of human presence in ape conservation areas continues to be a rich area of debate (e.g., see Commentaries, American Journal of Primatology Volume 70, Issue 8, 2008).

Many of the above-mentioned great ape health investigations have focused specifically on disease outbreaks, their potential sources of infection, and outbreak-related mortality that could cause catastrophic declines in population size. However, very little is known about baseline (i.e., non-outbreak) levels of health in wild ape populations and how or whether baseline illness is correlated to a variety of human, species-specific or ecological factors. In this study, we (1) analyze a retrospective set of standardized data from 1979 to 1987 in order to establish baseline rates of respiratory illness in chimpanzees at Gombe National Park, Tanzania, and (2) analyze the impact of several risk factors which may contribute to the introduction and spread of these agents.

The Jane Goodall Institute's research on wild chimpanzees at Gombe is the longest continuous study of any great ape population. Chimpanzees at Gombe conform to the typical chimpanzee fission–fusion social structure in which members form temporary subgroups or "parties" within a permanent community (Goodall, 1986). The total chimpanzee population at Gombe has declined from 120–150 (Pusey et al., 2007) in the 1960s to about 100 by 2009 (Rudicell et al., 2010). Major epidemics at Gombe included suspected polio in 1966, mortality accompanied by observable signs of respiratory disease in 1968, 1987, 1996, 2000, and 2002, and Sarcoptic mange in 1997 (Goodall, 1983, 1986; Nutter, 1996; Pusey, 1998; Mlengeya, 2000). A recent analysis of the causes of death in the main study community (Kasekela) showed that there were observable signs of clinical disease associated with 58% of deaths of known cause. Roughly half (48%) of the disease signs that were associated with mortality were respiratory (e.g., coughing, runny nose, etc.) (Williams et al., 2008). Not surprisingly, respiratory illness has also been demonstrated to be critically important at other chimpanzee field sites, including the Taï Forest and Mahale populations described above.

Observations of human–chimpanzee interactions predate the annexation of Gombe as a National Park in 1968 (Pusey et al., 2008). Thomas (1961) describes interactions between chimpanzees and people in the 1950s, including chimpanzees raiding crops such as oil palms and bananas, and sometimes attacking human infants. However, the initiation of research and the subsequent habituation process greatly increased the amount of time that chimpanzees were in close proximity to humans. These are outlined in detail by Pusey et al. (2008) but briefly, the habituation process included feeding bananas to chimpanzees, locating researcher living quarters within the home range of the chimpanzee study community, and conducting lengthy (usually all day) research follows of target individuals for behavioral data collection.

To better understand the factors correlated with variation in chimpanzee respiratory illness rates at Gombe, we utilized a retrospective set of standardized health data that was collected for an 8+ year period from January 1979 to April 1987. During this time, there were no outbreaks of respiratory illness; defined as 20% or more of the population observed with the same symptoms during a short period (up to 3 months) and more than one chimpanzee death (Williams et al., 2008). In addition, a wealth of standardized data on human and other species-specific risk factors was available. Human-related risk factors included time spent near staff quarters (the location of trash pits and pit latrines, etc.), time spent being followed by research staff and frequency of banana feeding. Non-human-related factors included time spent in close proximity to baboons (a suggested intermediate vector between humans and chimpanzees), sociality, and season (see Table 1 for summary of human-related factors). We used linear mixed models to investigate the relative contribution of these factors to observable chimpanzee respiratory illness. Using these data, we tested the hypothesis that human-related risk

Table 1. Identification code, sex, and data quantities for individuals included in the study

ID	Sex	Total follow time (h)	Years in data set	Mean follow time (h) per quartile season	Mean days bananas received per quartile season	Mean proportion of follow time near staff quarters per quartile season
AL	M	441.7	7	19	7	0.17
AT	F	544.0	8	22	3	0.06
EV	M	1226.2	All	36	10	0.22
FD	M	450.9	7	17	10	0.21
FF	F	2443.8	All	70	11	0.25
GB	M	3153.7	All	88	13	0.25
GG	F	437.9	8	16	7	0.14
GM	F	1270.9	All	39	15	0.20
JJ	M	1037.8	All	32	9	0.22
LB	F	744.6	8	25	9	0.16
MF	F	586.4	8	21	6	0.13
ML	F	1586.1	8	50	14	0.33
MU	M	213.0	5	10	8	0.20
PF	M	364.2	5	26	9	0.16
PI	F	691.1	All	23	10	0.17
PL	F	397.1	4	28	10	0.33
PM	F	662.2	5	37	8	0.01
SS	F	339.6	5	21	8	0.27
ST	M	1310.3	All	39	9	0.14
WK	F	2390.7	All	66	13	0.12
WL	M	86.2	3	14	11	0.17

Metrics are averaged across the quartile seasons for human-related factors. The maximum number of years in the data set is 8 years and 4 months.

factors increase individual baseline rates of respiratory disease in the Gombe chimpanzees.

Methods

Study Population

Gombe is a small (35 km^2) park located on the western border of Tanzania and is currently home to three chimpanzee communities. Our study focused on the Kasekela community which ranges in the center of the park and has been studied continuously since 1960. Figure 1 shows a map of the park, including chimpanzee ranges and major human settlements, both within and outside the park. Since 1973, researchers and Tanzanian field assistants have conducted full-day focal follows on individual chimpanzees, during which they record group composition and location every 15 min and continuous data on feeding behavior. In addition, they note all instances of aggressive and submissive behavior, and the presence of other primate species. Researchers typically follow each adult chimpanzee at least once per month. For this study, we analyzed data collected from January 1979–April 1987, when systematic health data were collected in addition to the behavioral and demographic information described above.

The Kasekela community contained between 50 and 58 individuals during the study period, including 7–12 adult males and 19–21 adult females (adult age >12 years old). Data from 2,339 follows were included in our analyses. We included only those individuals that had been observed in all four seasons, at least 30 times per season (mean = 84, range = 30–113) during the course of the entire study. Thus, 9 males and 12 females were included in the analysis; these individuals ranged in age from approximately 8.5 to 29.5 years at first appearance in the dataset (see Table 1).

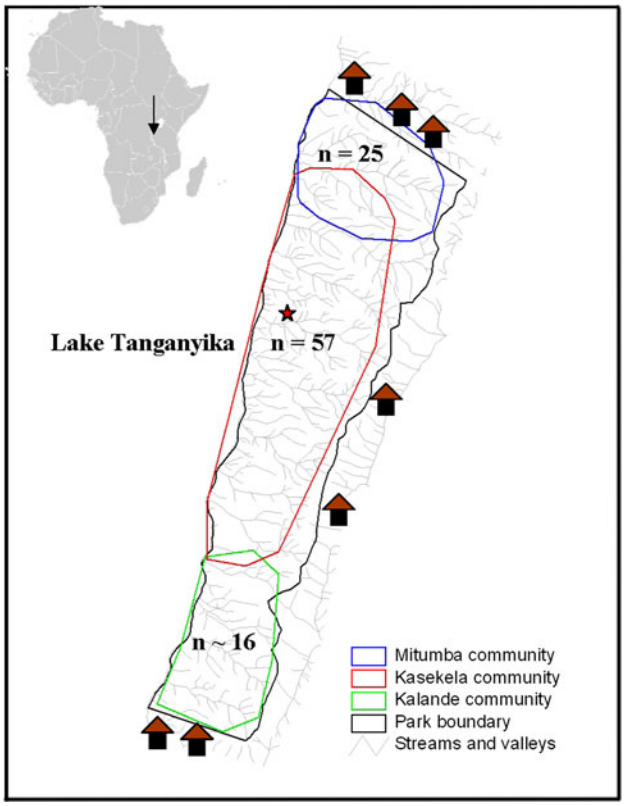

Figure 1. Location and current chimpanzee community ranges and sizes for Gombe National Park, Tanzania. Community ranges were delineated as 100% MCPs for all community locations, indicating the degree to which those individuals may interact with neighboring villages. The feeding station is located at the *star* (★)

Behavioral Metrics

Response Variable—Respiratory Illness Rate

During the study period, individual chimpanzees were assessed during the course of focal behavioral follows (as described above) by experienced Tanzanian field assistants for clinical signs of ill health. These observers (n = 15) had a minimum of 100 h observation time during the study period (range 168–2976 h). Clinical signs of ill health included elevated rates of coughing and/or sneezing, excessive nasal discharge, diarrhea, wounds, and sores. Severity was not measured quantitatively, but rather on a normal versus abnormal scale (e.g., occasional sneezing is normal, repetitive sneezing throughout the day with a runny nose is not). Daily monitoring times were by nature not equivalent, given that observers sometimes lost focal individuals in the dense forest. However, we have been conservative in our analyses by only including those chimpanzees with sufficient observation time. These observations were confirmed and compiled onto standardized checksheets by Goodall (see Table 2). Since respiratory disease is the major concern at Gombe and other study sites (see above), we focused on clinical signs associated with respiratory illness (e.g., coughing, runny nose). From these sheets, we calculated the dependent variable "respiratory illness rate" for each of 21 individual chimpanzees, by dividing the number of times the individual was observed with abnormal respiratory signs by the total number of times the individual was seen (No. of days observed ill/total no. of days seen) for each quartile season.

Because the prevalence of signs associated with respiratory illness was low in this population for any single year, metrics were averaged over all years within the study period. Both the response variable and predictors (risk factors) were summarized by quartile season (see below). For example, the average group size during the early wet season for an individual represented the average over all early wet seasons from 1979 to 1987.

During this time period, fecal sampling, necropsies, and other diagnostics were not conducted due to limitations in diagnostic technology at the time of the study. Therefore, these analyses focus only on observational clinical signs of respiratory illness; the particular infectious agent could not be determined.

Predictor Variables—Non Human-Related Factors

Season

The climate in Gombe is highly seasonal based on rainfall. Several studies have reported seasonal differences in chimpanzee behavior which indicate that food is most abundant during the wet season (e.g., party size: Wrangham, 1977; activity budgets: Lodwick et al., 2004; body mass: Pusey et al., 2005). We followed the precedent of previous studies (Goodall, 1986; Wallis, 2002) and divided the year into quartile seasons to control for this known seasonal variation: the early wet (November–February), late wet (March–April), early dry (May–July), and late dry (August–October) seasons.

Time Spent with Baboons

Chimpanzees often encounter olive baboons (*Papio anubis*), the most common large-bodied semi-terrestrial primate in the park. Large portions of the chimpanzee and baboon diets overlap, and the two species have been ob-

Table 2. Recreation of a 1979 chimpanzee health chart

Chimpanzee health charts—1979					
ID	Date	Diarrhea	Cough	Cold	Wound
ML	2-Jan-79	0	1	1	
WK	4-Jan-79	1	0	0	
WN	7-Jan-79	0	0	0	
WN	11-Jan-79	0	0	1	
SH	11-Jan-79	0	0	1	
EV	7-Feb-79	0	0	0	Under right eye after fight with FG and GB
PM	8-Feb-79	0	0	0	
HM	14-Feb-79	0	1	1	
EV	14-Feb-79	0	0	0	Lame, wound bottom left foot
FR	28-Feb-79	0	1	1	
FD	28-Feb-79	0	0	0	Bad. During a display he hurts bottom of left foot
FF	28-Feb-79	0	0	0	After attack by SH. Very slow. Limps on hand
FR	3-Mar-79	0	0	1	

served to have a variety of interactions, including young chimpanzees playing with young baboons, and adult chimpanzees killing and consuming baboons. In addition, baboons have been proposed to represent an intermediate vector between humans and chimpanzees in the park as they are more frequently found around human living areas. Behavioral records indicate the presence of baboons in a full-day follow. We calculated the daily percentage of time spent with baboons for each individual and then averaged over season.

Sociality—Average Group Size

The risk of infection with a respiratory pathogen may increase with the number of social contacts. In order to estimate how social an individual was during our study period, we relied on group composition data from full-day follows. We assigned a group size for each 15-min point sample during which the individual was the subject of the follow. We then calculated a seasonal average group size for each individual.

Predictor Variables—Human-Related Factors

Banana Provisioning

From 1962 to 2000, Kasekela chimpanzees were provisioned with bananas at an artificial feeding station located in the center of the community range (see Fig. 1). This practice facilitated habituation and regular monitoring of community members. Bananas were dispensed in a variety of ways over the course of the study, from being loaded into and released from remote-controlled boxes, to being directly handed to chimpanzees with un-gloved hands if the remote-controlled boxes were not functioning (Wallis and Lee, 1999; Pusey et al., 2008). By 1967, and during the course of this study, the degree of provisioning was reduced such that one individual received an average of 2–15 bananas once every 7–10 days (Pusey et al., 2005). Goodall (1986) previously reported that bananas were used to administer medication to chimpanzees during outbreaks. However, there were no outbreaks during this time period that necessitated targeted banana feeding. For these analyses, we calculated the average number of days on which an individual received bananas within a given season.

Follow Time

Close contact (distance and time) between humans and chimpanzees increases the risk of disease transmission. Therefore, a measure of chimpanzee time being followed by humans represents potential exposure and thus risk of disease transmission. In this study, the total time each individual was followed by researchers within a season was calculated and then scaled by the number of years the individual was present in the data set, thus accounting for individuals that died or disappeared during the study period (see Table 1).

Proximity to Staff Quarters

Researchers and park staff live in staff quarters on the shores of Lake Tanganyika. Since this area represents a place with a higher risk for chimpanzee–human interactions, we calculated the proportion of follow time spent in staff quarters for each individual. This proportion was derived from full-day follow data as the number of point samples within 100 m of staff quarters divided by the total number of point samples an individual was followed within a season.

Statistical Analyses

We used Statistical Analysis Software version 9.1 (SAS; Cary, NC) for all statistical analyses. Linear regression using a mixed model format (PROC MIXED) was chosen to account for random effects and repeated measures on the same individual (i.e., each individual represented in four different quartile seasons). We first conducted bivariate regression to identify those covariates demonstrating a significant relationship with the outcome. Multivariate analysis was then conducted using Type 3 tests and likelihood ratio χ^2 tests for model comparison. Forward selection was used to find the best model, and the significant covariates were examined for interaction.

To estimate effect sizes for significant variables, we relied on a method previously used in similar models (Murray et al., 2006, 2009). Effect size was calculated from log likelihood values as the log likelihood of the full model minus the log likelihood of the reduced model without the predictor of interest, divided by the log likelihood of the reduced model. This gives the relative increase in model fit for the predictor of interest.

Results

Descriptive Results

Overall, rates of respiratory illness were relatively low for this 8+ year time period. In Fig. 2, each monthly data point represents the study population's prevalence (average of 21 individuals) of respiratory illness and shows that the maximum prevalence of recorded observable respiratory signs during the study period was less than 3.5%. In addition, Fig. 2 shows that illness rates are strongly negatively associated with rainfall (source: BBC weather station for Kigoma, Tanzania, which lies 16 km south of Gombe).

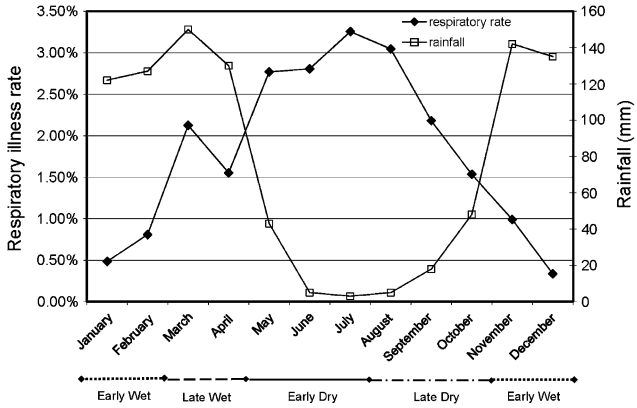

Figure 2. Respiratory illness rates and rainfall by month

Analytical Results

The model that provides the best fit for respiratory illness rate includes two of our proposed correlates: banana feeding ($F_{56,1} = 5.60$, $P = 0.0214$) and season, with the effect of season showing significance as an interaction with banana feeding ($F_{56,3} = 3.91$, $P = 0.0133$). Estimated effect sizes were 0.081 for season and 0.023 for bananas. Across seasons, respiratory illness rates were highest in the early dry season (mean = 3.03% ± 0.004 SE) followed by the late dry (mean = 2.34% ± 0.003 SE), late wet (mean = 1.61% ± 0.003 SE), and early wet (0.58% ± 0.003) seasons (see Fig. 3). Banana feeding was positively correlated to respiratory illness rates in the early dry season (Fig. 3). None of the other human- or non-human-related factors were significant.

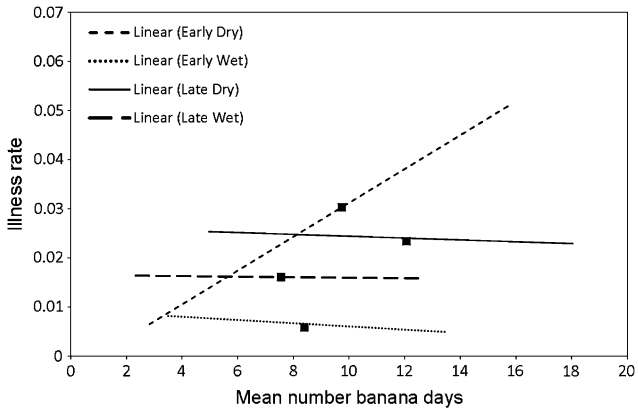

Figure 3. The interaction between season and banana feeding as predictors for illness rate. Linear trendlines are displayed for each quartile season with the mean of illness rate within the season indicated by the single marker

Discussion

Investigating the ecology of disease in wild animals is complex given the potential interaction between multiple species (hosts), pathogens (agents), and characteristics of the tropical environment. In addition, the high risk associated with immobilization of wild chimpanzees often precludes the collection of blood and tissue samples (Travis et al., 2008), hindering confirmatory diagnoses. Non-invasive diagnostic techniques are developing quickly and will hopefully become more widely available in the near future, but the initial detection of illness in wild primates is typically through observable clinical signs. In this study, we utilized a historical data set on observable signs of illness as well as human- and non-human-associated risk factors for respiratory illness. There are acknowledged difficulties when working with historical and longitudinal datasets. Among these are that multiple different observers over the study period collect data that is less detailed than what would be ideal for a focused prospective study. In this case, diagnostic tools were also not at a sufficient stage of sophistication to provide information on infectious agents. The strengths in this approach lie in the ability to analyze relationships and patterns over a longer period of time than is typically possible for a single field study and to incorporate detailed individual behavioral data that relate to proposed disease risks. Moreover, data from multi-year studies are less subject to biases caused by the effect of any single abnormal year. Ideally, studies such as the one presented here provide insight into complex ecological relationships while also providing ideas for variables that should be examined as part of more sophisticated syndromic health surveillance in wild animals (e.g., Lonsdorf et al., 2006; Decision Tree Writing Group, 2006).

Our analysis of 8+ years of data from Gombe National Park's Kasekela chimpanzee community suggests that the baseline rate of respiratory illness was below 3.5% prevalence per month, and that seasonality and banana feeding were the significant predictors of non-epidemic respiratory illness during this period. Average rates of illness were highest in the early dry season (May–July), followed by the late dry (August–October), late wet (March–April), and early wet (November–February) seasons (see Fig. 3). The maximum population average of respiratory clinical signs was 3.25% for the month of July (see Fig. 3). We consider this illness rate "relatively low," however, without comparable baseline data from other ape study sites, this is very difficult to assess. Figure 3 illustrates the statistical significance of the interaction term, which shows that banana provisioning is significantly and positively correlated with respiratory illness rates in the early dry season. Somewhat surprisingly, two human-related factors that were assumed to be of grave concern and positively correlated to chimpanzee respiratory illness, "follow time" and "proximity to staff quarters," were not significant predictors in our analyses.

As bananas themselves do not cause respiratory illness, the significant effect of banana feeding in the dry season has two possible interpretations. The dry season is a time of potential food stress for Gombe chimpanzees as evidenced by lower body masses (Pusey et al., 2005). While they were dispensed at low levels, bananas may represent a high-quality and reliable food source for predominantly frugivorous chimpanzees. Our result may therefore reflect an increased number of visits to the feeding station during the dry season when food is less abundant and subsequently a higher likelihood of disease transmission via human-handling of bananas. Alternatively, it is possible that chimpanzees may have been more likely to frequent the banana feeding station when they were already feeling ill, as a potentially low effort source of food.

We included the categorical variable for season given the strong seasonal differences in chimpanzee behavior demonstrated by prior research at Gombe. Season was a significant factor despite the fact that no outbreaks of disease occurred during the study period. Seasonal cycles of disease outbreaks are well documented, yet a single mechanistic explanation for this phenomenon remains elusive (Dowell, 2001; Dowell and Ho, 2004). Dowell (2001) summarizes the three main types of theories for seasonal emergence of illness as: (1) pathogens appear and disappear seasonally and upon appearance, spread via a direct transmission from one infected individual to another, (2) environmental changes, including changes in temperature and humidity, increase the probability of pathogen spread, and (3) seasonal changes in host behavior increase the probability of spread. Dowell (2001) also proposes a fourth possibility that seasonal changes in host physiology increase or decrease host susceptibility. With respect to respiratory infections, and influenza virus in particular, early laboratory experiments suggested that the virus is more stable in dry conditions (Hemmes et al., 1960), and more recent research suggests that low absolute humidity coincides with the onset of seasonal influenza (Shaman and Kohn, 2009;

Shaman et al., 2010). Our data concurs and shows higher rates of illness in the dry season. While the complexity of our system does not allow us test the mechanisms proposed above, we maintain that it is valuable to document the underlying seasonal and other influences on illness in chimpanzees as a starting point for further investigations.

Disease outbreaks are occurrences of disease greater than what would be expected in a given time and place. Therefore, understanding rates and patterns of disease during non-outbreak periods help us to determine baseline expectations and define outbreaks. Importantly, reported respiratory outbreaks at both Gombe and Mahale National Park (which is less than 150 km south of Gombe) have occurred at various times during the year and have not followed any strict seasonal patterns. At Gombe, two occurred during the early wet season (one in January and one in February) and one during the early dry (late May/early June) (Williams et al., 2008). Fatal respiratory epidemics at Mahale have occurred during the early or late dry seasons (between June and September) (Nishida et al., 2003; Kaur et al., 2008) and two non-fatal outbreaks occurred at Mahale during the early wet (late October/November) (Lucasik-Braum and Spelman, 2008). Whether wet versus dry season outbreaks represent different pathogens, environmental influences or particular transmission events remain to be determined. However, an understanding of baseline disease dynamics is the foundation upon which outbreak investigation occurs.

Understanding the ecological and anthropogenic factors that correlate to observable signs of respiratory illness may help us to manage and prevent the introduction and spread of infectious diseases in ape populations. In this study, we focused on human-related risk factors; it is important to note that humans are not the only source population for infectious disease for wild primates, but they are potentially the most manageable. For example, of the historical factors we analyzed for Gombe, the non-human-related factors (i.e., seasonality, sociality, and baboon interactions) cannot be actively managed. However, several protocols have been implemented in Gombe in recent years to reduce the likelihood of human-induced disease risk to the primates in the park (Collins, 2003). Baboon management strategies include improving sanitation in staff quarters by baboon-proofing toilets and garbage pits, and constructing mesh-protected areas for dish and clothes washing to prevent scrounging. These protocols also aim to directly reduce the human-related risk factor of "proximity to staff quarters" for chimpanzees. In addition, preventative measures have already been put in place to reduce the potential risk of researchers as disease vectors, including increasing the minimum viewing distance for researchers and implementing a quarantine period for researchers upon arrival to the park. We were not able to include data on tourist visits to Gombe as the records during this period were collected annually versus seasonally. However, we suspect that tourist visits are much higher during the dry season, so this is an important focus for future research. The one human-related predictor that was significant in this study—banana feeding—was eliminated in 2000. The analyses presented in this article provide strong post hoc scientific evidence for this assumption-based management decision. As conservation management becomes more evidence based, analyses that test such assumptions are critical.

As a result of increasing concern about the impacts of disease for wild apes, a prospective health-monitoring system was put into place for the Gombe chimpanzees in 2004 (Lonsdorf et al., 2006). From the 11 necropsies conducted since the project started, none of the causes of death were attributable to respiratory causes (Keele et al., 2009; Terio et al., in revision). While it is difficult to say whether this is a direct result of the more recent management initiatives, it is still encouraging. As human–chimpanzee interaction has had a long history at Gombe, it is also possible that the main study community has become somewhat immune (through consistent high level exposure and competent immune reactions) to these daily and moderate levels of human interaction (Pusey et al., 2008). However, even if the Gombe chimpanzees are or were somewhat immune to "regularly" circulating human diseases, emerging pathogens continue to be of grave concern and policies to prevent the introduction of these continue to be reviewed. Moreover, whether or not non-fatal respiratory illness impacts important conservation measures such as maturation rates and reproduction is an important next step for this research.

In this contribution, we have examined historic and site-specific information about potential human-related health risks at Gombe using observational data. With recent advances in diagnostic techniques, as well as an increased focus on health-monitoring of wild apes, there are many potential future avenues for this research. For example, integration of human illness data will provide important information regarding risks of exposure to specific pathogens. This should include information from local workers and research staff, villages surrounding the protected area,

as well as information on precise numbers and country of origin of tourists. Examination of ape disease outbreaks across study sites and their relationship to global human health information will also be valuable. As diagnostic capabilities develop, identification of specific pathogens and whether they are of human origin will also be possible in some cases. Moreover, long-term prospective health-monitoring programs have now been implemented at many sites which will allow for analyses that expand and complement the work we have presented here, especially when combined with detailed demographic and behavioral data on individuals. This will allow for baseline levels of disease to be established at each site and therefore more precise detection of outbreaks. Furthermore, comparison of disease levels and risk factors across sites will also be feasible.

Given the long history of human–chimpanzee interaction at Gombe, it is possible that younger study sites or new areas that are initiating studies or ecotourism projects would report different effects. Therefore, preventative protocols should be put in place, enforced, and regularly reassessed and updated at any field site where apes and humans have the potential to interact. In addition, as each ape study area may have differing ecology, the impacts of ecological variables such as seasonality may be more or less important. Gombe is a unique case in which a stable, long-term research presence and database has allowed us to investigate a variety of factors and begin to understand the complexity of one particular infectious disease scenario for wild apes. As such, a concerted and collaborative long-term effort among ape study sites will be the best way to fully understand the relative impacts and risks of disease for ape conservation.

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