Catastrophic ape decline in western equatorial Africa

Peter D. Walsh*, Kate A. Abernethy†‡, Magdalena Bermejo§, Rene Beyers||, Pauwel De Wachter¶, Marc Ella Akou¶, Bas Huijbregts¶, Daniel Idiata Mambounga#, Andre Kamdem Toham¶, Annelisa M. Kilbourn||, Sally A. Lahm☆, Stefanie Latour||, Fiona Maisels||, Christian Mbina||, Yves Mihindou||, Sosthène Ndong Obiang#, Ernestine Ntsame Effa#, Malcolm P. Starkey||††, Paul Telfer†‡‡, Marc Thibault¶, Caroline E. G. Tutin†‡, Lee J. T. White|| & David S. Wilkie||**

* *Department of Ecology and Evolutionary Biology, Guyot Hall, Princeton, New Jersey 08540, USA*
† *Centre International de Recherches Médicales, BP 769, Franceville, Gabon*
‡ *Department of Biological and Molecular Sciences, University of Stirling, Stirling FK9 4LA, UK*
§ *Departamento Biología Animal (Vertebrados), Facultad de Biología, Universidad de Barcelona, Avda. Diagonal 645, 08028 Barcelona, Spain*
|| *Wildlife Conservation Society, Bronx, New York, New York 10460-1099, USA*
¶ *WWF Central Africa Regional Program Office, BP 9144, Libreville, Gabon*
# *Ministère de l'Economie Forestière, des Eaux, de la Pêche chargé de l'Environnement et de la Protection de la Nature, Direction de la Faune et de la Chasse, BP 1128, Libreville, Gabon*
☆ *Institut de Recherche en Ecologie Tropicale, BP 13354, Libreville, Gabon*
** *Institute of Cell, Animal and Population Biology, Edinburgh University, Edinburgh EH9 3JT, UK*
†† *Department of Geography, University of Cambridge, Downing Place, Cambridge CB2 3EN, UK*
‡‡ *New York University, Department of Anthropology, 25 Waverly Place, New York, New York 10003, USA*

Because rapidly expanding human populations have devastated gorilla (*Gorilla gorilla*) and common chimpanzee (*Pan troglodytes*) habitats in East and West Africa, the relatively intact forests of western equatorial Africa have been viewed as the last stronghold of African apes[1]. Gabon and the Republic of Congo alone are thought to hold roughly 80% of the world's gorillas[2] and most of the common chimpanzees[1]. Here we present survey results conservatively indicating that ape populations in Gabon declined by more than half between 1983 and 2000. The primary cause of the decline in ape numbers during this period was commercial hunting, facilitated by the rapid expansion of mechanized logging. Furthermore, Ebola haemorrhagic fever is currently spreading through ape populations in Gabon and Congo and now rivals hunting as a threat to apes. Gorillas and common chimpanzees should be elevated immediately to 'critically endangered' status. Without aggressive investments in law enforcement, protected area management and Ebola prevention, the next decade will see our closest relatives pushed to the brink of extinction.

The plight of apes in western equatorial Africa (WEA; Fig. 1) has not been appreciated widely because previous assessments have assumed that the amount of intact forest cover is the primary determinant of ape abundance (Congo and Gabon retain about 60% and 80% of original forest cover, respectivley[3,4]). A widely cited 1995 estimate assuming moderate ape densities in all forested habitat put gorilla abundance in WEA at 110,000 (ref. 2). What this estimate did not take into account was the impact of threats other than deforestation. Rather than assuming that all forest held apes at some 'typical' density, from 1998 to 2002 we conducted surveys of ape sleeping nests at sites spread widely across Gabon. We compared our results with data from a national survey conducted in 1981–1983 (ref. 5), when high-density ape populations spanned Gabon (Fig. 2a). Our recent surveys suggest that high-density ape populations are now restricted to the southwest and northeast of the country (Fig. 2b). By far the best predictor of ape distribution in both time periods was distance from the nearest of Gabon's four major urban centres, which explained 61% of the variance in nest group encounter rate (Fig. 3). The effect of cities was already evident in 1983, but ape distribution has since contracted markedly, with healthy ape populations found only in very remote areas. The other good predictor of encounter rate of nest groups was distance from the nearest documented human Ebola outbreak site[6] ($R^2 = 0.63$ for a model including both variables, $P = 0.02$, $n = 89$). When data from the two time periods are compared, they indicate an ape decline of 56% (95% confidence interval = 35–70%). This figure may underestimate substantially the true magnitude of ape decline (see Methods).

Sharp declines in ape abundance are almost certainly not restricted to Gabon. Neighbouring Congo has a higher rural human density (http://apps.fao.org) and deforestation rate[4] than Gabon, and apes in northwest Congo are in the midst of a devastating Ebola epidemic (http://www.who.int). The situations in other WEA countries that still hold appreciable ape populations (that is, Cameroon, Central African Republic and Equatorial Guinea[1]) are probably worse as a consequence of their higher human densities (http://apps.fao.org) and deforestation rates[4]. Also of great concern is the suspected but largely undocumented crash of ape populations in eastern Democratic Republic of Congo, the consequence of hunting spurred by recent civil unrest.

The World Conservation Union (IUCN) red list of threatened species now classes both *G. gorilla* and *P. troglodytes* as 'endangered' (http://www.redlist.org). Our results suggest that there should be an immediate reclassification of both species to 'critically endangered' status. Under criterion CR-A2, a species should be considered critically endangered if it is expected to suffer "A reduction of at least 80% … within the next 10 years or three generations." Assuming a constant decline rate between the end of the early surveys (1983) and the midpoint of recent surveys (2000), the annual

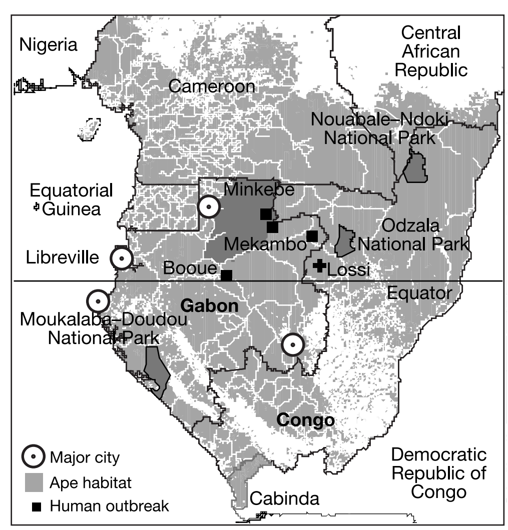

Figure 1 Western equatorial Africa. Commercial hunting is concentrated near transport routes (major roads in white), whereas Ebola impact has been heaviest in remote areas. Ape density in the Minkébé forest block (shaded area in northern Gabon) has dropped by about 99% over the past decade. The Ebola epidemic is currently most severe between Lossi and Odzala National Park. Observations of unpredated ape carcasses span 600 km, from 40 km west of Booue to the Nouabale–Ndoki region of northern Congo.

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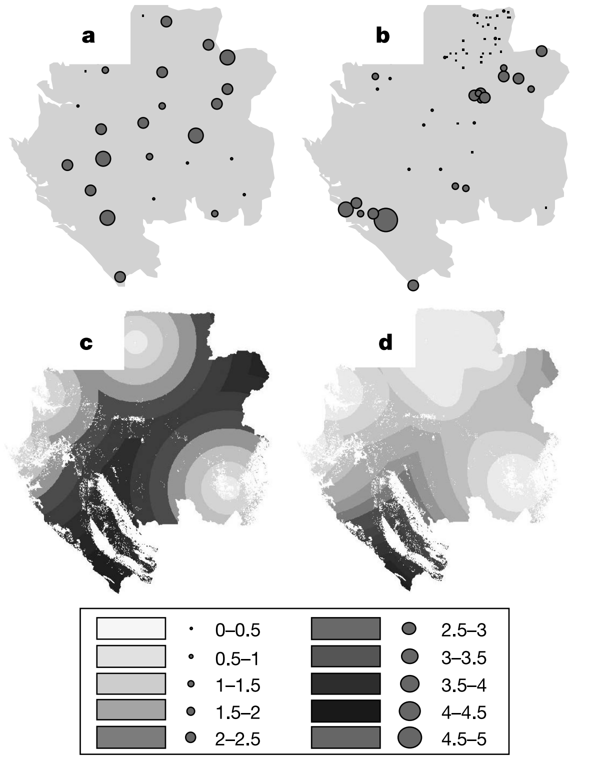

Figure 2 Ape nest encounter rates in Gabon. **a**, **b**, Encounter rates of ape nest groups (nest groups per km) from early 1980s (**a**) and recent surveys (**b**). The smallest circles include sampling sites with zero nest group encounters. **c**, **d**, Individual nest encounter rate (nests per km) predicted by distance from nearest major urban centre and distance from nearest human Ebola outbreak (see Methods): **c**, early 1980s; **d**, recent surveys. Predictions are corrected to reflect positive correlation between nest group size and distance from nearest human Ebola outbreak. Regression surfaces do not accurately represent smaller-scale variation in encounter rate.

decline rate is 4.7%. At this rate, ape populations would decline by an additional 80% within 33 years: a generation and one half for chimpanzees and perhaps two generations for gorillas (Fig. 4a). Given that our decline estimates are conservative and that decline rates have probably been accelerating during recent years, the 80% threshold will probably be reached much sooner. Even if decline can be halted, ape demographic rates are so low that population recovery will be very slow (Fig. 4b).

Over the past decade, the intensity and spatial extent of commercial hunting have increased greatly—driven by the rapid expansion of mechanized logging and by economic migration and resettlement policies[7,8], which have concentrated salaried bushmeat customers in towns and cities (http://apps.fao.org)[9]. The transportation infrastructure provided by logging has transformed hunting from a primarily subsistence activity into a commercial enterprise. Villages near logging roads hunt much more intensively than villages that lack market access[9]. Furthermore, hunting is no longer confined to local villagers or to the immediate proximity of villages. Organized groups of hunters use logging roads and vehicles to penetrate deep into remote areas (including parks and wildlife reserves)[10], then export bushmeat to nearby logging towns (where logging employees eat more bushmeat than local villagers[9]), regional transportation hubs, and even large cities hundreds of kilometres away[11]. For the four market towns where we observed gorilla sales, time of travel from the Gabonese capital Libreville was an excellent predictor of bushmeat price per kg ($n = 31$ species, $F = 67.86$, $P < 0.001$). Bushmeat costs about one-third as much as alternative sources of protein (frozen chicken, beef and fish) in remote villages, but 50% more in Libreville ($R^2 = 0.91$, $P = 0.048$),

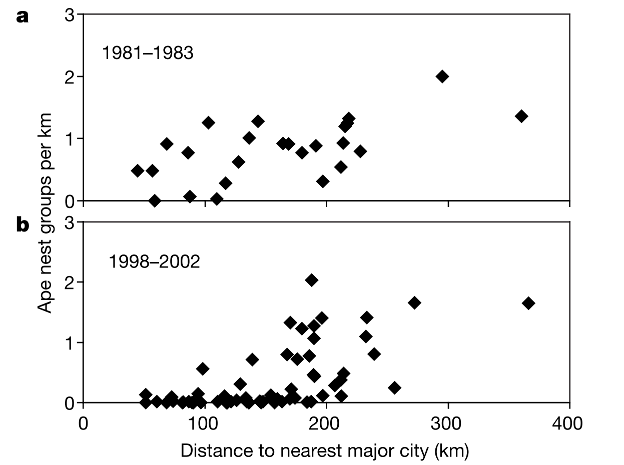

Figure 3 Encounter rate of ape nest groups plotted as a function of distance to the closest of Gabon's four major urban areas (anticlockwise from Libreville are Port Gentil, Franceville and Oyem).

where it is consumed on only about 2% of days. Most ape hunting in Gabon is probably not driven by a specific consumer demand for gorilla or chimpanzee meat. Forty-one (42%) out of 98 people that we interviewed in Libreville cited gorilla as a meat that they did not eat. Now that bushmeat has become too expensive for poor Librevillois, smaller regional cities and towns have probably become the principal centres of urban bushmeat consumption. But even in rural areas, ape meat does not make a substantive contribution to food security: maximum sustainable yield of chimpanzee meat is 10–50-fold lower than that of preferred market species (Supplementary Information).

Since 1994, Gabon has had four well-documented human Ebola epidemics, all in the northeast. Ape carcasses have been found near the sites of three of the human epidemics, with apes testing positive for Ebola in two cases[6] (http://www.who.int). The impact of Ebola on ape populations has been most extensive in the Minkébé region, a lightly settled, roadless block of about 32,000 km^2 (Fig. 1)[12]. Minkébé showed moderate[5] to high[13] encounter rates of ape nest groups in pre-Ebola surveys, including a 1991 study in which 75 ape nest groups were observed in only 20 km of line transects, a rate higher than all but one published report from WEA[14]. By 2000, nest group encounter rates on reconnaissance surveys (2,700 km) and line transects (17 km) yielded only 91 nest groups, a drop of about 99%. Hunting was not a probable cause of this marked decline, but hunters described finding large numbers of dead apes both near human epidemic sites and in other sectors of Minkébé[12]. Other remote areas of central and northeastern Gabon covered in our surveys also showed little sign of hunting pressure (for example, they had high encounter rates of elephant dung comparable to rates from the late 1980s[15]), but exhibited unexpectedly low ape densities.

The ape Ebola epidemic is gradually working its way south and west. Over the past 18 months, wildlife conservation workers and an international research team have found many ape carcasses in Congo, across the border from the 2001 human epidemic site at Mekambo (http://www.who.int). Since December, the carcasses of seven gorillas from a study population at Lossi have been found, along with five chimpanzee carcasses. The study population originally included 143 individually identified gorillas, but after exhaustive searches only seven have been found alive. The epidemic is now approaching Odzala National Park, which boasts the world's highest recorded gorilla and chimpanzee densities[16].

The precipitous decline of apes in WEA is a major conservation crisis. Responding effectively to the Ebola epidemic will require intensified research on reservoir and host dynamics, with a more quantitative, ecological emphasis. Research on vaccines and modes

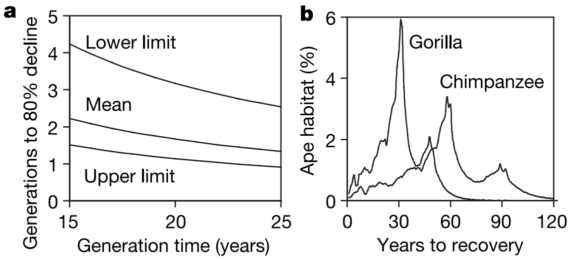

Figure 4 Decline and recovery projections. **a**, Generations until Gabonese apes decline by an additional 80%, assuming the mean decline rate observed between 1983–2000 (4.7%), and upper and lower 95% confidence limits for that decline rate. Chimpanzee generation time is about 22 years, whereas gorilla generation time is slightly shorter. **b**, Frequency distribution of time necessary for gorilla and chimpanzee populations across Gabon to recover to 99% of 1982 levels. Projections are based on ideal conditions, including no hunting, no Ebola, no density-dependent population regulation, and highly optimistic birth rates (see Supplementary Information for details).

of deployment is also a high priority. Other interventions in the Ebola transmission chain should be investigated actively. The solution to the hunting crisis will not result from investment in poverty alleviation or sustainable development. Rural poverty is too intractable to be solved before hunting further demolishes ape populations, and the social and economic contexts in WEA are such that alternative use strategies such as gorilla tourism cannot provide national governments with enough income to offset the large opportunity costs of forgoing extractive use of resources[17,18]. The bulk of conservation investment should, instead, be focused on formally protected areas that still have enough apes to be viable in the long run. The immediate priority is a massive investment in law enforcement, which has long been underfunded in WEA. The long-term priority should be building national capacity to conduct all aspects of protected area management. In addition, logging and oil companies should be compelled to control illegal bushmeat hunting, transport and consumption on their concessions. Funds to pay for hunting and Ebola control efforts must be generated in developed countries where apes are cherished as a vital element of our natural heritage. We must also provide national governments with economic incentives, linking aid and debt relief to verifiable measures of conservation performance. The stark truth is that if we do not act decisively our children may live in a world without wild apes. □

Methods

Surveys

Our data for the recent survey period come from 261 km of formal line transects[19] and 4,793 km of reconnaissance surveys ('recces'[20]) performed while evaluating existing and potential protected areas in Gabon. The sampling sites were chosen because they were thought to contain uncharacteristically high large-mammal densities, whereas sampling locations from the national survey in 1981–1983 were spread more uniformly across Gabon. The survey data were also collected before the ongoing Ebola epidemic in northeast Gabon and neighbouring Congo (http://www.who.int). Therefore, the figures for decline that we report below are likely to underestimate substantially the true magnitude of ape decline.

Surveys in both sampling time periods were based on counts of sleeping nests rather than live gorillas or chimpanzees, which are secretive and difficult to observe during surveys. Because discriminating between gorilla and chimp nests can be difficult, we pooled gorilla and chimp data and analysed the rate at which ape nest groups (not individual nests) were encountered along line transects and recces. Raw encounter rate data are shown in Fig. 2. Evidence that encounter rates of ape nest groups should be directly proportional to ape density is provided in Supplementary Information, along with a detailed discussion of analytical methods.

Measurement of ape decline

To estimate the magnitude of ape decline, we took a 'spatial modelling' approach[21]. For each sampling period, we estimated the functional relationship between nest group encounter rate and important predictor variables, cut Gabon into a 30 arcsec grid (approximately 1 km^2 cells), and interpolated encounter rate in each grid cell given the predictor variable values for that cell. We confined ourselves to analysing the effects of two predictor variables: distance from the closest of Gabon's major urban centres and distance from documented human Ebola outbreaks. We do not include analyses with predictor variables that varied on a smaller scale because our sampling sites tended not to include the full range of predictor values on smaller scales. For example, few sampling sites were near towns or heavily deforested areas, so that analyses of the effects of these factors on encounter rates of nest groups tended to produce obviously spurious results. Our analyses indicated a strong increase in nest group size with increasing distance from human Ebola outbreak sites ($R^2 = 0.012$, $P = 0.00002$, $n = 1{,}434$). Therefore, when interpolating the value for each cell in the Gabon grid, we multiplied the predicted nest group encounter rate by the predicted nest group size. We then estimated the percentage ape decline by averaging nest encounter rates across grid cells, dividing the average for the recent surveys by the 1981–1983 average, subtracting the quotient from one, and multiplying by 100. Without including the effect of declining group size, the analysis suggested a nest group encounter rate decline of 46% (95% confidence interval = 23–63%).

Analysis of bushmeat sale and consumption

Sales of bushmeat were recorded at 11 markets in Gabon between January 2000 and July 2002. Analysed surveys included between 21 and 426 days per market and 80,528 bushmeat sales from 42 species, of which 7,686 (9.5%) were of whole animals. Prices per unit mass for whole animal sales were calculated using published average adult body weights[22]. Prices of alternative protein sources were recorded monthly in a sample of shops in each town. In Libreville, we visited 518 randomly chosen households once each between January and April 2001 for a total of 1,793 consumption days. We asked about: (1) consumption of meat over the previous three days; (2) household income in the previous month; and (3) household assets.

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Correspondence and requests for materials should be addressed to P.D.W. (e-mail: pwalsh@princeton.edu).

