International Journal of Primatology, Vol. 25, No. 2, April 2004 (© 2004)

Densities, Distributions, and Seasonal Movements of Gorillas and Chimpanzees in Swamp Forest in Northern Congo

John R. Poulsen[1,2] **and Connie J. Clark**[1]

Received December 5, 2002; revised August 11, 2003; accepted August 23, 2003

*The conservation of gorillas (*Gorilla spp.*) and chimpanzees (*Pan troglodytes*) depends upon knowledge of their densities and distribution throughout their ranges. However, information about ape populations in swamp forests is scarce. Here we build on current knowledge of ape populations by conducting line transect surveys of nests throughout a reserve dominated by swamp forest: the Lac Télé Community Reserve in northern Congo. We estimated gorilla and chimpanzee densities, distributions across habitats, and seasonal changes in abundance. Gorilla density was 2.9 gorillas km*$^{-2}$*, but densities varied by habitat (0.3–5.4 gorillas km*$^{-2}$*) with highest densities in swamp forest and* terra firma *mixed forest. Average chimpanzee density is 0.7 chimpanzees km*$^{-2}$ *(0.1–1.3 chimpanzees km*$^{-2}$*), with highest densities in swamp forest. Habitat was the best predictor of ape nest abundance, as neither the number of human indices nor the distance from the nearest village predicted nest abundance. We recorded significantly greater numbers of apes in* terra firma *forest during the high-water season than the low-water season, indicating that many gorillas and chimpanzees are at times concentrated in* terra firma *forest amid a matrix of swamp forest. Seasonally high numbers of apes on* terra firma *forest islands easily accessible to local people may expose them to substantial hunting pressure. Conversely, the nearly impenetrable nature of swamp forests and their low value for logging makes them promising sites for the conservation of apes.*

KEY WORDS: Gorilla; chimpanzee; swamp forest; Congo; Lac Télé Community Reserve.

[1]Wildlife Conservation Society, Lac Télé Community Reserve Project, BP 14537, Brazzaville, Republic of Congo.
[2]To whom correspondence should be addressed at 223 Bartram Hall, Department of Zoology, University of Florida, Gainesville, FL 3261-8525; e-mail: jpoulsen@zoo.ufl.edu.

INTRODUCTION

The status of ape populations in central Africa is a hotly debated topic. Population estimates of gorillas and chimpanzees not only vary widely depending on how they are calculated (Harcourt, 1996), but they also guide conservation efforts, deciding whether we attempt to conserve apes across their ranges or focus only on protected areas. In Gabon, Walsh *et al.* (2003) documented a precipitous decline of gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes troglodytes*) over the last 17 years, concluding that the very survival of apes in equatorial west Africa is threatened. However, deficiencies in our knowledge of ape populations makes their status uncertain (Harcourt, 1996). First, even though the primary causes of population declines—commercial hunting, disease, and habitat destruction by mechanized logging—occur across most of central Africa (Walsh *et al.*, 2003; Wilkie *et al.*, 2000), we have no idea how they translate to reductions in ape numbers (Oates, 1994). Second, little is known about the distribution and density of gorillas and chimpanzees in large parts of their ranges. Although the extrapolation of results from Gabon to the entirety of Central Africa may be premature, it underscores the immediate need for reliable information on the density and distribution of ape populations and the threats they face.

Much of our current information on ape populations comes from protected areas (but see Tutin and Fernandez, 1984). Traditionally, most conservation and research efforts have prioritized the establishment of parks in pristine habitats (Oates, 1996). Therefore, despite the fact that the majority of tropical forests are outside of parks or have experienced some level of anthropogenic disturbance (Chapman *et al.*, 1999), our knowledge of ape populations is largely derived from studies in untouched, primary rain forest. To more accurately assess the status of apes, it is critical to survey sites throughout the ranges of gorillas and chimpanzees, in a variety of habitat types, and with various levels of human disturbance.

Swamp forest represents a promising, though infrequently studied, habitat for gorilla and chimpanzee populations. Previous surveys of the Likouala swamps in the Republic of Congo indicated that gorilla densities are high in swamps relative to other habitats (Blake *et al.*, 1993; Fay *et al.*, 1989; Fay and Agnagna, 1992). Studies from sites not dominated by swamp forest have also revealed relatively high gorilla densities in swamp forests compared to other forest types, though chimpanzee densities tend to be low (Bermejo, 1999; but see Tutin and Fernandez, 1984; Lahm, 1993; Williamson and Usongo, 1996). However, most studies of ape populations in swamp forest were based on few km's of transects with little replication. More importantly, we have little information concerning the seasonal use of swamp forest or the ecological factors determining ape abundance in swamp forest.

If inundated forests support large numbers of gorillas and chimpanzees, they may be ideal to conserve apes because they are less subject to human pressures—hunting, logging and agriculture—than non-inundated forests (Gautier-Hion, 1996; Lahm, 1993). But swamp forests also present substantial environmental constraints for some animals. Seasonal fluctuations in water level may flood previously dry areas with $\geq$0.5 m of water. During the high-water season, many species may be driven from swamp forest to higher, dry habitats. If apes are seasonally dependent upon relatively small areas of accessible habitat, their numbers may be constrained by limitations of space or food. Moreover, the concentration of apes and other animals onto *terra firma* islands surrounded by a matrix of swamp forest could make them highly susceptible to hunting.

This study contributes to current knowledge of ape populations by a) documenting ape density, distribution, and seasonal movements in a reserve dominated by swamp forest, and b) assessing ecological and anthropogenic factors that affect ape density. We present results of the first systematic survey of apes conducted in the Lac Télé Community Reserve in northern Republic of Congo. Specifically, we address 4 questions: 1) What is the average density of apes in the reserve? 2) What is the distribution of apes by habitat? 3) What variables explain the distribution of apes? 4) Are ape densities substantially higher on the *terra firma* habitat during the high-water season (September–December) than during the low-water season (February–June)?

STUDY AREA

The Lac Télé Community Reserve (4440 km^2) is situated between the Sangha and Oubangui Rivers in northern Republic of Congo. The Likouala-aux-Herbes River runs from the northeast corner of the reserve to the southern point, cutting it into two blocks–the northern and southern blocks. Annual rainfall between 1995 and 2001 averaged 1526 mm (range = 1377–1794 mm, N = 7 years). Mean monthly rainfall varied between 15.4 and 288.9 mm, and was typically greatest between August and November. Low rainfall from December to March constituted the major dry season. Variation in rainfall results in fluctuations in the water level throughout the reserve. We recognized 2 seasons based on the water level in the Likouala-aux-Herbes river: a low-water season (February–June) and a high-water season (September–December).

The reserve contains a diversity of habitats, including swamp forest, seasonally flooded swamp forest, savanna, *terra firma* mixed forest, and riparian forest (Fig. 1). The northern block is composed almost entirely of swamp forest (49% of the reserve area), whereas the southern block

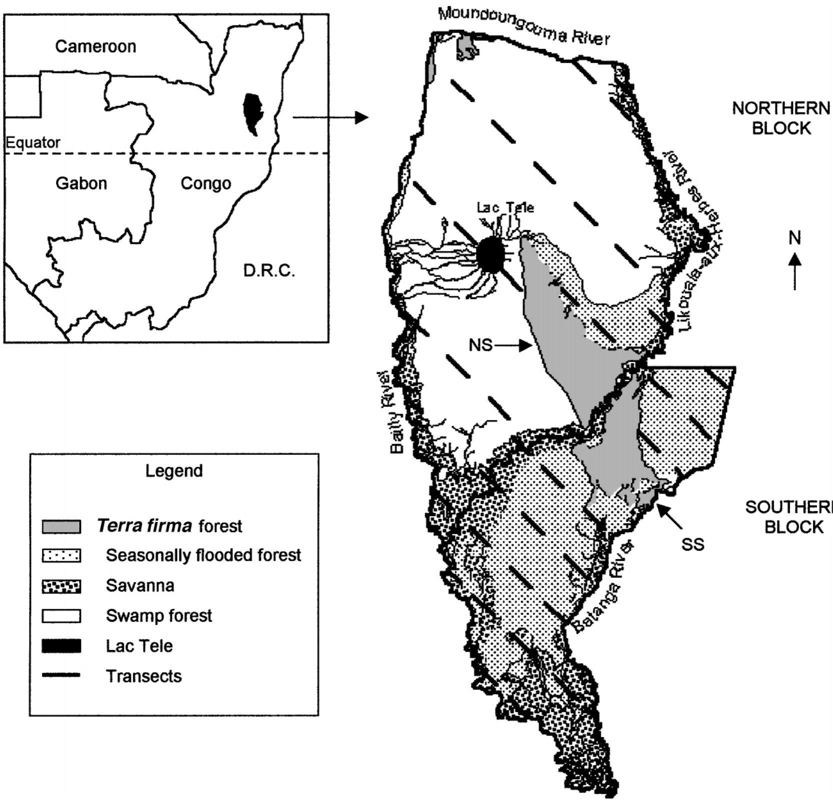

Fig. 1. Location of the Lac Télé Community Reserve in Central Africa and a map of the reserve with the transect sampling design. The northern and southern blocks of the reserve are separated by the Likouala-aux-Herbes River. The northern (NS) and southern (SS) sectors represent the northern and southern halves of the main spit of *terra firma* forest; the sectors are naturally divided by the Likouala-aux-Herbes River. Complete lines in all habitats but the *terra firma* forest represent transects 5 km in length. Complete lines in the *terra firma* forest represent transects a distance of 2 km.

contains higher proportions of seasonally flooded swamp and savanna. Swamp forest is almost always flooded and is dominated by *Mitragyna stipulosa*, *Alstonia boonei*, *Nauclea pobeguinii*, *Uapaca guineensis*, *U. heudelotii*, *U. paludosa*, *Macaranga schweinfurthii, Xylopia rubescens*, and *Coelocaryon botryoides* (Heymans and Oyo, 1999). Seasonally flooded forest (17%) is located around the periphery of swamp forest and is primarily flooded in the high-water season. Dominant tree species include *Lophira alata*, *Gambeya perpulchra*, *Uapaca heudelotii*, and *Sterculia bequaertii*. Riparian forest (8%) occurs along waterways dominated either by *Uapaca heudelotii* and *Parinari excelsa* or by *Guibourtia demeusia* and *Uapaca heudelotii*. Mixed forest habitat on *terra firma* (10%) is primarily located in the center of the reserve. The principal *terra firma* forest is surrounded by wet forest types and is naturally divided into northern and southern sectors by the Likouala-aux-Herbes River (Fig. 1). The most abundant tree species in mixed forest are *Entandrophragma* spp., *Terminalia superba*, *Pterocarpus soyauxii, Piptadeniastrum africanum*, *Pycnanthus mechowianus*, *Lophira alata*, *Staudtia gabonensis*, and *Autranella congolensis*. Seasonally flooded savannas (16%) occur along rivers and are composed of grasses (Poaceae), attaining heights of 2 to 3 m.

In the Lac Télé Community Reserve, *ca.* 17,000 people live in 27 villages along the rivers. Fishing and agriculture are the principal economic activities. Only 1% of the population claim to be hunters as a primary occupation, though a small percentage of people also cite hunting as a secondary or tertiary economic activity (1–4%) (Poulsen and Clark, 2002). According to interviews of 247 hunters from 21 villages, most hunting (51%) takes place during the 4-mo high-water season in the reserve (Poulsen and Clark, 2002). Hunters use firearms (80%) more frequently than other weapons: crossbows (10%), traps (8%), spears (8%), or harpoons (3%). Even though the Lac Télé Community Reserve was formally gazetted on May 2002, conservation activities in the form of research and environmental education have been ongoing since 1997. However, there has been no formal enforcement of hunting laws, and conservation activities have probably had a very small impact on poaching.

METHODS

Transect Establishment

We used satellite images to identify habitat types so that ape abundance could be calculated later for each habitat. To ensure that each habitat type was surveyed proportionally to its representation in the reserve, we used Arcview 3.2. to create polygons for each habitat type and calculated the area of each polygon. Because it was difficult to distinguish between seasonally flooded swamp forest and riparian forest habitats on the satellite images, we combined them into a single polygon. We positioned a digital grid oriented roughly perpendicular to the Likouala-aux-Herbes River over the reserve. Transects were placed at intervals along the gridlines using a systematic design with a random origin, and start and end GPS coordinates were determined for each transect (Fig. 1). We established transect length as 5 km with 5-km intertransect spacing to insure independence of transects while allowing 15–25 replicates (transects) per habitat. The *terra firma* forest has a relatively small area (437 km^2) compared to the other habitat types; therefore, we reduced transect length to 2 km with 3.5-km intertransect spacing to provide adequate numbers of transects to estimate densities for the northern and southern sectors.

We first walked transects in mixed forest on *terra firma* during the high-water season (November 15–December 15, 2001). Then we conducted line transects in each habitat including *terra firma* forest during the low-water season (March 1–June 10, 2002). During the 5 mo between the first and second samplings of the *terra firma*, the vegetation had largely regrown, closing transects.

Data Collection

Arriving at the predetermined coordinates, we cut straight line transects following a fixed compass bearing. Three local field guides scanned the transect line and its surroundings for signs of gorillas and chimpanzees, including feeding sites, tracks, nests, and dung. We also recorded all signs of humans, including hunting trails, traps, cut marks, camps, and tracks. We measured perpendicular distances to all signs of apes or humans from the transect line to the nearest cm. When an ape nest was encountered, guides searched the area intensively to locate additional nests. For each nest site, we recorded: distance along transect, animal species, perpendicular distance from the center of transect to the center of each nest, side of transect on which the nest occured, nest height, nest age, nest type, and habitat type. Nest height was measured to the nearest cm whenever possible, but the heights of nests high in trees were estimated to the nearest m. We scored nest age and type following White and Edwards (2000) for age classes—fresh, recent, old, and very old—and for nest types: ground, minimum, herbaceous, mixed, wood, and tree. A nest site was defined as a group of nests of the same age $\leq$25 m apart.

Taxonomy of Nests

We scored nest sites as gorilla when (1) $\geq$1 ground nest was present or (2) an obvious gorilla sign, e.g., dung, of the same age as the nest site was on the ground below the site. However, discriminating between gorilla and chimpanzee nests can be difficult. Data from Lopé, Gabon show that as many as 26% of gorilla nest sites can be mistakenly recorded as chimpanzee nest sites when only tree nests remain visible (Tutin *et al.*, 1995). Thus we may have underestimated gorilla density and overestimated chimpanzee density. We also calculated overall ape abundance and density for the reserve as a measure of combined gorilla and chimpanzee densities that does not depend on nest identification.

Density Estimates and Statistical Analysis

From the transect data, we estimated densities of ape nest sites with the computer program DISTANCE (Laake *et al.*, 2001). To improve model estimation, we truncated our data set to exclude the 5% of observations occurring farthest from the transect line (Buckland *et al.*, 2001). DISTANCE models the distance from the transect line to an observation to estimate density of observations in a study area. We considered 4 models for the detection function: Uniform + cosine, Uniform + simple polynomial, Half normal + hermite polynomial, and Hazard rate + cosine. We computed Akaike's Information Criterion (AIC) for each model, and based the choice of the final model on a combination of a low AIC value and low variance (Buckland *et al.*, 2001).

Because it is commonly assumed that weaned chimpanzees and gorillas make one nest per night, we calculated the density of weaned individuals with the following formula (Tutin and Fernandez, 1984):

Weaned individuals per km^2 = (nest site density × mean group size)/nest decay time.

The differential disappearance of nests from older nest sites may lead to underestimates of group size (Remis, 1993; Tutin *et al.*, 1995). Therefore, we based mean group sizes on sites with fresh and recent nests for which we were confident that all nests were counted.

Mean gorilla nest site duration varies depending on the proportion of different nest types within nest sites (Tutin *et al.*, 1995). Therefore, we calculated nest site duration for each habitat based on the proportions of fresh and recent nests of each nest type within that habitat (Table I). Over 90% of all observed nests in *terra firma* forest were constructed of herbaceous material (91%-high-water season; 96%-low-water season) so we used the same mean nest site lifespan for both seasons. Tutin and Fernandez (1984) estimated that chimpanzee nests remained visible for 113.6 days, which we

Table I. Gorilla nest type and mean nest life span by habitat

Nest type	Mean nest life-span (days)[a]	% Observations *Terra firma* forest	% Observations Swamp forest	% Observations Seasonally flooded forest
Tree	129	3	66	44
Herbaceous	61.7	96	19	17
Palm/woody	50.9	1	11	22
Mixed	52.7	0	3	17
Ground	4.3	0	2	0
Mean nest life-span (days)		63.6	104.1	86.4

Note. All chimpanzee nests recorded during the study were tree nests.
[a]Tutin *et al.* (1995).

used in our calculations. The lack of information on nest decay rates for the swamp forest and the fact that our results do not take into account seasonal differences in nest decay rate most certainly introduced error into our density estimates (Tutin *et al.*, 1995; Tutin and Fernandez, 1984).

We conducted one-tailed tests of the hypothesis that apes are more abundant in *terra firma* forest during the high-water season than in the low-water season. Before conducting the research, we reasoned that apes would likely move from the swamp forest to the higher *terra firma* forest during seasonal flooding, a hypothesis substantiated by conversations with local hunters. All other statistical tests are two-tailed, unless otherwise noted.

We fitted and evaluated generalized linear models (GLIM) using R (R Development Core Team 2003) to determine if nest site abundance is associated with habitat and human presence. Generalized linear models are an extension of traditional linear models to situations where the response variable follows any member of the exponential family of probability distributions. Because the data did not fit a Poisson distribution (variance in the response variable was greater than the mean response), we built a model for the mean and variance of the response simultaneously via a quasilikelihood function with a log-link (Agresti, 1996; McCullagh and Nelder, 1989). If the sampling variance of a response variable is significantly greater than that predicted by an expected probability distribution, e.g. Poisson, the response variable is aggregated or overdispersed. Ignoring overdispersion will result in underestimates of the standard errors of parameter estimates and higher than stated Type 1 error rates (Connor *et al.*, 1997; McCullagh and Nelder, 1989).

As a preliminary analysis, we first assumed that the number of ape nests has a Poisson distribution. We constructed each model hierarchically using two explanatory components. First, we forced transect distance into the model as an offset to adjust for among-transect variation in sampling effort. Second, we constructed each model with the following explanatory variables: habitat, number of human indices, and distance from nearest village. We examined the contribution of each explanatory variable via a deviance difference test. We compared the residual deviance of a model to the residual deviance of the corresponding null model, scaling it by the overdispersion parameter. The quasi-link function estimates the overdispersion parameter as $\Phi = X^2/\mathrm{df}$, wherein X^2 is the Pearson chi-square statistic, and df is the degrees of freedom. The difference in deviance between nested models follows a X^2 distribution with degrees of freedom equal to the difference in the number of parameters between the models being compared (Connor *et al.*, 1997). In the final models, the standard error of covariates was adjusted by a multiplicative factor $\sqrt{\Phi}$, and the estimated effects of the covariates were evaluated with t-tests.

RESULTS

Ape Density and Distribution

During the low-water season, we conducted 75 straight line transects (24 in *terra firma* and 51 in the other three habitat types) for a distance of 234 km. We counted 341 ape groups (144 gorilla nest sites, 197 chimpanzee nest sites) and 1205 nests (719 gorilla nests, 486 chimpanzee nests; gorilla: mean = 4.99 nests per group, range = 1–34; chimpanzee: mean = 2.47 nests per group, range = 1–11). Ape nests were in all habitat types with the exception of the savanna (Table II). The mean density of apes for the reserve was 3.6 apes km^{-2} (95% CI: 2.0, 6.2). Mean gorilla density (2.9 gorillas km^{-2}) is higher than the density of chimpanzees (0.7 chimpanzees km^{-2}), although errors in the identification of nests may underestimate gorilla density and overestimate chimpanzee density. By multiplying the area of each habitat in the reserve by the mean density of apes per habitat, we derive estimates of the total number of apes, gorillas, and chimpanzees in the reserve and for each habitat type (Table III).

Ape Density and Distribution in *Terra Firma* Mixed Forest During High- and Low-Water Seasons

To evaluate seasonal fluctuations in habitat use, we conducted 24 transects (45.9 km) in the *terra firma* forest at the center of the reserve during both the high- and low-water seasons. In the high-water season, we counted 180 ape nest sites and 657 nests. The majority of the nest sites (95.6%) were in the northern sector of the *terra firma* forest. In the low-water season, we counted 35 ape nest sites and 105 nests, and 94.3% of nest sites were in the northern sector. Because distinguishing between gorilla and chimpanzee nest sites is sometimes difficult, we list the encounter rate and density of apes in Tables IV and V. By multiplying the area of the *terra firma* forest (437 km^2) by the density of apes, we estimated 4732 weaned apes in the habitat during the high-water season compared to 865 weaned apes during the low-water season.

Gorilla Survey

In the high-water season, 657 gorilla nests were found in 146 nest sites. In the low-water season, 105 gorilla nests were in 31 nest sites (Tables V and VI). Gorilla nest site encounter rates are significantly greater during the high-water than the low-water season ($Z = 1.91$, $P = 0.03$, one-tailed Wilcoxon

Table II. The number of groups and nests and estimates of group density and individual (ind) density for apes, gorillas, and chimpanzees by habitat

Habitat type	Transect distance (km)	Groups and (nests)	Groups and (ind's) km	Density (groups/ km^2)	Density (ind's/ km^2)[a]	95% CI (ind's/km^2)	CV[b]
Swamp forest	78						
Ape		279 (1019)	3.6 (13.1)	1.3	6.7	[3.8, 12.0]	28.2
Gorilla[c]		109 (607)	1.4 (7.8)	0.7	5.4	[3.0, 9.8]	29.6
Chimpanzee		170 (412)	2.2 (5.3)	0.6	1.3	[0.7, 2.4]	29.3
Seasonally flooded forest	58						
Ape		23 (68)	0.4 (0.2)	0.1	0.3	[0.2, 0.6]	26.9
Gorilla[d]		3 (13)	0.1 (0.2)	0.1	0.3	[0.1, 1.6]	94.5
Chimpanzee		20 (55)	0.3 (1.0)	0.1	0.2	[0.1, 0.3]	28.3
Savanna	47						
Ape		0 (0)	0 (0)	NA	NA	NA	NA
Gorilla		0 (0)	0 (0)	NA	NA	NA	NA
Chimpanzee		0 (0)	0 (0)	NA	NA	NA	NA
Terra firma	51						
Ape		39 (118)	0.8 (2.3)	0.7	2.3	[1.1, 5.1]	40.0
Gorilla[d]		32 (99)	0.6 (1.9)	0.6	1.9	[0.8, 4.2]	40.8
Chimpanzee[d]		7 (19)	0.1 (0.4)	0.1	0.1	[0.0, 0.1]	40.8
Total[e]	234						
Ape[f]		341 (1205)	1.9 (7.0)	0.72	3.63	[2.0, 6.2]	
Gorilla		144 (719)	0.8 (4.1)	0.42	2.91	[1.6, 5.6]	
Chimpanzee		197 (486)	1.2 (2.9)	0.31	0.70	[0.4, 1.3]	

[a]Density (ind's km^{-2}) = density (groups km^{-2}) × average number of nests per site (using only fresh and recent nests for the calculations).
[b]CV = coefficient of variation.
[c]The hazard-rate + cosine model best fit the data with the lowest Akaike's Information Criterion (AIC) value (614.66), giving a group density estimate of 1.0 groups km^{-2} and an individual density of 8.2 weaned gorillas per km^{-2}. However, because of the increased coefficient of variation (CV) associated with the hazard-rate cosine model and the fact that the other 3 candidate models provided similar group density estimates (0.5–0.7 groups per km^{-2}), we report the next best model and the more conservative density estimate of the uniform + cosine model (AIC: 620.43).
[d]Buckland *et al.* (2001) recommend a minimum of 40 observations to perform density estimations with DISTANCE. The small number of groups that we observed led to reduced precision and a large coefficient of variation (CV).
[e]We calculated total encounter rate (groups and individuals per km) and total density as: (abundance or density per habitat × area of habitat type)/total area of reserve.
[f]The estimates of mean ape densities for the reserve also take into account savanna habitat, despite the fact that we saw no apes in savanna.

rank-sum test). We estimated a density of 12.2 weaned gorillas per km^2 during the high-water season and a density of 2.0 weaned gorillas per km^2 during the low-water season. Using the area of the *terra firma* forest (437 km^2), we obtained abundance estimates of 5327 weaned gorillas in this habitat type during the high-water season and 887 weaned gorillas during the low-water season.

Table III. Estimates of the number of weaned individuals by habitat [95% CI] and for the entire reserve

Habitat type	Area (km^2)	Ape	Gorilla	Chimpanzee
Swamp forest	2244	15,124 [8505, 26,883]	12,050 [6620, 21,946]	2962 [1616, 5386]
Seasonally flooded forest	1164	372 [198, 698]	349 [67, 1816]	210 [116, 384]
Savanna	706	0 [0]	0 [0]	0 [0]
Terra firma forest	437	1018 [468, 2224]	822 [367, 1835]	17 [9, 44]
Total	4551	16,514 [9171, 28,049]	13,221 [7054, 25,597]	3,189 [1741, 5814]

Note. The number of apes is not equal to the number of gorillas + number of chimpanzees for each habitat. Observation of nest sites for gorillas, chimpanzees, and apes (gorillas + chimpanzees) produce different distributions of nest sites with distance from the transect. Thus, the detection functions fitted to the data by DISTANCE have different parameters and result in different estimates of density. We estimated ape, gorilla, and chimpanzee numbers by multiplying the density estimate for each category by the area of the habitat type.

Gorilla nest site encounter rates are greater in the northern sector of the *terra firma* than the southern sector (high-water season: $Z = -4.02$, $P < 0.01$; low-water season: $Z = -3.28$, $P = <0.01$, Wilcoxon rank-sum test) for both seasons. The majority of nest sites (94–97%) and nests (96–98%) were in the northern sector during both seasons. The density of gorillas in the northern sector was *ca.* 5.2 groups km^{-2} and 20.6 individuals km^{-2} (95% CI = [9.1, 46.5], CV = 40.1%) in the high-water season and 0.9 groups km^{-2} and 2.8 individuals km^{-2} (95% CI = [1.1, 7.1], CV = 44.3%) in the low-water season. We did not make enough observations of gorilla nest sites in the southern sector in either season to calculate reliable density estimates.

In addition to a north-south divide in gorilla abundance and density, nest sites were patchily distributed, with many nest sites being counted on some transects and none being counted on others. Transects with many nest sites commonly cut through thick patches of Marantaceae. There is a strong correlation between the presence and abundance of nest groups on transects during the high- and low-water seasons ($r = 0.96$, N = 24, $P < 0.01$).

Table IV. Encounter rate of ape nest groups and (individual nests) per km of transect walked in *terra firma* forest by season

	High-water season			Low-water season		
Terra firma forest	Gorilla	Chimpanzee	Ape	Gorilla	Chimpanzee	Ape
Southern sector	0.2 (0.9)	0.1 (0.2)	0.4 (1.3)	0.1 (0.2)	0.0 (0.0)	0.1 (0.2)
Northern sector	5.7 (22.2)	1.2 (1.9)	6.9 (24.3)	1.2 (3.6)	0.2 (0.4)	1.3 (4.1)
Total	3.2 (12.4)	0.7 (1.1)	3.9 (13.8)	0.7 (2.0)	0.1 (0.2)	0.8 (2.3)

Table V. Density of apes in *terra firma* forest during the high-water and low-water seasons

Apes	N (groups)	N (nests)	Density (groups/km^2)	Density (ind's/km^2)[a]	95% CI (ind's/km^2)	CV
High-water season						
Ape	180	657	3.1	10.8	[5.3, 24.1]	35.6
Gorilla	146	570	3.1	12.2	[5.5, 26.9]	39.9
Chimpanzee[b]	34	87	0.3	0.4	[0.2, 0.9]	40.0
Low-water season						
Ape	35	105	0.6	2.0	[0.9, 4.4]	40.1
Gorilla	31	94	0.6	2.0	[0.9, 4.7]	42.8
Chimpanzee[b]	4	11	0.1	0.1	[0.0, 0.4]	54.3

[a]Density (ind's km^{-2}) = Density (groups km^{-2}) × average number of nests per site (using only fresh and recent nests for the calculations). Average number of ape nests/group during the high-water season = 3.5; average number of gorilla nests/group = 4.0; average number of chimpanzee nests/group = 1.5. Average number of ape nests/group during the low-water season = 3.2; average number of gorilla nests/group = 3.3; average number of chimpanzee nests/group = 2.8.
[b]The small number of chimpanzee groups led to reduced precision and a large coefficient of variation (CV).

Transects with many nest sites during the high-water season tended to have a relatively high number of nest sites during the low-water season.

Chimpanzee Survey

The 87 chimpanzee nests in *terra firma* mixed forest during the high-water season were in 34 nest sites, with a mean of 1.5 nests per group (range = 1–8). By contrast, in the low-water season, there were only 11 chimpanzee nests in 4 nest sites, with a mean of 2.8 nests per site (range = 1–3). Like gorilla nest sites, chimpanzee encounter rates are significantly greater during the high-water than the low-water season ($Z = 2.20, P = 0.01$, one-tailed Wilcoxon rank-sum test).

We estimated a density of 0.4 weaned chimpanzees per km^2 in the high-water season and 0.1 weaned chimpanzees per km^2 in the low-water season (Table V). We obtained an abundance estimate of 179 weaned chimpanzees and 52 weaned chimpanzees in this habitat type for each season. There is a significantly greater abundance of chimpanzee nest sites in the northern sector than the southern sector during the low-water season ($Z = -2.27, P = 0.02$ Wilcoxon rank-sum test) and a marginally significant abundance in the high-water season ($Z = -1.93$, $P = 0.05$, Wilcoxon rank-sum test).

Nest Characteristics in Different Habitats

Gorilla nest types varied according to habitat (Fig. 2). The majority of gorilla nests in swamp forest and seasonally flooded forest were tree

Table VI. Results of generalized linear models examining the contribution of habitat and human indices to ape nest abundance

Model	Explanatory variables	df	Residual deviance	Deviance ($\Phi = 1$)	Deviance ($\Phi > 1$)	*P*
(A) All habitats						
1	Null	74	3490.5			
2	Hab	71	2006.5	1484.0	35.54	<0.01
3	Hab + Humin	70	1884.6	121.9	2.84	0.09
4	Hab + Humind + Distvill	64	1616.5	268.2	7.74	0.25
(B) Swamp forest and terra firma *forest*						
1	Null	44	2379.5			
2	Hab	43	1911.1	468.4	7.14	0.01
3	Hab + Humin	42	1800.5	110.6	1.64	0.20
4	Hab + Humind + Distvill	36	1498.5	301.9	5.58	0.47
Covariate	Coefficient.	SE	*t*	*P*		
(A)						
Intercept	−4.38	0.20	−21.93	<0.01		
Seasonally flooded forest	−2.63	0.94	−2.78	0.01		
Terra firma forest	−0.17	0.63	−2.71	0.01		
Savanna	−10.60	33.08	−0.32	0.75		
(B)						
Intercept	−4.38	0.25	−17.50	<0.01		
Terra firma forest	−0.854	0.40	−2.159	0.04		

Note. (A) The null model includes only the intercept term. Explanatory variables include habitat (Hab), number of human indices (Humind), and distance to nearest village (Distvill). We used difference in deviance tests scaled by the overdispersion parameter for each model to determine which explanatory variables to include in the final model. (B) We adjusted the covariate standard errors by the overdispersion parameters to determine the significance of each covariate to ape nest abundance (model A: $\Phi_A = 34.659$; model B: $\Phi_B = 65.56$). Test of the hypothesis that a coefficient differs significantly from 0 provided by *t* value (coefficient/standard error) in column 4. Model (A) includes all transects conducted in the low-water season; whereas model (B) includes only transects in swamp forest and *terra firma* forest in the low-water season.

nests; whereas nearly all nests on *terra firma* were constructed of herbaceous material near the ground (Table I). The average height of tree nests is 7.1 m ($SD = 4.35$, N = 386, range = 0.75–20 m) and 5.2 m ($SD = 4.65$, N = 5, range = 2–6 m) for the swamp forest and seasonally flooded forest. Of the nest sites that contained herbaceous nests in the swamp forest, 75% also had tree nests. The average height of these tree nests is 7.3 m ($SD = 4.28$, N = 235, range = 1.05–20 m).

Gorilla nest sites in *terra firma* forest rarely contained tree nests. The majority of gorilla nests in the high-water season were herbaceous (91%), with only 7% of nests in trees, 1% woody, and 1% of mixed construction. During the low-water season, nest sites included 96% herbaceous nests, 1%

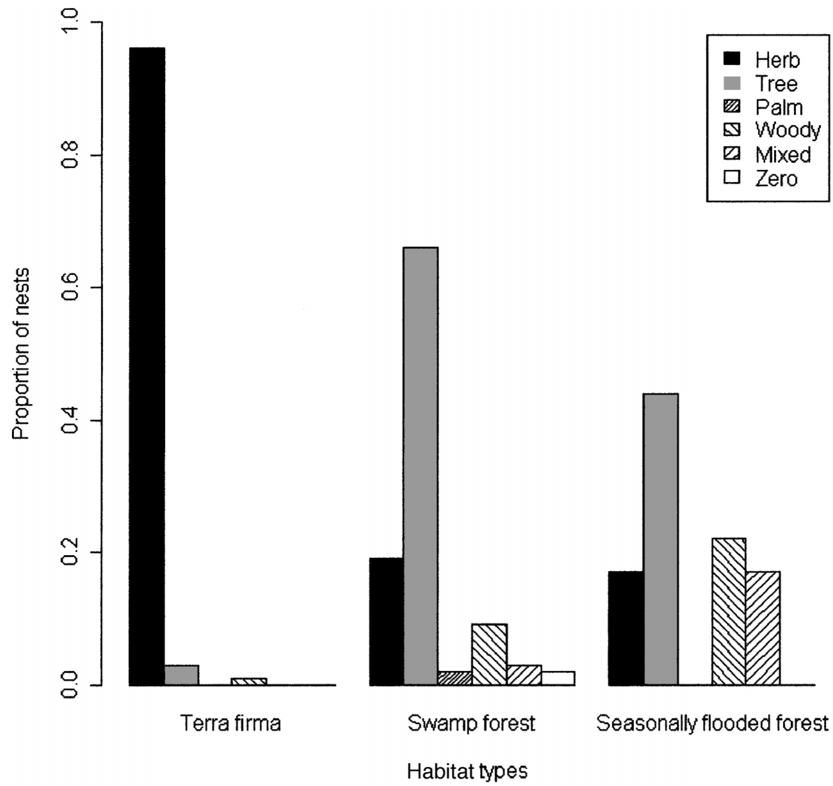

Fig. 2. The proportion of gorilla nests of each nest type by habitat.

tree nests, 2% woody nests, and 1% of mixed construction. Most nests were built near the ground with an average height of 1.0 and 1.2 m during the high- and low-water seasons.

Chimpanzee nests in swamp forest have an average height of 9.3 m ($SD = 6.21$, N = 329, range = 1.2–50 m); and the average height of nests in seasonally flooded forest is 18.9 m ($SD = 9.07$, N = 55, range = 3–42 m). The average heights of chimpanzee nests in mixed forest on *terra firma* are 12.5 m ($SD = 8.68$, N = 79, range = 3–30) and 10.7 m ($SD = 2.10$, N = 15, range = 7–15) in the high- and low-water seasons, respectively.

Nest Abundance Relative to Habitat and Human Presence

The encounter rates of gorilla nest sites in the swamp forest and *terra firma* forest are not correlated with human sign per transect (swamp forest:

$r = -17.9$, N = 19, $P = 0.46$; *terra firma* $r = -19.9$, N = 26, $P = 0.31$). Similarly, the encounter rate of chimpanzee nest sites in the swamp forest is not correlated with human sign per transect ($r = -19.1$, N = 19, $P = 0.43$). Even though the chimpanzees and gorillas demonstrated much higher densities in the northern sector of the *terra firma* forest than the southern sector, human indices for the high- and low-water seasons are independent of sector ($X^2 = 0.124$, df = 1, $P = 0.73$).

When we fitted the generalized linear model with explanatory variables of habitat (3-factor), number of human indices, and distance of transect from nearest village (6-factor) to the abundance of ape nests, human indices and distance to nearest village were nonsignificant (X^2 test of change in deviance). The final fitted model only included the effects of habitat (Table VI). The residual deviance of the model is 2006.5 with 71 degrees of freedom. The estimated coefficients in the final model are −0.17 for *terra firma* forest, −2.63 for seasonally flooded forest, and −10.60 for savanna. The coefficients indicate that relative to swamp forest, where the coefficient is set at zero, the number of ape nests decreased in all other habitats.

Because few nest sites were in seasonally flooded forest and savanna, generalized linear models were built excluding transects from these habitats. Only habitat remained as a significant explanatory variable for ape nest abundance in the final model (Table VI). The residual deviance of the model is 1911.1 with 43 degrees of freedom. The coefficients demonstrate that *terra* firma forest has fewer ape nests relative to swamp forest.

DISCUSSION

Gorilla and Chimpanzee Densities

The Lac Télé Community Reserve contains high densities of gorillas relative to other sites in central Africa; whereas estimates of chimpanzee densities from other sites are similar to those that we report (Table VII). Gorillas and chimpanzees occurred in all forest habitats, but each species had the highest density in swamp forest. This study may overestimate chimpanzee density because gorilla tree nests can often be mistaken for chimpanzee nests. Even so, the density of chimpanzees is 30% higher in swamp forest than *terra firma* forest; a difference slightly greater than the 26% error rate in nest identification documented by Tutin *et al.* (1995). Thus, in the Lac Télé Community Reserve, both gorilla and chimpanzee densities are high in swamp forest compared to other habitats.

The high density of Lac Télé gorillas may be explained by the permanently high abundance of non-fruit food plants typical of swamp forests.

Table VII. Density estimates of western gorillas and chimpanzees based on nest counts across Central Africa

Location	General habitat	Weaned individuals km^{-2}	Source
Gorilla			
Equatorial Guinea	*Terra firma* forest	NA (0.58–0.86)[a]	Jones and Sabater-Pi (1971)
Gabon	*Terra firma* forest	0.18 (0.008–0.44)[a]	Tutin and Fernandez (1984)
Lopé Reserve, Gabon	*Terra firma* forest	NA (0.3–1.0)[a]	White (1994)
Petit Loango Reserve, Gabon	*Terra firma* forest	0.21 (0.21–0.64)[a]	Furuichi *et al.* (1997)
Dja Reserve, Cameroon	*Terra firma* forest	1.71 (1.02–2.86)[b]	Williamson and Usongo (1996)
Dzanga-Ndoki, CAR	*Terra firma* forest	NA (0.89–1.45)[a]	Carroll (1988)
Dzanga-Ndoki, CAR	*Terra firma* forest	1.6 (1.1–2.0)[a]	Fay (1989)
Dzanga-Ndoki, CAR	*Terra firma* forest	1.63 (1.18–2.14)[b]	Blom *et al.* (2001)
Ngotto Forest, CAR	*Terra firma* forest	0.30 (0.17–0.52)[b] 0.40 (0.23–0.69)[b]	Brugiere and Sakom (2001)
Dzanga-Sangha, CAR	*Terra firma* forest	1.52 (0.84–1.96)[a]	Remis (2000)
Odzala National Park, Congo	*Terra firma* forest	5.40 (1.10–11.3)[a]	Bermejo (1999)
Northern Congo	Swamp forest	0.04 (0.01–1.2)[a]	Fay and Agnagna (1992)
Likouala Region, Congo	Swamp forest	NA (0–5.88)[a]	Blake *et al.* (1993)
Lac Télé Community Reserve, Congo	Swamp forest	3.4 (0.3–5.8)[a]	This study (savanna excluded)
		2.9 (0–5.4) [a]	This study (all habitats)
Chimpanzee			
Budongo Forest, Uganda	*Terra firma* forest	NA (0.8–1.6)[a]	Plumptre and Reynolds (1996)
Kibale National Park, Uganda	*Terra firma* forest	NA (0.82–4.81)[a]	Balcomb *et al.* (2000)
Gabon	*Terra firma* forest	0.49 (0–1.78)[a]	Tutin and Fernandez (1984)
Lopé Reserve, Gabon	*Terra firma* forest	NA (0.32–0.70)[a]	White (1994)
Petit Loango Reserve, Gabon	*Terra firma* forest	0.78 (0.65–0.94)[a]	Furuichi *et al.* (1997)
Dja Reserve, Cameroon	*Terra firma* forest	0.79 (0.60–1.04)[b]	Williamson and Usongo (1996)
Odzala National Park, Congo	*Terra firma* forest	2.2 (1.5–3.0)[a]	Bermejo (1999)
Lac Télé Community Reserve, Congo	Swamp forest	0.8 (0.1–1.3)[a]	This study (savanna excluded)
		0.7 (0–1.3) [a]	This study (all habitats)

Note. We provide 2 density estimates for comparison with those from other studies. Most studies do not include habitats where apes are absent in the density estimation for a site. Here we provide density estimates for the reserve that include and exclude savanna, where no apes was counted. Country names above have been abbreviated: CAR – Central African Republic, Congo – Republic of Congo, Gabon – Republic of Gabon, Cameroon – Republic of Cameroon.
[a]Overall mean density (minimum and maximum mean density values for different habitats).
[b]95% confidence limits.

Although fruit is also an important food resource when it is available (Nishihara, 1995; Remis, 1997; Rogers and Williamson, 1987), highest gorilla densities in central Africa occur in habitats with abundant ground vegetation (Brugière and Sakom, 2001), which has led previous researchers to hypothesize that gorilla populations are regulated by the availability of herbaceous plants (Bermejo, 1999; Goldsmith, 1999; Remis *et al.*, 2001; Williamson *et al.*, 1990).

Our observations of feeding sign are primarily of stems of *Afromomum* in *terra firma* forest and of *Pandanus candelabrum* in the swamp forest. Likewise, previous research showed gorillas to feed extensively on *Pandanus candelabrum* and other plants common in the Likouala swamps; and the abundance of *Raphia* sp. was thought by Fay and Agnagna (1992) and Blake *et al.* (1993) to determine gorilla distribution and density. Swamp forest in the Dja Reserve, Cameroon, also contains abundant foods for gorillas (Williamson and Usongo, 1996). Thus gorillas appear to forage on species from several monocotyledonous families. Therefore, the hypothesis that the abundance of herbaceous vegetation (species of Marantaceae and Zingiberaceae) determines gorilla density should be broadened to include other forms of ground vegetation (Fay and Agnagna, 1992; Tutin and Fernandez, 1984).

A competing explanation for the high density of gorillas in swamp forest is refuge from hunters (Blake *et al.*, 1993). Kano and Asato (1994) reported that gorilla densities in northeastern Congo increased with distance from the nearest village. Similarly, the best predictor of ape distribution in Gabon is distance from the nearest major urban centers (Walsh *et al.*, 2003). As in many parts of Africa, gorillas are hunted for food and traditional medicine in the Lac Télé Community Reserve (Poulsen and Clark, 2002); however, gorilla nest abundance is not correlated with human sign. Neither the number of human indices per transect nor the distance from the transect to the nearest village accounts for variation in ape nest abundance in our generalized linear models. Given the low numbers of hunters in the reserve and the greater dependence upon fish as a protein source, the current level of hunting probably does not substantially influence gorilla populations or behavior.

The higher density of chimpanzees in swamp forest than other forest habitats is difficult to explain without a greater knowledge of fruiting patterns and fruit abundance in each of the habitats. Three species of *Uapaca* are among the dominant tree species in the swamp forest of the Lac Télé Community Reserve. In the Dja Reserve, Cameroon, chimpanzees frequently consumed the succulent fruits of *Uapaca*, with 40% of their fecal clumps containing intact seeds (Poulsen *et al.*, 2001). *Uapaca guineensis* is also listed by Tutin and Fernandez (1993) as an important food in the diets of chimpanzees at Lopé Reserve, Gabon. Thus, swamp forest may provide adequate fruit resources for chimpanzees, particularly given their dietary flexibility. More detailed research is necessary to determine why densities of chimpanzees were 30% greater in swamp forest than in other habitats.

Distribution and Fluctuation of Ape Populations in *Terra Firma* Forest

Ape populations in *terra firma* forest were not evenly distributed. Gorillas, in particular, showed extremely clumped distributions, probably due to microhabitat differences. Transects with the highest abundance of gorilla nest sites in the northern sector of the *terra firma* crossed vast thickets of *Marantaceae*. *Marantaceae* forest is known to be attractive for gorillas that range in search of herbaceous plant food (Fay and Agnagna, 1992; Nishihara, 1995; Rogers and Williamson, 1987; White, 1994). Thus a large part of the variance in distribution of gorilla nest sites may be due to the presence or absence of these thickets.

Gorilla and chimpanzee densities changed significantly in *terra firma* forest, with greater numbers of apes during the high-water season compared to the low-water season. Our results suggest a gorilla density 6 times higher and a chimpanzee density 3.4 times higher in the high-water season than the low-water season. Therefore, *ca.* 4400 gorillas and 130 chimpanzees leave the *terra firma* in the low-water season, presumably moving into the surrounding swamp forest.

We propose two possible explanations for the changes in ape densities between the 2 seasons. First, gorillas and chimpanzees may move onto *terra firma* during the high-water season because mobility is restricted when the forest is flooded. However, Blake *et al.* (1993) found high densities of gorilla nests in an area 15 km from isolated islands of *terra firma* and concluded that gorillas are capable of living in flooded swamps without needing to retreat to *terra firma* forest. Thus, it may be that when *terra firma* is in close proximity, gorillas prefer to use it for nesting during flooded seasons. Conversely, although phenological studies have not been conducted in the Lac Télé Community Reserve, fruit was clearly more abundant on the *terra firma* during the high-water season, whereas the low-water season corresponded with the flowering season (Poulsen personal observation). Gorillas and chimpanzees may move into the *terra firma* forest in the high-water season because fruit is more abundant than in the swamp forest.

While swamp forest appears to support large populations of gorillas and chimpanzees, the seasonal movements by apes onto *terra firma* forest underscores the importance of both swamp forest and *terra firma* forest types. This raises the question of whether swamp forest alone can support a high number of gorillas and chimpanzees, or if it is the combination of swamp forest and *terra firma* habitats that allows ape populations to occur at high densities in swamp forest. Further research on the ecology and movements of apes in swamp forest is necessary to determine the reason for seasonal fluctuations in ape density and the relative importance of each habitat for gorillas and chimpanzees.

Conservation and Management Implications

Of significance for the management of apes in the Lac Télé Community Reserve, we document the seasonal concentration of a large number of apes in the *terra firma* forest. The high abundance of gorillas and chimpanzees in a relatively small area makes these populations vulnerable to hunting, particularly because over 90% of these apes are found on the northern sector of this habitat island. Focusing law enforcement efforts on this area during three or four months of the year could result in the protection of over 5000 gorillas and nearly 200 chimpanzees.

Of more widespread application for conservation is our finding that swamp forests can support a large number of apes, suggesting that it may be a promising habitat for the conservation of gorillas and chimpanzees. Swamp forests are extensive in the Congo Basin, with estimates of 60,000 km^2 of permanent swamps and 400,000 km^2 of seasonally inundated swamps (Sayer *et al.*, 1992). Over 80,000 km^2 of the Congo River floodplain is permanently or seasonally flooded. In addition, these forests may be particularly valuable for conservation because they often support biologically distinct communities, but are difficult to exploit for timber and generally have lower value for commercial logging (Frumhoff and Losos, 2001). Flooded on a seasonal basis and carpeted with mud and knee-high stilt roots year-round, swamp forests present a real obstacle for hunters, and support less agriculture and settlement than *terra firma* forests (Poulsen and Clark, 2002). Although current human pressure in swamp forests is low, this could change as access to them is improved and as populations of bushmeat species, including gorillas and chimpanzees, decline in more accessible habitats. To accurately assess the status of gorillas and chimpanzees in Central Africa, more survey data is needed, particularly outside of parks and reserves where apes face the largest threats to their existence.

ACKNOWLEDGMENTS

We are grateful to the Republic of Congo, in particular the Ministry of Forestry Economy and the Department of Protected Areas, for their support of our work in the Lac Télé Community Reserve. The US Fish and Wildlife Service Great Ape Fund and the Wildlife Conservation Society generously provided financial support for this research. We sincerely thank the people from reserve villages for welcoming us into their localities, access to their forests, and for their help as guides. For dedicated and skillful work in the forest, we acknowledge G. Malanda, F. Iyenguet, B. Modzoke, and F. Ntalassani. B. Curran and J. Mokoko provided logistical and administrative support for this research. Special thanks to S. Strindberg for advice on the survey design, and to C. Chapman, B. Bolker, T. Gillespie, N. Seavy, and 3 anonymous reviewers for their contributions to the manuscript.

REFERENCES

Agresti, A. (1996). *An Introduction to Categorical Data Analysis*, Wiley, New York.

Balcomb, S. R., Chapman, C. A., and Wrangham, R. W. (2000). Relationship between Chimpanzee (*Pan troglodytes*) density and large, fleshy-fruit tree density: Conservation implications. *Am. J. Primatol.* 51: 197–203.

Bermejo, M. (1999). Status and conservation of primates in Odzala National Park, Republic of Congo. *Oryx* 33(4): 323–331.

Blake, S., Rogers E., Fay, J. M., Ngangoué, M., and Ebéké, G. (1993). Swamp gorillas in northern Congo. *Afr. J. Ecol.* 33: 285–290.

Blom, A., Almasi, A., Heitkönig, I. M. A., Kpanou, J.-B., and Prins, H. H. T. (2001). A survey of the apes in the Dzanga-Ndoki National Park, Central African Republic: A comparison between the census survey method of estimating the gorilla (*Gorilla gorilla gorilla*) and chimpanzee (*Pan troglodytes*) nest group density. *Afr. J. Ecol.* 39: 98–105.

Brugiere, D., and Sakom, D. (2001). Population density and nesting behaviour of lowland gorillas (*Gorilla gorilla gorilla*) in the Ngotto forest, Central African Republic. *J. Zool.* 255: 251–259.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., and Thomas, L. (2001). *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*, Oxford University Press, Oxford, UK.

Carroll, R. W. (1988). Relative density, range extension and conservation potential of the lowland gorilla *Gorilla gorilla gorilla* in the Dzanga-Sangha region of southwestern Central African Republic. *Mammalia* 52: 309–323.

Chapman, C. A., Gautier-Hion, A., Oates, J. F., and Onderdonk, D. A. (1999). African primate communities: Determinants of structure and threats to survival. In Fleagle, J.G., Janson, C., and Reed, K.E. (eds.), *Primate Communities*, Cambridge University Press, Cambridge, UK, pp. 1–37.

Connor, E. F., Hosfield, E., Meeter, D. A., and Niu, X. (1997). Tests for aggregation and size-based sample-unit selection when sample units vary in size. *Ecology* 78: 1238–1249.

Fay, J. M. (1989). Partial completion of a census of the western lowland gorillas in southwestern Central African Republic. *Mammalia* 53: 203–215.

Fay, J. M., and Agnagna, M. (1992). Census of gorillas in the northern Republic of Congo. *Am. J. Primatol.* 27: 275–284.

Fay, J. M., Agnagna, M., Moore, J., and Oko, R. (1989). Gorillas (*Gorilla g. gorilla*) in the Likouala swamp forests of North Central Congo: Preliminary data on populations and ecology. *Int. J. Primatol.* 10: 477–486.

Frumhoff, P. C., and Losos, E. C. (2001). Where should natural forest management be promoted to conserve wildlife? In Fimbel, R.A., Grajal, A., and Robinson, J.G. (eds.), *The Cutting Edge*, Columbia University Press, New York, pp. 453–472.

Furuichi, T., Igagaki, H., and Angoue-Ovono, S. (1997). Population density of chimpanzees and gorillas in the Petit Loango Reserve, Gabon: Employing a new method to distinguish between nests of the two species. *Int. J. Primatol.* 18: 1029–1045.

Gautier-Hion, A. (1996). Statut des Populations de Primates au Sein du Bloc Forestier d'Afrique Centrale, Technical report to Projet ECOFAC, CEE DGVIII (AGRECO-CTFT).

Goldsmith, M. L. (1999). Ecological constraints on the foraging effort of western gorillas at Bai Hokou, Central African Republic. *Int. J. Primatol.* 20: 1–24.

Harcourt, A. H. (1996). Is the gorilla a threatened species? How should we judge? *Biol. Conserv.* 75, 165–176.

Heymans, J. C., and Oyo, P. (1999). Plan d'amenagement de la Réserve Communautaire du Lac Télé/Likouala-aux-Herbes. Technical report to the IUCN.

Jones, C., and Sabater-Pi, J. (1971). Comparative ecology of *Gorilla gorilla* (Savage and Wyman) and *Pan troglodytes* (Blumenbach) in Rio Muni, West Africa. *Bib. Primatol.* 13: 1–96.

Kano, T., and Asato, R. (1994). Hunting pressure on chimpanzees and gorillas in the Motaba River Area, northeastern Congo. *Afr. Study Monogr.* 15: 143–162.

Laake, T. L., Strindberg, S., Marques, F. F. C., Borchers, D. L., Buckland, S. T., Anderson, D. R., Burnham, K. P., Hedley, S. L., and Pollard, J. H. (2001). Distance 4.0. Beta 4. Research Unit for Wildlife Population Assessment, University of St. Andrews, Scotland, UK. http://www.ruwpa.st-and.ac.uk/distance/.

Lahm, S. A. (1993). *Ecology and Economics of Human/Wildlife Interactions in Gabon*, PhD Thesis, New York University.

McCullagh, P., and Nelder, J. A. (1989). *Generalized Linear Models*, 2nd edn., Chapman and Hall, London.

Nishihara, T. (1995). Feeding ecology of western lowland gorillas in the Nouabalé-Ndoki National Park, Congo. *Primates* 36(2): 151–168.

Oates, J. F. (1994). Africa's primates in 1992: Conservation issues and options. *Am. J. Primatol.* 34: 61–71.

Oates, J. F. (1996). Habitat alternation, hunting and the conservation of folivorous primates in African forests. *Aust. J. Ecol.* 21: 1–9.

Plumptre, A. J., and Reynolds, V. (1996). Censusing chimpanzees in the Budongo Forest, Uganda. *Int. J. Primatol.* 17: 85–99.

Poulsen, J. R., and Clark, C. J. (2002). Feasibility study report of the Lac Télé Community Reserve. Technical report to the Wildlife Conservation Society, New York.

Poulsen, J. R., Clark, C. J., and Smith, T. B. (2001). Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *J. Trop. Ecol.* 17: 787–808.

R Development Core Team. (2003). R: A language and environment for statistical computing, Vienna, Austria. http://www.R-project.org.

Remis, M. J. (1993). Nesting behaviour of lowland gorillas in the Dzanga-Sangha Reserve, Central African Republic: Implications for population estimates and understandings of group dynamics. *Tropics* 2: 245–255.

Remis, M. J. (1997). Western lowland gorillas as seasonal frugivores: Use of variable resources. *Am. J. Primatol.* 43: 87–109.

Remis, M. J. (2000). Preliminary assessment of the impacts of human activities on gorillas *Gorilla gorilla gorilla* and other wildlife at Dzanga-Sangha Reserve, Central African Republic. *Oryx* 34(1): 56–65.

Remis, M. J., Dierenfeld, E. S., Mowry, C. B., and Carroll, R. W. (2001). Nutritional aspects of western lowland gorilla (*Gorilla gorilla gorilla*) diet during seasons of fruit scarcity at Bai Hokou, Central African Republic. *Int. J. Primatol.* 23: 231–250.

Rogers, M. E., and Williamson, E. A. (1987). Density of herbaceous plants eaten by gorillas in Gabon. *Biotropica* 19(3): 278–281.

Sayer, J. A., Harcourt, C. S., and Collins, N. M. (1992). *The Conservation Atlas of Tropical Forests. Africa*, Macmillan, London, UK.

Tutin, C. E. G., and Fernandez, M. (1984). Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. *Am. J. Primatol.* 6: 313–336.

Tutin, C. E. G., and Fernandez, M. (1993). Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. *Am. J. Primatol.* 30: 195–211.

Tutin, C. E. G., Parnell, R. J., White, L. J. T., and Fernandez, M. (1995). Nest building by lowland gorillas in the Lopé Reserve, Gabon: Environmental influences and implications for censusing. *Int. J. Primatol.* 16: 53–76.

Walsh, P. D., Abernathy, K. A., Bermejo, M., Beyers, R., De Wachter, P., Akou, M. E., Huijbregts, B., Mambounga, D. I., Toham, A. K., Kilbourn, A. M., Lahm, S. A. Latour, S., Maisels, F., Mbina, C., Milhindou, Y., Obiang, S. N., Effa, E. N., Starkey, M. P., Telfer, P., Thibault, M., Tutin, C. E. G., White, L. J. T., and Wilkie, D. S. (2003). Catastrophic ape decline in western equatorial Africa. *Nature* 1566: 1–3.

White, L. J. T. (1994). Biomass of rain forest mammals in the Lopé Reserve, Gabon. *J. Anim. Ecol.* 63: 499–512.

White, L. J. T., and Edwards, A. (2000). *Conservation Research in the African Rain Forests: A Technical Handbook*, Wildlife Conservation Society, New York, 444 pp.

Wilkie, D. S., Shaw, E., Rotberg, F., Morelli, G., and Auzel, P. (2000). Roads, development, and conservation in the Congo Basin. *Conserv. Biol.* 14: 1614–1622.

Williamson, E. A., Tutin, C. E. G., Rogers, M. E., and Fernandez, M. (1990). Composition of the diet of lowland gorillas at Lopé in Gabon. *Am. J. Primatol.* 21: 265–277.

Williamson, L., and Usongo, L. (1996). Survey of Gorillas *Gorilla gorilla* and Chimpanzees *Pan troglodytes in* the Reserve de Faune du Dja, Cameroun. *Afr. Primates* 2(2): 67–72.