

Natural History Miscellany

Potential for Ebola Transmission between Gorilla and Chimpanzee Social Groups

Peter D. Walsh,^{1,*} Thomas Breuer,^{1,2} Crickette Sanz,¹ David Morgan,^{2,3} and Diane Doran-Sheehy⁴

1. Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany;

2. Wildlife Conservation Society, Bronx, New York 10460;

3. Lester E. Fisher Center for the Study and Conservation of Great Apes, Lincoln Park Zoo, Chicago, Illinois 60614;

4. Department of Anthropology, Stony Brook University, Stony Brook, New York 11794

Submitted June 17, 2006; Accepted October 17, 2006;

Electronically published March 21, 2007

Online enhancements: videos.

ABSTRACT: Over the past decade Ebola hemorrhagic fever has emerged repeatedly in Gabon and Congo, causing numerous human outbreaks and massive die-offs of gorillas and chimpanzees. Why Ebola has emerged so explosively remains poorly understood. Previous studies have tended to focus on exogenous factors such as habitat disturbance and climate change as drivers of Ebola emergence while downplaying the contribution of transmission between gorilla or chimpanzee social groups. Here we report recent observations on behaviors that pose a risk of transmission among gorilla groups and between gorillas and chimpanzees. These observations support a reassessment of ape-to-ape transmission as an amplifier of Ebola outbreaks.

Keywords: ape decline, epidemiology, frugivory, Congo, disease network, emergent disease.

Since the mid-1990s, the Zaire strain of Ebola virus (ZEBOV) has repeatedly emerged in human populations in Gabon and the Republic of Congo (Leroy et al. 2004). Simultaneously, nearby gorilla and chimpanzee populations have experienced massive declines in numbers, with ape populations in certain forests falling by more than 90% in just a few years (Huijbregts et al. 2003; Walsh et

al. 2003; Bermejo et al. 2006). Ape carcass sampling at several die-off locations has confirmed ZEBOV as a cause of death (Leroy et al. 2004; Rouquet et al. 2005). Further insight into the ecology of the virus is essential for understanding why ZEBOV has emerged so explosively in recent years, predicting future impact on ape populations, and determining the feasibility of control measures.

A critical issue is the extent to which the virus is transmitted between apes, rather than solely through spillover from reservoir hosts (recently suggested to be bats; Leroy et al. 2005). The consensus has been that some ape-to-ape transmission might occur within ape social groups (hereafter "group") because close proximity is common and direct physical contact not unusual. Indeed, mother-infant contact and sexual contact were both significant risk factors during an outbreak of the Côte d'Ivoire strain of Ebola in a chimpanzee community of Tai Forest, Côte d'Ivoire (Formenty et al. 1999). Group-living adult male gorillas (silverbacks) at Lokoué, in northwest Republic of Congo, also suffered a higher ZEBOV mortality rate (97%) than did solitary silverbacks (77%; Caillaud et al. 2006). Caillaud et al. (2006) felt that group-to-group transmission probably played an important role in the Lokoué die-off, although their data did not discriminate decisively between group-to-group transmission and reservoir spillover. In contrast, previous authors have tended to dismiss the notion that transmission between ape groups could contribute substantially to amplifying ape die-offs because, they note, direct physical contact between groups is rare (see, e.g., Tutin 2000; Leroy et al. 2004; Rouquet et al. 2005). The possibility of cross-species transmission between gorillas and chimpanzees appears not to have been seriously considered.

Until now, conclusions about the potential for between-group and cross-species transmission were based on a very sketchy understanding of ape behavior and feeding ecology. Direct observations of western gorillas (*Gorilla gorilla*) have been extremely limited until quite recently, as have observations on central chimpanzees (*Pan troglodytes troglodytes*) living in sympatry with gorillas. Here we present new observations from three study sites in northeast Congo, which

* Corresponding author; e-mail: walsh@eva.mpg.de.

inform the debate. First, we present an observation that bears on the tendency of gorillas to closely approach and inspect dying or dead gorillas from other groups. Second, we report on the extent to which gorillas from different groups feed in the same trees in close temporal succession, thus providing a means of cross-group contact with infective bodily fluids. Third, we quantify the rate at which gorillas and chimpanzees feed simultaneously in the same tree, thereby providing a potential mechanism for cross-species transmission. Our observations suggest that the potential for ZEBOV transmission between ape groups and between ape species may have been underestimated.

Our first observation was made by D. Doran-Sheehy and colleagues at the Mondika Research Center, which straddles the border with Central African Republic. A group of western gorillas (including one silverback, six adult females, and their offspring) has been observed there on a near-daily basis since April 2001 (Doran-Sheehy et al. 2004). On June 18, 2004, we conducted an all-day focal follow of the group's silverback. The silverback was foraging apart from other group members when we heard female gorillas screaming from a distance, which we later measured (by GPS) to be 400 m. The silverback immediately ran in the direction of the screams. We followed to find the females of the group agitated and displaying close (frequently <1 m) to a mortally wounded adult female gorilla who was neither a member of their group nor known to us. We did not observe the source of the fresh bloody lacerations along her back but suspect it may have been a leopard. The silverback displayed repeatedly, beating his chest and running near (≤ 1 m) the wounded female. He remained close to her for 80 min and then moved off 45 m to join the group of females. We were unable to make observations on the following day, but 43 h later the group returned to the same location where the female had died. The silverback approached the now-scavenged corpse, brushed flies away, and sniffed the rotting flesh. All group females, juveniles, and infants also approached the carcass to distances of less than 1 m. The group remained near the carcass for 160 min, making repeated close inspections of the carcass and resting close to it, although we never saw any of the gorillas directly touch the wounded female or her carcass.

Although inspection of great ape carcasses has been observed before (Fossey 1983; Boesch and Boesch-Achermann 2000), this is the first record of the behavior being directed at a member of a different group. This may not have been observed previously in African apes for at least two reasons. First, because chimpanzees defend community territorial boundaries, the carcass of an individual from another group would rarely be encountered within the home range (but see Muller 2002). Second, western gorillas in the Ebola outbreak zone live at higher densities (Bermejo 1999; Mor-

gan et al. 2006) than the better-studied mountain gorilla (McNeilage et al. 1997; Kalpers et al. 2003). They also have a more frugivorous diet and, therefore, have longer daily path lengths, larger home ranges, more contemporaneous home range overlap, and more frequent encounters with other groups (Bermejo 2004; Doran-Sheehy et al. 2004). Thus, under normal circumstances, western gorillas may be more likely to encounter the carcass of an extragroup member than are other African apes. During an Ebola outbreak, the rate of carcass encounter would be much higher than normal because the monthly mortality probability of each individual in a group hit by Ebola is about 0.45 (M. Bermejo, unpublished data), or about 50 times higher than the long-term mean adult mortality rate (conservatively assuming a mean adult life span of 10 years).

Direct contact with carcasses presents a serious transmission risk because blood in the secreted and excreted body fluids (e.g., saliva, vomit, urine, feces) of late-stage Ebola victims has a high virus titer (Geisbert et al. 2003). During a 1994 outbreak of the Côte d'Ivoire strain of Ebola, 10 different chimpanzees were observed touching the carcass of a deceased juvenile. Two of these individuals then died after an interval consistent with Ebola infection (Formenty et al. 1999). Under laboratory conditions, surfaces infected with the closely related Marburg virus remain infective for up to 4–5 days (Leffel and Reed 2004). The Reston strain of Ebola has repeatedly caused large outbreaks in separately caged monkeys at captive primate facilities (Miranda et al. 2002). Tissues from wild ape carcasses yield viable ZEBOV virus for up to 3 days after death, and handling ape carcasses found in the forest has been the primary mode of human outbreak initiation in Gabon and Congo (Leroy et al. 2004, 2005). Thus, Ebola stability also appears to be great enough for viable virus to persist on carcasses long enough for other groups to encounter still-infective carcasses.

In fact, direct contact with carcasses may not even be necessary for infection. Very close approaches of the kind we observed may also represent a substantial infection risk. Immobile final-stage Ebola victims often excrete large quantities of infective body fluids, so the vegetation and ground surrounding a carcass could be infective. In addition, scavenging of carcasses could spread infective blood and body tissues over a wide area. The rapid scavenging observed in our case occurred well within the reported 3-day limit for Ebola viability in carcass tissues and is typical of large mammal carcasses in the central African forest.

The immediate vicinity of carcasses is not the only place where infective body fluids might be encountered. Exposure of other frugivores to infective saliva or feces deposited on fruit by bats has been proposed as a major mechanism of viral disease transmission in general (Dobson 2005) and Ebola transmission in particular (Formenty

et al. 1999; Leroy et al. 2005). Less considered, however, is that fruit trees may also serve as focal points for disease transmission between groups or species of apes. Gorillas and chimpanzees frequently urinate and defecate while either foraging in or resting near fruit trees (C. Sanz, unpublished data). For example, one chimpanzee in the Côte d'Ivoire outbreak showed symptoms 6 days before his disappearance, and another continued feeding in fruit trees up to the day before her death. Carcasses of several others were discovered within a few days of their last observed feeding bout (Formenty et al. 1999). Given that the virus appears in excreted body fluids several days before death (Dowell et al. 1999; Geisbert et al. 2003), these chimpanzees were likely shedding infective virus while feeding in trees, and subsequent visits to these trees by other apes could potentially lead to infection.

Gorillas and chimpanzees are also highly selective in their fruit consumption. They prefer ripe to unripe fruit (Wrangham et al. 1998), have strong preferences for particular and often rare species (Rogers et al. 2004), incorporate ripe fruit in their diets on the basis of availability (Wrangham et al. 1998), and travel farther to obtain it when available (Doran 1997; Wrangham et al. 1998; Doran-Sheehy et al. 2004). Many preferred fruit species are highly synchronous in their fruiting patterns, fruiting for short periods of time and either rare or highly localized in the environment. Apes are often choosy about which fruits they eat, testing fruits by sniffing and/or biting, possibly leaving mucous or saliva, and discarding uneaten parts (see video 1, available in the online edition of the *American Naturalist*) so that food items left by one group



Video 1: Still photograph from a video (available in the online edition of the *American Naturalist*) depicting a juvenile gorilla sniffing, tasting, and discarding *Nauclea* fruits. Apes are often very choosy about the fruits they eat, which can result in many discarded food items at “magnet” resources that have been handled or tested by previous visitors. Video by Thomas Breuer (Max Planck Institute and Wildlife Conservation Society).



Video 2: Still photograph from a video (available in the online edition of the *American Naturalist*) showing a lone silverback gorilla named Campo arriving at a *Chrysophyllum lacourtianum* tree. He collects and feeds on several fruits near the path. Twenty-seven minutes later, another lone silverback (Vince) arrives at the same location and smells the location where Campo had been feeding. He then proceeds to consume the feeding remains that were left behind by Campo. Video by Thomas Breuer (Max Planck Institute and Wildlife Conservation Society).

may be subsequently encountered by individuals of different groups (see video 2, available in the online edition). Because gorilla group home ranges overlap with those of as many as 36 other groups (Gatti et al. 2004) and one or more chimpanzee communities, and because sympatric gorillas and chimpanzees show high dietary overlap (Tutin and Fernandez 1993; Morgan and Sanz, forthcoming), many different gorillas and/or chimpanzees may be drawn to these “magnet” resources on the same or successive days, creating conditions that increase the probability of contact with feces, urine, or saliva of nongroup individuals. Exactly how frequently this occurs is unknown.

We recently made two sets of observations that allowed us to quantify the extent of overlap at fruiting trees, both among gorilla groups and between gorillas and chimpanzees. The first observations were made by T. Breuer at Mbeli Bai, a large swampy clearing where gorillas have been monitored since 1995 (Parnell 2002; Stokes et al. 2003). During the study, the clearing was visited by 11 different western gorilla groups and 10 lone males. For most of the year, gorillas feed primarily on aquatic and semiaquatic herbs while visiting the clearing (Parnell 2002). However, during September and October they also feed on the fruits of *Nauclea* (*Sarcocephalus*) *pobeguini*, which grows only in the inundated forest surrounding the clearing and shows strong supra-annual pulses in fruit reproduction (mast fruiting). During a *Nauclea* mast fruiting event in 2003, we observed 15 different gorilla social units (four solitary silverbacks and 11 groups of two or more individuals) foraging in 37 different *Nauclea* trees.

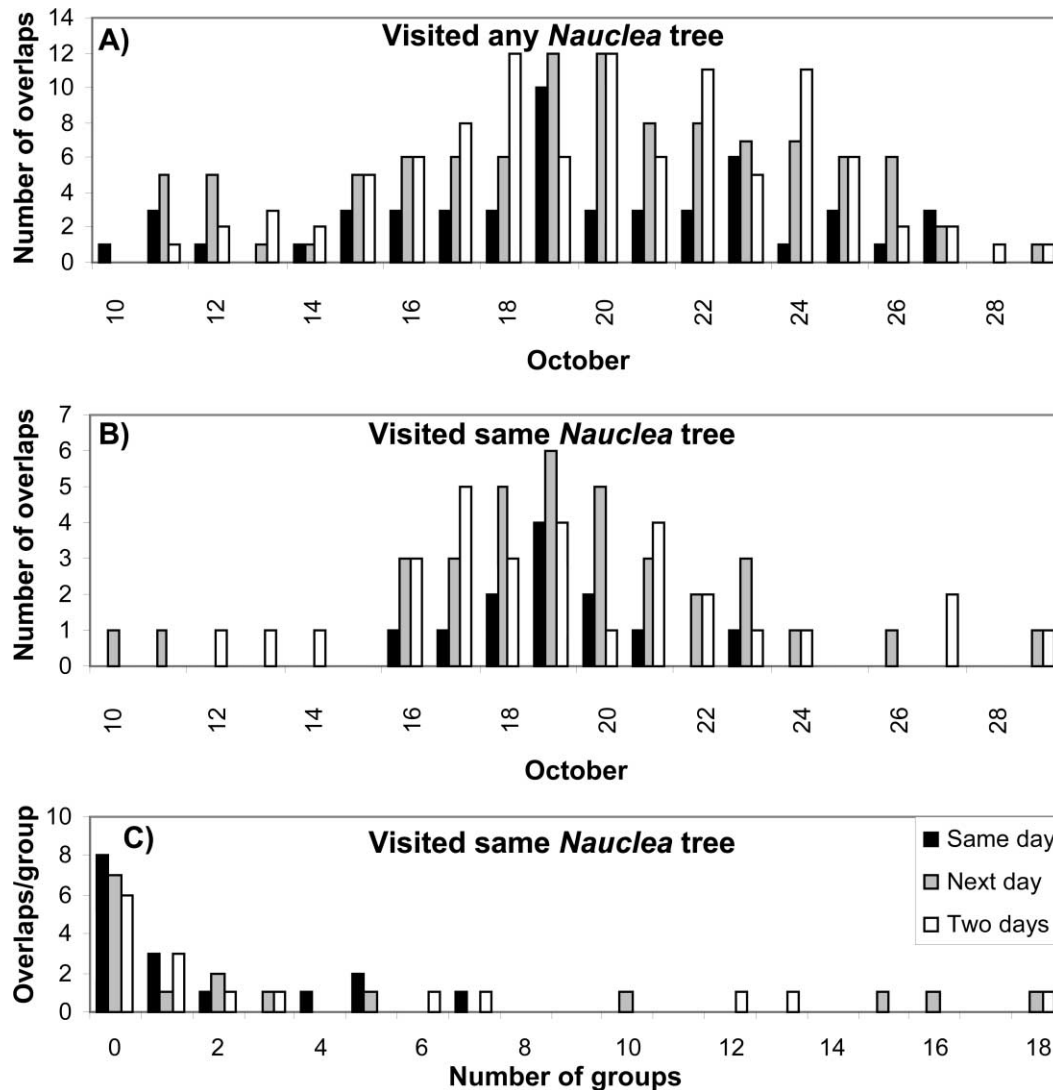


Figure 1: Overlap frequency for gorillas foraging in *Nauclea* trees surrounding Mbeli clearing. *A*, Time series of cases in which two different social units foraged at any *Nauclea* tree in the clearing on the same day or separated by one or two days. *B*, Number of cases when members of two different social units foraged in exactly the same *Nauclea* tree on the same day or separated by one or two days. *C*, Frequency histogram for number of overlaps per social unit.

There were 56 cases (involving 14 of 15 units) in which a pair of social units fed in the same stand of *Nauclea* trees on the same day (fig. 1A) and frequently used the same travel routes to and from the trees where they were likely to have encountered the traces (feces, urine, discarded feeding remains, etc.) of another group.

Different gorilla social units also fed in exactly the same fruiting tree in close temporal succession. In 13 cases, gorilla(s) from one social unit fed in the same tree on the same day as gorilla(s) from another unit. Eight of 15 social units were involved in same-day overlaps in trees, and up to four different units used a single *Nauclea* tree on the

same day (fig. 1B). Each case of same-day tree use involved an average of 9.5 individuals from a pair of social units, with each individual spending on average 16.4 min foraging in overlap trees. Instances in which a different social unit fed in the same tree the next day or 2 days later were even more frequent (37 and 32 cases involving, respectively, 11 and 14 different units). These observations include only time intervals when gorillas were clearly visible from an observation platform up to 200 m away, so true overlap may have been even greater.

Of particular interest was the fact that overlaps pivoted on a few social units that were frequently present during



Video 3: Still photograph from a video (available in the online edition of the *American Naturalist*) showing a young silverback gorilla and a subadult chimpanzee feeding in the canopy of the same *Treculia africana* tree. Researchers at this site have observed co-feeding events of gorillas and chimpanzees at several important food resources shared by these apes, which indicates a potential intersection for virus transmission between species. Video by Crickette Sanz (Max Planck Institute and Wildlife Conservation Society) and David Morgan (Wildlife Conservation Society and Lincoln Park Zoo).

the mast fruiting event (fig. 1C). One unit visited the *Nauclea* trees on 26 of the 36 September and October days on which gorillas were observed in *Nauclea* trees. It accounted for 38% of same-day overlaps, 49% of consecutive-day overlaps, and 56% of 2-day overlaps. It overlapped with nine of the other 15 units in at least one of the three time intervals (four, seven, and nine units, respectively). These observations suggest that some gorilla social units may play a disease-transmission role analogous to that of prostitutes in the spread of HIV in southern Africa (Anderson et al. 1991), rapidly disseminating Ebola among networks of individuals that would otherwise interact little. Such “super spreaders” have recently been shown to play a critical role in the dynamics of explosively emerging diseases, including Ebola in humans (Lloyd-Smith et al. 2005).

Our third set of observations concerns the possibility of cross-species ZEBOV transmission and were made by C. Sanz and D. Morgan at the Goulougo Triangle Research Center in Nouabalé-Ndoki National Park (Morgan and Sanz, forthcoming). From 2002 to 2004, we observed chimpanzees from four different communities foraging in fruiting trees from the genus *Ficus*. On 5 of 75 days (i.e., once for every 15 days of feeding observations at *Ficus* trees) chimpanzees occupied a tree simultaneously with gorillas (see video 3, available in the online edition). Co-occupancy lasted for an average of 47 min, with an average of 10.4 chimpanzees and 3.8 gorillas involved. True rates of co-occupancy are probably higher because gorillas appeared to be deterred by the presence of observers. Al-

though shared use of resources has been reported (Kuroda et al. 1996), this is the first study documenting that co-feeding occurs on a regular basis.

Although we have reported only on *Nauclea* and *Ficus* trees, gorillas and chimpanzees commonly exploit many other tree species that produce fruit crops large enough to attract and satiate multiple ape groups (Kuroda et al. 1996; Yamagiwa et al. 1996). These same trees also attract other species to which Ebola is virulent, including duikers (Leroy et al. 2004; Rouquet et al. 2005), whose carcass-scavenging habits put them at greater risk of infection. The role of these other hosts in the dynamics of ZEBOV remains unclear.

In conclusion, our intention is not to argue that these observations provide strong evidence that between-group transmission plays a major role in the transmission of ZEBOV. Rather, they illustrate potential means of transmission between groups or species that have previously failed to enter in the debate because of the paucity of available data on gorilla and chimpanzee socioecology. ZEBOV poses a grave threat to humans and apes in central Africa in the near future, and examining potential modes of transmission between groups and species is critical for improving our understanding of the ecology of this virus and assessing the feasibility of potential control measures. Considering the toll that this virus has already taken on ape populations in Gabon and Congo, determining the principles that govern the emergence and spread of ZEBOV may be an important means of ensuring the conservation of great apes in the Congo Basin.

Acknowledgments

We thank the Ministère de l'Économie Forestière of the Republic of Congo for permission to work in and around Nouabalé-Ndoki National Park. The Wildlife Conservation Society's Congo Program provided logistical support to all of the research projects in this study. Special thanks are due to B. Djoni, P. Elkan, M. Gatley, P. Ngouembe, and E. Stokes. Financial support was provided by Brevard Zoo, Columbus Zoo and Aquarium, Cincinnati Zoo and Botanical Garden, Lincoln Park Zoo, Lowry Park Zoo, Max Planck Society, National Geographic Society, SeaWorld and Busch Gardens Conservation Fund, Toronto Zoo, U.S. Fish and Wildlife Service, and Woodland Park Zoo.

Literature Cited

- Anderson, R. M., R. M. May, M. C. Boily, G. P. Garnett, and J. T. Rowley. 1991. The spread of HIV-1 in Africa: sexual contact patterns and the predicted demographic impact of AIDS. *Nature* 352: 581–589.
- Bermejo, M. 1999. Status and conservation of primates in Odzala National Park, Republic of the Congo. *Oryx* 33:323–331.

- . 2004. Home-range use and intergroup encounters in western gorillas (*Gorilla g. gorilla*) at Lossi Forest, North Congo. *American Journal of Primatology* 64:223–232.
- Bermejo, M., J. D. Rodríguez-Teijeiro, G. Illera, A. Barroso, C. Vilà, and P. D. Walsh. 2006. Ebola outbreak killed 5000 gorillas. *Science* 314:1564.
- Boesch, C., and H. Boesch-Achermann. 2000. *The chimpanzees of the Tai Forest: behavioural ecology and evolution*. Oxford University Press, Oxford.
- Caillaud, D., F. Levréro, R. Cristescu, S. Gatti, M. Dewas, M. Douadi, A. Gautier-Hion, M. Raymond, and N. Ménard. 2006. Gorilla susceptibility to Ebola virus: the cost of sociality. *Current Biology* 16:R489–R491.
- Dobson, A. P. 2005. What links bats to emerging infectious diseases? *Science* 310:628–629.
- Doran, D. 1997. Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Tai chimpanzees. *International Journal of Primatology* 18:183–206.
- Doran-Sheehy, D. M., D. Greer, P. Mongo, and D. Schwindt. 2004. Impact of ecological and social factors on ranging in western gorillas. *American Journal of Primatology* 64:207–222.
- Dowell, S. F., R. Mukunu, T. G. Ksiazek, A. S. Khan, P. E. Rollin, and C. J. Peters. 1999. Transmission of Ebola hemorrhagic fever: a study of risk factors in family members, Kikwit, Democratic Republic of the Congo, 1995. *Journal of Infectious Diseases* 179(suppl.):S87–S91.
- Formenty, P., C. Boesch, M. Wyers, C. Steiner, F. Donati, F. Dind, F. Walker, and B. Le Guenno. 1999. Ebola virus outbreak among wild chimpanzees living in a rain forest of Côte d'Ivoire. *Journal of Infectious Diseases* 179(suppl.):S120–S126.
- Fossey, D. 1983. *Gorillas in the mist*. Houghton Mifflin, Boston.
- Gatti, S., F. Levréro, N. Menard, and A. Gautier-Hion. 2004. Population and group structure of western lowland gorillas (*Gorilla gorilla gorilla*) at Lokoué, Republic of Congo. *American Journal of Primatology* 63:111–123.
- Geisbert, T. W., L. E. Hensley, T. Larsen, H. A. Young, D. S. Reed, J. B. Geisbert, D. P. Scott, et al. 2003. Pathogenesis of Ebola hemorrhagic fever in cynomolgus macaques: evidence that dendritic cells are early and sustained targets of infection. *American Journal of Pathology* 163:2347–2370.
- Huijbregts, B., P. de Wachter, L. S. Ndong Obiang, and M. Ella Akou. 2003. Ebola and the decline of gorilla *Gorilla gorilla* and chimpanzee *Pan troglodytes* in Minkebe Forest, north-eastern Gabon. *Oryx* 37:437–443.
- Kalpers, J., E. A. Williamson, M. M. Robbins, A. McNeilage, A. Nzamurambaho, N. Lola, and G. Mugiri. 2003. Gorillas in the crossfire: population dynamics of the Virunga mountain gorillas over the past three decades. *Oryx* 37:326–337.
- Kuroda, S., T. Nishihara, S. Suzuki, and R. A. Ooko. 1996. Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. Pages 71–81 in W. C. McGrew, L. F. Marchant, and T. Nishida, eds. *Great ape societies*. Cambridge University Press, Cambridge.
- Leffel, E. K., and D. D. Reed. 2004. Marburg and Ebola viruses as aerosol threats. *Biosecurity and Bioterrorism* 2:186–191.
- Leroy, E. M., P. Rouquet, P. Formenty, S. Souquiere, A. Kilbourne, J. M. Froment, M. Bermejo, et al. 2004. Multiple Ebola virus transmission events and rapid decline of central African wildlife. *Science* 303:387–390.
- Leroy, E. M., B. Kumulungui, X. Pourrut, P. Rouquet, A. Hassanin, P. Yaba, A. Delicat, J. T. Paweska, J. P. Gonzalez, and R. Swanepoel. 2005. Fruit bats as reservoirs of Ebola virus. *Nature* 438:575–576.
- Lloyd-Smith, J. O., S. J. Schreiber, P. E. Kopp, and W. M. Getz. 2005. Superspreading and the effect of individual variation on disease emergence. *Nature* 438:355–359.
- McNeilage, A., A. J. Plumptre, A. Brock-Doyle, and A. Vedder. 2001. Bwindi Impenetrable National Park, Uganda: gorilla census 1997. *Oryx* 35:39–47.
- Miranda, M. E. G., Y. Yoshikawa, D. L. Manalo, A. B. Calaor, N. L. J. Miranda, and F. Cho. 2002. Chronological and spatial analysis of the 1996 Ebola Reston virus outbreak in a monkey breeding facility in the Philippines. *Experimental Animals* 51:173–179.
- Morgan, D., and C. Sanz. 2006. Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goualougo Triangle, Republic of Congo. Pages 97–122 in G. Hohmann, M. M. Robbins, and C. Boesch, eds. *Feeding ecology of apes and other primates*. Cambridge University Press, Cambridge.
- Morgan, D., C. Sanz, J. R. Onononga, and S. Strindberg. 2006. Ape abundance and habitat use in the Goualougo Triangle, Republic of Congo. *International Journal of Primatology* 27:147–179.
- Muller, M. N. 2002. Agonistic relations among Kanyawara chimpanzees. Pages 112–123 in C. Boesch, G. Hohmann, and L. F. Marchant, eds. *Behavioural diversity in chimpanzees and bonobos*. Cambridge University Press, Cambridge.
- Parnell, R. J. 2002. Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. *American Journal of Primatology* 56:193–206.
- Rogers, M. E., K. Abernethy, M. Bermejo, C. Cipolletta, D. Doran, K. McFarland, T. Nishihara, M. Remis, and C. E. G. Tutin. 2004. Western gorilla diet: a synthesis from six sites. *American Journal of Primatology* 64:173–192.
- Rouquet, R., J. M. Froment, M. Bermejo, A. Kilbourn, W. Karesh, P. Reed, B. Kumulungui, et al. 2005. Wild animal mortality monitoring and human Ebola outbreaks, Gabon and Republic of Congo, 2001–2003. *Emerging Infectious Diseases* 11:283–290.
- Stokes, E. J., R. J. Parnell, and C. Olejniczak. 2003. Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behavioural Ecology and Sociobiology* 54:329–339.
- Tutin, C. E. G. 2000. Ecology and social organisation of African rainforest primates: relevance for understanding the transmission of retroviruses. *Bulletin de la Société de Pathologie Exotique Filiales* 93:157–161.
- Tutin, C. E. G., and M. Fernandez. 1993. Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. *American Journal of Primatology* 30:195–211.
- Walsh, P. D., K. A. Abernethy, M. Bermejo, R. Beyers, P. De Wachter, M. Ella Akou, B. Huijbregts, et al. 2003. Catastrophic ape decline in western equatorial Africa. *Nature* 422:611–614.
- Wrangham, R. W., N. L. Conklin-Brittain, and K. D. Hunt. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology* 19:949–970.
- Yamagiwa, J., T. Maruhashi, Y. Yumoto, and N. Mwanza. 1996. Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaire. Pages 82–98 in W. C. McGrew, L. F. Marchant, and T. Nishida, eds. *Great ape societies*. Cambridge University Press, Cambridge.