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RESEARCH ARTICLE

Comparing Ape Densities and Habitats in Northern Congo: Surveys of Sympatric Gorillas and Chimpanzees in the Odzala and Ndoki Regions

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The conservation status of western lowland gorillas and central chimpanzees in western equatorial Africa remains largely speculative because many remote areas have never been surveyed and the impact of emergent diseases in the region has not been well documented. In this study, we compared ape densities and habitats in the Lokoué study area in Odzala National Park and the Goualougo Triangle in Nouabalé-Ndoki National Park in northern Republic of Congo. Both of these sites have long been considered strongholds for the conservation of chimpanzees and gorillas, but supposedly differ in vegetative composition and relative ape abundance. We compared habitats between these sites using conventional ground surveys and classified Landsat-7 ETM+ satellite images. We present density estimates via both standing-crop and marked-nest methods for the first time for sympatric apes of the Congo Basin. The marked-nest method was effective in depicting chimpanzee densities, but underestimated gorilla densities at both sites. Marked-nest surveys also revealed a dramatic decline in the ape population of Lokoué which coincided with a local Ebola epidemic. Normal baseline fluctuations in ape nest encounter rates during the repeated passages of marked-nest surveys were clearly distinguishable from a 80% decline in ape nest encounter rates at Lokoué. Our results showed that ape densities, habitat composition, and population dynamics differed between these populations in northern Congo. We emphasize the importance of intensifying monitoring efforts and further refinement of ape survey methods, as our results indicated that even the largest remaining ape populations in intact and protected forests are susceptible to sudden and dramatic declines. Am. J. Primatol. 70:1–13, 2008.

Key words: *Gorilla gorilla*; *Pan troglodytes*; ape density; remote sensing; conservation

INTRODUCTION

Western lowland gorillas (*Gorilla gorilla gorilla*) and central chimpanzees (*Pan troglodytes troglodytes*) live in sympatry across much of the Congo Basin of western equatorial Africa. Surveys across this region have yielded some of the highest [7.6 apes/km^2 in Odzala National Park; Bermejo, 1999] and lowest [<1 ape/km^2 at many sites in Gabon; Tutin & Fernandez, 1984] ape densities in the world. Such vast differences in ape abundance could be associated with the carrying capacities of diverse habitats, impacts of emergent diseases, degree of poaching pressure, human encroachment, or issues associated with the methodologies to survey ape populations. Despite significant survey effort in this region [A.P.E.S., 2007], it has proven problematic to evaluate the conservation status of gorillas and chimpanzees in the Congo Basin [Tutin et al., 2005].

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Efforts have been made to estimate the size of gorilla and chimpanzee populations based on available forest cover [Butynski, 2001; Teleki, 1989]. However, there is a wide range of habitat types within this region, which include monodominant evergreen forests, semi-deciduous forests, swamps, and savannas. In their nationwide ape surveys in Gabon, Tutin and Fernandez [1984] recognized 15 habitat types based on vegetative structure. Chimpanzee and gorilla densities differ in relation to the distribution and quality of habitats [Bermejo, 1999; Morgan et al., 2006; Poulsen & Clark, 2004; Tutin & Fernandez, 1984], but large-scale patterns of their relative abundance have not yet been determined. Furthermore, ape densities do not differ consistently relative to one another, which raises intriguing questions about niche partitioning with regard to ranging and resource utilization. It is also likely that other factors influence ape densities such as human encroachment, hunting pressure, and emergent diseases.

The high variability in reported ape densities may also be attributable to methodological issues, such as differences in survey techniques or low degrees of precision associated with density estimates. Most ape density estimates have been generated from ''standing-crop'' nest surveys, which involve recording the ape nests of all ages that are encountered on transects. These indirect ape traces are converted to absolute ape density estimates by conversion factors for nest creation and rate of decay. Chimpanzee nest creation rates are similar between sites [Morgan et al., 2006; Plumptre & Reynolds, 1997], but recent studies have shown variability in gorilla nest creation related to seasonal and climatic factors [Mehlman & Doran, 2002]. Ape nest decay rates are much less stable, with differences documented in relation to the species that constructed the nest, material used in nest construction, and climatic conditions [Tutin et al., 1995; Walsh & White, 2005]. To remove the nest decay rate conversion factor from the calculation of ape densities, the ''marked-nest'' method has been implemented to survey chimpanzee populations in East Africa [Hashimoto, 1995; Plumptre & Reynolds, 1996]. Application of the ''marked-nest'' method requires repeated surveys on the same transects to quantify the accumulation of new nests during discrete time intervals. In addition to yielding more precise ape density estimates, which are not dependent on nest decay rates, the marked-nest method also has the potential to detect trends in the ape population because surveys are repeated over time [Plumptre & Reynolds, 1996, 1997]. In light of recent reports of drastic ape declines due to human impact and disease epidemics in western equatorial Africa [Bermejo et al., 2006; Caillaud et al., 2006; Huijbregts et al., 2003; Walsh et al., 2003], survey and monitoring efforts are of particular importance to assess the status of ape populations in this region.

The Odzala National Park and Nouabalé-Ndoki National Park are both reputed to have relatively high ape densities [Bermejo, 1999; Morgan et al., 2006]. Although chimpanzee and gorilla densities have been estimated, these ape populations should be monitored because they are at high risk of Ebola hemorrhagic fever. Indeed, the Zaire strain of this virus (ZEBOV) has repeatedly emerged in the border region of Gabon and the Republic of Congo since 2000, causing hundreds of deaths in human and animal populations [Pourrut et al., 2005; Rouquet et al., 2005]. In the Lossi Sanctuary, which is adjacent to the southern border of Odzala National Park, it has been reported that at least 5,000 gorillas have succumbed to Ebola in 2002 and 2003 [Bermejo et al., 2006] and another 360 gorillas disappeared from Lokoué Bai, which is located in the National Park, in 2004 [Caillaud et al., 2006]. These studies indicate decline of up to 90% in ape populations. It had previously been assumed that ZEBOV outbreaks were independent events, but recent research has shown that this may be a single, spreading wildlife epizootic [Walsh et al., 2005]. Walsh et al. [2005] calculated a northeastern directional spread of 50 km/yr, which puts the apes of northern Congo at extremely high risk of ZEBOV in the present and near future. This information makes it an urgent priority to survey and monitor chimpanzee and gorillas in northern Congo.

In this study, we compare ape densities and habitat composition in the Goualougo Triangle and Lokoué study areas (200 km away from each other) in the Republic of Congo. Ape surveys were conducted before and during a ZEBOV outbreak in Odzala, and density estimates were calculated using both the standing-crop and marked-nest methods to assess their efficacy in depicting sympatric ape populations. We compare the results and applications of these methods to survey sympatric apes in this region. In addition, a combination of ground surveys and satellite imagery classification were used to consistently and rigorously compare habitats within these lowland forests. Calculating ape density estimates and examining factors shaping ape densities in northern Congo will not only improve our scientific understanding of chimpanzees and gorillas but also provide valuable insights for developing conservation strategies to preserve these apes.

METHODS

Study Sites

The Lokoué study site is located within the Odzala National Park (0.23′–1.10′N; 14.39′–15.11′E), Republic of Congo (Fig. 1). The study area encompasses 42 km^2 of lowland forest with altitudes ranging between 300 and 600 m. The climate can

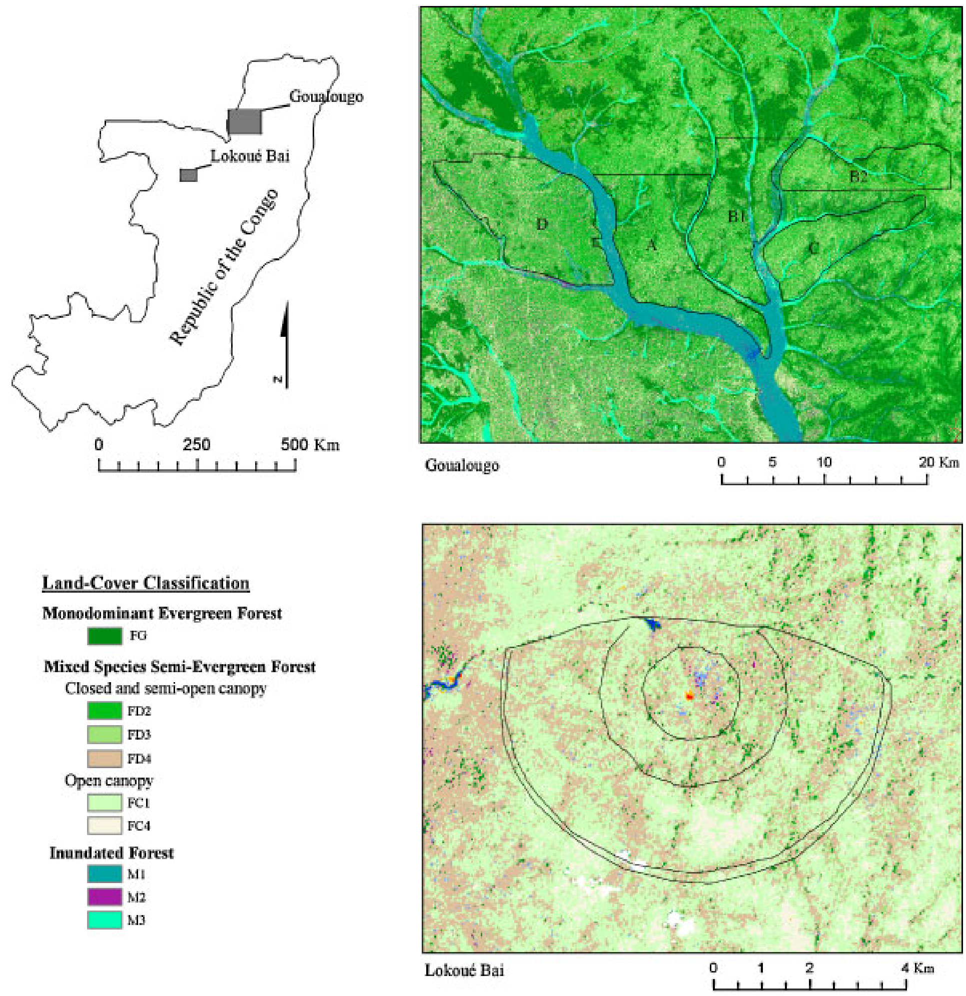

Fig. 1. Location of Lokoué Bai in Odzala National Park and the Goualougo Triangle in the Nouabalé-Ndoki National Park, Republic of Congo. The study areas are overlaid on a Landsat ETM+ satellite image (collected on 02.09.2001) displayed in bands 4,5,3 (RGB). The figure legend applies to both image classifications.

be described as transitional between the Congo-equatorial and sub-equatorial climatic zones [Harris, 2002]. Rainfall is bimodal with a main rainy season from August through November and a short rainy season in May. Total annual rainfall in 2002 was 1957 mm (recorded at Lokoué base camp) and average minimum and maximum temperatures ranged from 20.4 to 20.9°C and 31.3 to 31.5°C in 1994 and 1995 (Mboko database—about 40 km from Lokoué).

The Goualougo Triangle is located within the Nouabalé-Ndoki National Park (2.05′–3.03′N; 16.51′–16.56′E), Republic of Congo (Fig. 1). The study area covers 380 km^2 of lowland forest with altitudes, climate and bimodal rainfall patterns similar to Odzala's. Between 2000 and 2002, annual average rainfall was $1{,}728 \pm 47$ mm (recorded at Mbeli Bai base camp; 17 km from the study area; E. Stokes, unpublished data) and average minimum and maximum temperatures ranged from 21.1 to 21.9°C and 26.5 to 26.8°C, showing little seasonal variation.

Habitat Composition and Forest Structure

The lowland tropical forests of northern Congo are part of the regional center of endemism Guinea–Congolain that ranges from Nigeria to the Congo Basin [White, 1986]. The different habitat types relevant to our study sites are described below and related to the satellite imagery classifications depicted in Figure 1.

Monodominant *Gilbertiodendron dewevrei* forest (one type of the *Guinea–Congolain monodominant wet evergreen and semi-evergreen forest* described by White [1986]) is a single-species formation of *G. dewevrei* that has sparse or dense understorey. It occurs along watercourses as well as on interfluvial plateaus and has a relatively even canopy between 30 and 40 m in height. This corresponds to the FG satellite classification that represents monodominant evergreen forests, with greater than 90% canopy coverage.

Mixed-species forest (*Guinea–Congolain mixed wet semi-evergreen forest* [White, 1986]) occurs on *terra firma* and has high heterogeneity of species composition, canopy coverage, and understorey vegetation. This forest is semi-deciduous with a double or triple stratification of layers, which reaches heights of more than 40 m. The understorey may consist of herbs, shrubs, and diverse liana species. This corresponds to the Landsat image classifications of mixed-species semi-evergreen forest, with canopy coverage decreasing from 60 to 90% in the FD classes to less than 60% in FC classes.

Marantaceae forest (*Guinea–Congolain open forest with Marantaceae* [Devillers et al., 2002]) is a particular type of mixed-species forest, characterized by dense understorey vegetation dominated by the family *Marantaceae*. Trees are sparse and between 20 and 30 m in height, with emergents reaching up to 40 m high. There are few trees in the middle or understorey, which results in a generally open canopy. That is likely depicted in the FD4 and FC satellite habitat classifications. Subcategories based on density and height of the *Marantaceae* understorey and openness of the canopy were distinguished on ground surveys.

Gallery and Swamp forest (*Guinea–Congolain Marsh and Riverine forest* [White, 1986]) consists of diverse flora associated with watercourses. Canopy coverage varies. The ground layer may be inundated permanently or on a seasonal basis depending on geography and soil conditions. Forests of this type correspond to satellite classifications M1 and M3.

Study Design

Lokoué transect surveys

Three concentric circular transects were placed south of the Lokoué River at radial distances of 1, 2, and 4 km from the Lokoué Bai; totaling 29.5 km in length. An initial standing-crop nest survey and 14 subsequent marked-nest passages at monthly intervals were conducted on these transects. Total survey effort comprised 15 months.

Goualougo transect surveys

As described in previous publications, the Goualougo study area has been divided into zones for long-term monitoring [Morgan et al., 2006]. The automated survey design component of the custom DISTANCE software was used to generate systematically spaced line transects at 1.5 km intervals with a random start in each zone [Thomas et al., 2005], which totaled 30.5 km in Survey 1 and 25.3 km in Survey 2. Each independent survey consisted of an initial standing-crop nest survey and six marked-nest passages at 2-week intervals on the same transects. Total survey effort comprised 7 months.

Transect Data Collection

Standing-crop density estimates included all nests encountered during the first passage along transects. Nests encountered during subsequent passages were used in marked-nest density calculations. Each nest was ticketed (''marked'') so as not to be recounted on repeated passages. Specific data recorded for each nest included perpendicular distance, height, forest type, tree species, nest type [adopted from Tutin et al., 1995]. Nest sites were defined as all nests of the same age class within 50 m of one another.

We followed methods of Sanz et al. [2007] to distinguish between the nests of sympatric chimpanzees and gorillas. There were no certain chimpanzee nests in the Lokoué data set, so we used nests coded as possibly chimpanzee. Discriminant function analysis was calculated from fresh and recent nests for certain gorilla ($n = 122$) and possible chimpanzee ($n = 34$) nests. To verify the model, we tested its efficiency in classifying a sub-sample of nests with known builder that was not used to create the model. More than 90% of nests were correctly classified.

Data Analysis

Ape nest encounter rates

Encounter rates were calculated by dividing the number of nests encountered by the length of transects walked. The first passage of a new field season was excluded from average calculations of pre- and post-Ebola encounter rates.

Ape density estimation

Density estimates were calculated using DISTANCE analysis in which the probability of detecting a nest is modeled as a function of the observed distances which is combined with the nest encounter rate to calculate the density of nests in an area [Buckland et al., 2001; Thomas et al., 2005]. To ensure robust estimation of detection and consequently of the effective strip half-width, observations made at the furthest distances from the line were truncated [Buckland et al., 2001].

Nest surveys on the first passage were used to calculate standing-crop density estimates. Nest creation rates, identification of the ape species that created the nests, and nest decay rates are used to convert nest site density estimates to absolute chimpanzee or gorilla densities as follows:

$$\hat{D}_i = \frac{\hat{D}'_i}{\hat{r}_i \cdot \hat{t}_i} = \frac{\frac{1}{2} \cdot \frac{n'_i}{L} \cdot \hat{f}_i(0) \cdot \hat{E}(s_i)}{\hat{r}_i \cdot \hat{t}_i} \qquad (1)$$

where the subscript i is used to denote whether the estimate is for chimpanzees or gorilla, $\hat{D}'_i$ is the estimate of animal density, $\hat{D}'_i$ is the estimate of nest density, n'_i is the number of nest sites, L is the total length of the transect lines, $\hat{f}_i(0)$ corresponds to the probability density function of the perpendicular distances evaluated at zero, $\hat{E}(s_i)$ is the average nest site size, t_i is the length of time to nest decay (the reciprocal of decay rate), and r_i is the estimate of the nest creation rate.

Marked-nest density estimates were calculated following Plumptre and Reynolds [1996] and Hashimoto [1995]. The total number of days elapsed between marked-nest passages was substituted for the decay rate factor in the density equation. Therefore, in the density equation t_i is the elapsed time between the first and last survey of the marked-nest study.

To examine differences in study design and implications for data analysis, we pooled all data onto one side of the transect line and calculated separate detection functions for gorilla and chimpanzee nests. Comparison of the detection functions between the two sites showed that objects were well detected on the center-line and normally distributed with increasing distance from the survey line; hence, we proceeded with DISTANCE analysis. Several models of detection function were considered and selection was based on the lowest Akaike's Information Criteria [Buckland et al., 2001].

We examine the effect of different habitat types on nest encounter rates by comparing detection functions between habitats. As shown in Figure 2, the height and distance from the transect line differed between monodominant *Gilbertiodendron*, mixed-species, and *Marantaceae* forests.

As stated by Caillaud et al. [2006], an Ebola epidemic broke out at Lokoué study site in December 2003. To get a reasonable estimate of ape population density at Lokoué before the outbreak, we used only the first nine marked-nest counts (conducted before December 2003) in our calculation of density. The number of nests recorded in the last five walks (in the course of the epidemic) was not sufficient to yield density estimates hence we estimated ape population decline from encounter rates.

Nesting habitat selection

G tests [log-likelihood ratio; Sokal & Rohlf, 1995] were used to examine observed nesting patterns vs. habitat composition of the respective study sites.

Satellite imagery

Habitats were assessed using unsupervised classification of Landsat-7 ETM+ 2001-02-09 image using bands 3, 4, and 5 (Red, NIR, MIR). Each class was examined, labeled, and split further if necessary (combinations of bands 4 and 5 or bands 4, 5, and 7, another MIR band, often highly correlated to band 5, are used in areas seriously affected by haze); manual delineation was involved in splitting some classes. Classes were aggregated using the following: calculated separability based on bands 4 and 5; spectral plotting of bands 1–5 and 7, focusing mostly on bands 4, 5, and 7; visual interpretation of the RGB-543 and RGB-547 color composite images; contextual information. The resulting image was then filtered using a 4-pixel sieve filter. All clusters less than 4 pixels were combined into the largest nearest neighboring cluster.

RESULTS

Comparing Habitat Composition and Classifications

Although climate and altitude were very similar between the two study sites, satellite image classification and ground surveys clearly showed that habitat composition differed dramatically between the two sites (Fig. 3). Lokoué was dominated (97% of the study area by satellite imagery analysis) by mixed- species semi-evergreen forest, more than half of which was characterized by an open canopy (less than 60% canopy coverage). Ground surveys revealed that this consisted mostly of *Marantaceae* forest (62% of transects surveyed). Mixed species semi-evergreen forest was also the most common forest type in the Goualougo Triangle, accounting for 72% of the study area. In contrast to Lokoué, more than 90% of the forests at this site had 60–90% canopy coverage.

We found that forest types recorded on ground surveys and differentiated by canopy characteristics were readily depicted by habitat classification of satellite imagery, whereas those defined by understorey characteristics on ground surveys did not correspond as well because they were differentiated by canopy cover in Landsat images. Monodominant formations of *Gilbertiodendron* forest with >90% canopy coverage in the Goualougo study area were clearly differentiated by remote sensing (22% of the study area) and showed almost identical agreement with ground survey data of this forest type (23% of transects surveyed). Mixed-species forest with a closed canopy on transect surveys in Goualougo (36% of transects surveyed) was best represented by the FD2 satellite classification (38% of the study area), which represents mixed-species semi-evergreen forest with 60–90% canopy coverage. Our general definition of mixed-species forest with an open canopy (37% of transects surveyed in Goualougo) seemed to be represented by a combination of several gradations of mixed-species semi-evergreen forest (FD3, FD4, FC1) ranging from closed to open

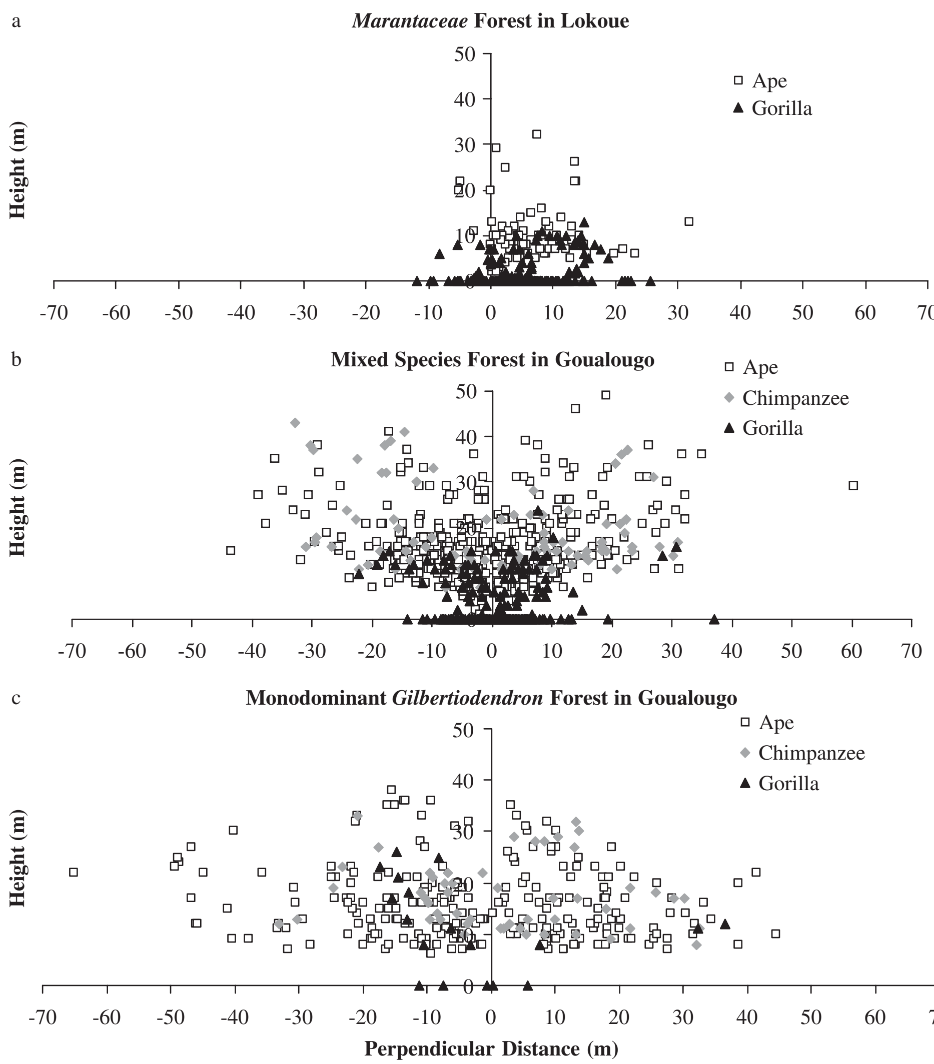

Fig. 2. Comparison of nests detected in different forest types of Goualougo and Lokoué. (**a**) shows that the shortest nest detection distances were documented in the *Marantaceae* forests of Lokoué, which are characterized by dense understorey vegetation. Nests were detected at greater heights and farther from transects in the mixed-species forests of Goualougo (**b**). Almost all nests located in monodominant *Gilbertiodendron* forest in Goualougo (**c**) were located in the forest canopy. The average greatest nest detection distances were found in the monodominant *Gilbertiodendron* forest of Goualougo (c). Differences in nest detection are likely related to the degree of visibility in these habitats and warrants against comparing nest encounter rates between sites where habitats may differ.

canopy, totaling 34% of this study area. Satellite imagery classification showed that inundated forest (M1, M3) totaled 7% of the Goualougo study area, which closely corresponded with our swamp forest classification on 5% of transect surveys.

The Lokoué study site is characterized as having a relatively open canopy, and during ground surveys we differentiated several types of *Marantaceae* forest based on understorey vegetation. This information was insightful when interpreting satellite imagery that provides little if any information on habitat characteristics beneath the canopy. Satellite imagery depicted 50% of the Lokoué study area as mixed-species semi-evergreen forest with less than 60% canopy cover (FC1). It is likely that this corresponds to our ground survey classification of *Marantaceae* forest with a low canopy which comprised 51% of the transects surveyed. The FC4 classification—described as mixed-species semi-evergreen forest with minimal or open canopy and *Marantaceae* understorey vegetation—represented 4% of the study area, and corresponds to our ground surveys of *Marantaceae* forest with an open canopy (recorded on 11% of transects). Mixed-species forest with a closed canopy was detected on 8% of transects surveyed, and corresponds to the combination of closed and semi-open satellite imagery classes of FD2 and FD3 (7% of the Lokoué study area). The FD4 classification of mixed-species semi-evergreen with 60–90% canopy cover, which comprised 36% of the

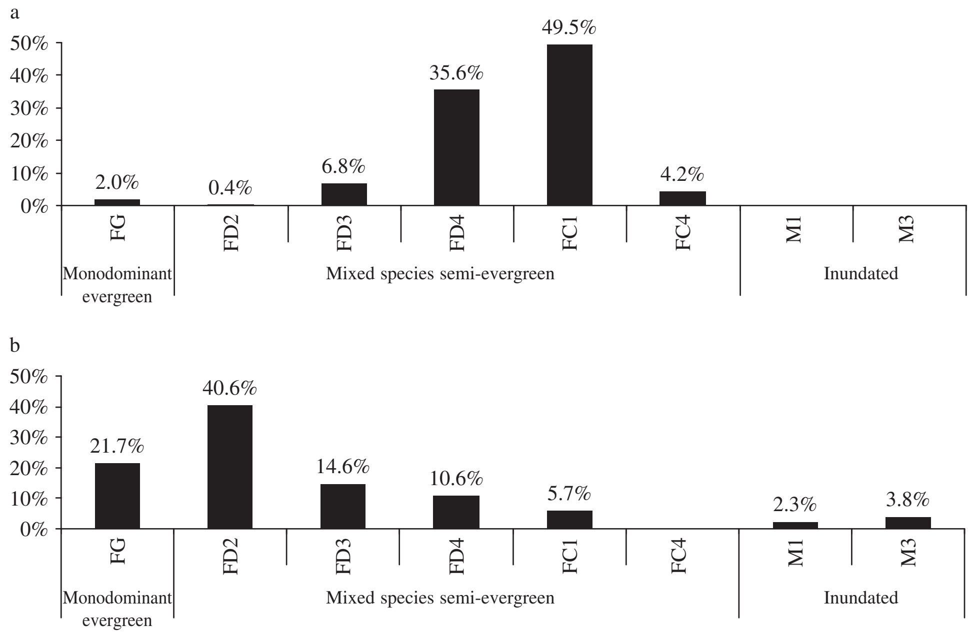

Fig. 3. Habitat composition as depicted by satellite imagery of Lokoué (**a**) and Goualougo (**b**). Habitat classification codes are standardized across western equatorial Africa by N. Laporte, with forests decreasing in canopy coverage from the FG to FC classes. The prevalence of FG (monodominant *Gilbertiodendron* forests with 90% coverage) and FD (mixed-species with 60–90% coverage) in Ndoki indicates that there is greater canopy coverage than Odzala which shows a higher prevalence of FD and FC forests that have <60% canopy coverage.

study area, is likely to correspond to our ground survey classification of *Marantaceae* forest with a closed canopy (23% of transects). Remote sensing indicated that 2% of the study area consisted of monodominant *Gilbertiodendron* forest, but this forest was not detected on transect surveys in Lokoué. Transects were concentrated around Lokoué Bai; hence, it is not surprising that 7% of the distance surveyed consisted of swamp or gallery forests, whereas satellite imagery indicated that less than 1% of the study area consisted of inundated forests.

Ape Abundance and Habitat Use

At Lokoué, 413 ape nests comprising 112 nest sites were encountered before the Ebola outbreak (November 2002–February 2003, June 2003–November 2003) and 64 nests comprising 22 nest sites during the outbreak (February 2004–June 2004). One thousand two hundred and fifty-four ape nests that comprised 439 nest sites were encountered on ape nest surveys in the Goualougo study area (August–December 2002, March–July 2003). Initial comparison of overall nest encounter rates on standing-crop surveys indicated that gorilla nest encounter rates were higher in Lokoué (standing crop: 5.5 gorilla nests/km; 1.0 chimpanzee nests/km) than Goualougo, where chimpanzee nests were much more frequently encountered on the initial transect passage (standing crop: 3.5 gorilla nests/km; 7.2 chimpanzee nests/km). In Figure 4, the opposite pattern is seen on the repeated passages of marked-nest surveys where gorilla nest encounter rates were higher during 2-week survey intervals in Goualougo (0.9 gorilla nests/km, 1.4 chimpanzee nests/km) than monthly surveys in Lokoué (0.7 gorilla nests/km, 0.2 chimpanzee nests/km). This difference can be partially attributed to differences in nest detection from transect line, which differ between forest types, as shown in Figure 2.

DISTANCE calculations of density estimates take into account the detection function of nests encountered on transects. In Table I, we compare density estimates from the standing-crop and marked-nest surveys. Although chimpanzee densities differed between sites, the results produced by the two survey methods were remarkably similar within Lokoué (standing crop: 0.33 chimpanzees/km^2, marked nest: 0.35 chimpanzees/km^2) and Goualougo (standing crop: 1.76 chimpanzees/km^2, marked nest: 1.75 chimpanzees/km^2). The chimpanzee density estimates from Lokoué are lower than previous reports of 2.2 chimpanzees/km^2 from the Odzala region [Bermejo, 1999], but results from Goualougo are similar to previous standing-crop estimates from the Goualougo site [Morgan et al., 2006]. The standing-crop surveys yielded higher gorilla density estimates in Lokoué (3.22 gorillas/km^2) than Goualougo (2.63 gorillas/km^2), whereas

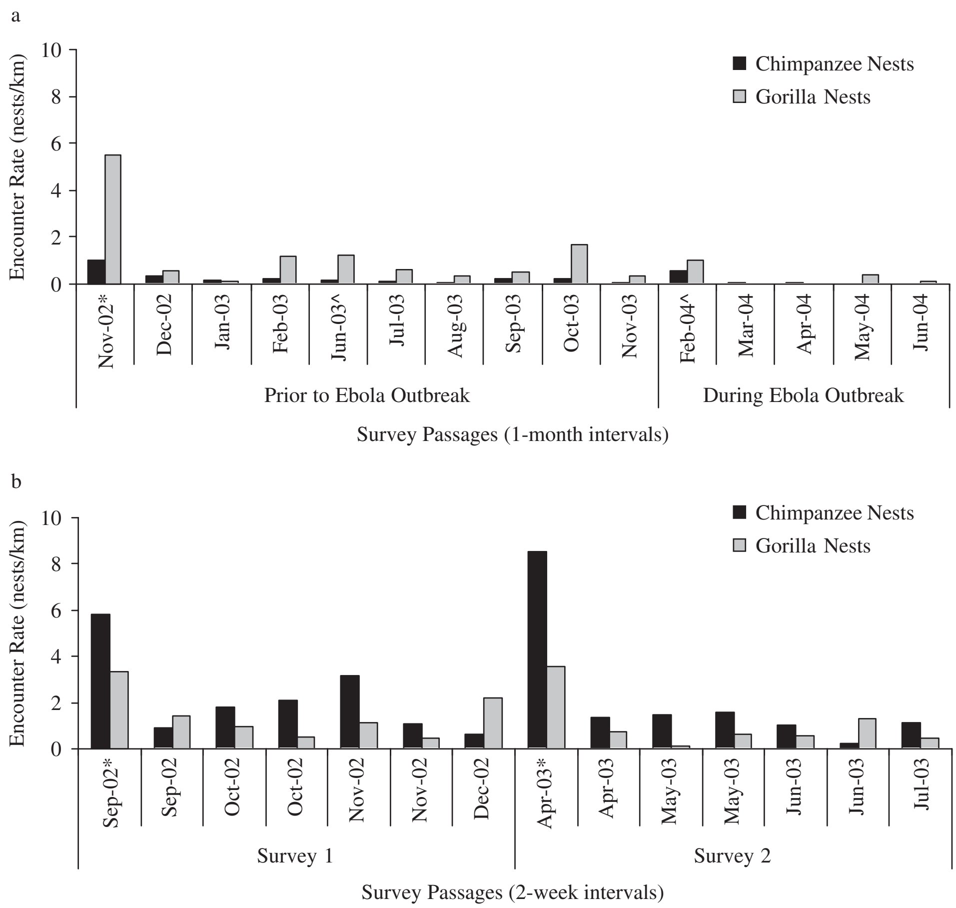

Fig. 4. Encounter rates of ape nests on standing crop and marked-nest passages in Lokoué (**a**) and Goualougo (**b**). Encounter rates are higher in standing crop surveys (*) because these involve inventories of nests of all ages, whereas marked-nest survey include only nests detected during passage intervals. Surveys conducted before Ebola are differentiated from those occurring during the Ebola outbreak in Lokoué. The first passage of a new field season (^) was excluded from average calculations of pre- and post-Ebola encounter rates. Two independent surveys are depicted for Goualougo, with no evident differences in nest encounter rates between these time periods.

TABLE I. Comparison of Gorilla and Chimpanzee Density Estimates in Lokoué and Goualougo Generated From Standing-crop and Marked-nest Count Analyses

Density estimate analysis	Density (indiv/km^2)	95% LCI[a] (indiv/km^2)	95% UCI[a] (indiv/km^2)	% CV[b]
Gorilla gorilla gorilla				
Lokoué, standing crop[c,d]	3.22[c]	1.61	6.44	34.7
Lokoué, marked nest[c,e]	1.37	0.35	5.29	42.6
Goualougo, standing crop[c,d]	2.63	1.42	4.90	31.6
Goualougo, marked nest[c,f]	1.70	0.88	3.29	33.3
Pan troglodytes troglodytes				
Lokoué, standing crop[g,h]	0.33	0.12	0.92	43.4
Lokoué, marked nest[e,g]	0.35	0.07	1.70	48.7
Goualougo, standing crop[g,h]	1.76	1.17	2.69	21.7
Goualougo marked nest[g,f]	1.75	1.12	2.75	22.4

[a]LCI, lower confidence interval; UCI, upper confidence interval.
[b]Coefficient of variation.
[c]Gorilla nest creation rate of 1.0.
[d]Nest decay rate of 90.0 days ($SE = 2.85$) from Goualougo.
[e]Number of days between the initial standing-crop passage in Lokoué and the final marked-nest survey passage before the Ebola outbreak, $n = 210$. This excludes the third passage, which was not completed.
[f]Number of days between the initial standing crop passage in Goualougo and the final marked-nest passage, $n = 90$.
[g]Chimpanzee nest creation rate of 1.09 ($SE = 0.05$).
[h]Nest decay rate of 90.0 days ($SE = 2.85$) from Goualougo.

the marked-nest estimates from Lokoué were lower (1.37 gorillas/km^2) than Goualougo (1.70 gorillas/km^2). The standing-crop results for Lokoué are more similar to pre-Ebola density estimates of 5.4 gorillas/km^2 reported from Odzala [Bermejo, 1999] than the marked-nest estimates, which seem to be underestimated for gorillas at both sites. The standing-crop and marked-nest surveys of gorillas from Goualougo were similar to previous reports from this site (2.52 gorillas/km^2; Morgan et al., 2006) and from Lac Tele (2.91 gorillas/km^2; Poulsen & Clark, 2004).

Chimpanzees and gorillas preferentially nested in particular habitat types at both sites. The distribution of gorilla and chimpanzee nests was significantly different than habitat composition in the two study areas (gorilla in Goualougo: $G = 451.5$, $df = 3$, $P < .01$/in Lokoué; $G = 547.9$, $df = 4$, $P < .01$; chimpanzee in Goualougo: $G = 363.7$, $df = 3$, $P < .01$/in Lokoué: $G = 14.4$, $df = 4$, $P < .01$). In the Goualougo study area, 81% of gorilla nests were located in mixed-species forest with an open canopy, which is typically characterized by dense understorey vegetation. In contrast, the majority of known chimpanzee nests were located in monodominant *Gilbertiodendron* forest (38%) and mixed-species forest with a closed canopy (42%). In the Lokoué study area, all gorilla nests were found in *Marantaceae* forest, with a preference for open canopy forests (54.8% of all nests). In contrast, chimpanzee nests were recorded in all types of forest but significantly more than expected by overall habitat representation in the area in both open and closed canopy *Marantaceae* forests.

Trend Detection

Different trends in ape population dynamics are clearly detected by repeat survey passages in the Goualougo and Lokoué study areas (Fig. 4). Nest encounter rates in Goualougo showed minor fluctuations from one passage to the next, but remained stable throughout the study period, which is in contrast to the sudden decline in encounter rate during the last four passages of the marked-nest study in Lokoué. As an indication of the magnitude of this decline, the nest encounter rates for ape signs during the first nine passages (0.67 ± 0.52 gorilla nests/km, 0.17 ± 0.10 chimpanzee nests/km) were 82% higher for gorillas and 85% higher for chimpanzees than those on the last four passages (0.12 ± 0.17 gorilla nests/km, 0.03 ± 0.03 chimpanzee nests/km).

DISCUSSION

Our results confirm that the Odzala and Ndoki forests supported some of the highest overall ape densities in this region previous to recent Ebola epidemics in northern Congo. We found significant ecological variation between these sites, which indicates that some areas can support higher ape densities in relation to habitat diversity, composition, and structure. Indeed, habitat composition between the two sites was dramatically different, with Lokoué predominantly consisting of *Marantaceae* forests with a semi-open canopy and Goualougo consisting mostly of mixed-species forest with a closed canopy. Gorilla densities in Lokoué were much higher than sympatric chimpanzee densities. In contrast, densities of the two species were similar in the Goualougo study area. The marked-nest method produced nearly identical results to standing-crop estimates of chimpanzees at each site, but seemingly underestimated gorilla densities. Continuous monitoring via marked-nest surveys at the two sites showed that ape populations in Odzala declined within the study period, whereas Ndoki ape populations were stable. Our results indicate that the conservation status of ape populations can dramatically change within relatively short time periods, which underscores the importance of survey and monitoring programs, particularly in zones at high risk for Ebola [Tutin et al., 2005].

Sympatric Apes and Their Habitats

Although we found that both the Odzala and Ndoki regions had relatively high ape densities, the relative abundance of the two ape species differed between these sites. Climatic factors were similar at Lokoué and Goualougo, but systematic comparison of satellite imagery showed that habitat composition and canopy coverage were very different. The majority of the Lokoué study area consists of *Marantaceae* forest, which represents a recolonization stage of peripheral savannas that occurs in Gabon, Republic of Congo, Cameroon, and equatorial Guinea. In contrast, the Goualougo study area comprised mixed-species forest and monodominant stands of *Gilbertiodendron* forest. Both sites contain a variety of forest clearings, but the density of salines and bais is higher in Odzala than Ndoki. Gorillas frequent these clearings to feed on aquatic vegetation, but chimpanzees have only rarely been observed to visit such clearings [Devos et al., 2002]. Surveys in Lokoué were conducted around a forest clearing, but this did not seem to result in elevated gorilla densities, which were lower in this study than previous surveys that had wider coverage [Bermejo, 1999].

Gorillas in western equatorial Africa are able to successfully exploit several types of habitat [Morgan et al., 2006; Poulsen & Clark, 2004; Tutin & Fernandez, 1984]. Gorilla densities in this study were highest in the *Marantaceae*-dominated habitat of Lokoué, but gorilla densities in Goualougo indicate that mixed-species forest is also a high-quality habitat for these apes. Our results show that both sites with very different types of mixed-species forest harbored substantial ape populations. However, more extensive surveys are needed to determine the distribution and abundance of gorillas throughout the region. Ape densities have been extrapolated across areas based on habitat, but future efforts should differentiate between the types of mixed-species forest (*Marantaceae* dominated, open canopy) that harbor higher ape densities than others (closed canopy). Furthermore, it is critical to incorporate the impacts of disease epidemics and poaching pressure into any models of ape distribution and abundance.

Although gorilla densities between the two sites were relatively similar, chimpanzee densities were much lower in Lokoué than the Goualougo Triangle. This could be because of differences in forest composition and structure as linked to the dietary needs of chimpanzees that are committed frugivores. The *Marantaceae* forests of Odzala have reduced canopy coverage resulting from lower tree densities in comparison to the more closed canopy forests of Ndoki. Lokoué may be a lower quality habitat for chimpanzees compared with Ndoki, which is rich in fruit-bearing tree species consumed by chimpanzees [Moutsambote et al., 1994].

Surveying Sympatric Apes Using the Standing-crop and Marked-nest Methods

In a recent nationwide survey of chimpanzees in Uganda, the marked-nest method was chosen over traditional standing-crop surveys [Plumptre & Cox, 2006]. However, detailed recommendations regarding the respective applicability of each method are lacking in the literature, making the choice between one and the other somewhat speculative. The present report describes the first application of both the standing-crop and the marked-nest method to determine the density of sympatric chimpanzees and gorillas in the Congo Basin. Our results show that chimpanzee density estimates calculated by the two methods were roughly equivalent, but that there were large differences between standing-crop and marked-nest density estimates for gorillas: at both sites, marked-nest density estimates were lower than standing-crop estimates. Although the marked-nest method seemingly underestimates gorilla densities, the repeated passages on transects required by the method enabled us to detect a drastic change in ape population status at Lokoué during the course of this study. Those results highlight the fact that there are several important considerations when making the choice between the standing-crop and marked-nest survey methods. First, it is necessary to decide whether the main objective of the study is to survey or to monitor the ape population. Second, one must determine the acceptable level of precision that will be associated with the resulting density estimates, which will determine survey effort and whether the standing crop can be used for trend detection. Finally, it is essential to assess the effectiveness of the marked-nest method in accurately depicting gorilla populations who build nests with shorter life spans than chimpanzee nests.

The standing-crop survey method involves a single count of ape nests of all ages along transects and when detection functions are considered, this method yields density estimates that can be compared between sites. The benefits of this method include its higher nest encounter rates and typically larger survey coverage. Its limitations are that it involves conversion factors for both nest creation and nest decay rates which can be highly variable within and between sites. In contrast, the marked-nest survey method involves repeated surveys for nests created between repeated passages along the same transects. Similar to the standing-crop method, it yields density estimates that can be compared between sites when detection functions are incorporated in calculations. The main benefits of this method are (1) that the nest decay rate is removed from the density calculation, (2) the data set includes only recently created nests, which is likely to yield more accurate nest group sizes, and (3) repeated passages along the same transects can also be used for monitoring the ape population, without the confounding effect of comparing different habitats. The drawbacks are that nest encounter rates on repeated passages are much lower than the initial standing-crop passage, as shown in Figure 4. The standing-crop method is typically used to assess the status of an ape population, but estimates generated from this method are often associated with high levels of variation that reduce their resolution and sensitivity to detect population trends. Plumptre [2000] recommends reducing the number of conversion factors used in density estimate calculation to increase the resolution of indirect survey methods, but as we have shown in this study there is a trade-off with loss of precision owing to smaller sample sizes associated with the marked-nest method.

In our comparison between sites, we had anticipated that both ape nest encounter rates and density estimates would be higher in Odzala than Ndoki. This prediction was based on the long sampling interval in the Lokoué surveys (which was monthly, compared to 2 weeks in Ndoki), proximity of transects to a swampy clearing, and previous reports of very high ape densities from the Odzala region. However, our results clearly showed that nest encounter rates were higher in Ndoki in habitats where ape nests could be detected further from the transect line (see Fig. 2). The longer sampling interval in the Lokoué surveys was not advantageous in terms of sample size and, further, seems responsible for the disparities between standing-crop and marked-nest gorilla density estimates in this study. Indeed, the premise of the marked-nest method is that all existing nests along transects will be marked and subsequent surveys will be repeated at short enough intervals so as to record all nests constructed since the last passage. A 2-week interval has generally been employed to survey chimpanzee nests in Eeast Africa [Furuichi et al., 2001; Plumptre & Cox, 2006; Plumptre & Reynolds, 1996]. In Goualougo, the 10–14 days interval between continuous passages seemed relatively effective in detecting newly created gorilla nest sites. In contrast, it is likely that certain types of gorilla nests were created and disappeared between monthly survey intervals and field seasons at Lokoué. This can also be deduced from Tutin and Fernandez's [1984] report that the longevity of gorilla nests ranged on average between 19 and 61 days depending on construction type. Differences in chimpanzee estimates are not as drastically affected by length of survey intervals, as the tree nests of chimpanzees have longer life spans. In future marked-nest studies of gorillas, intervals between passages should be shortened to account for short nest decay. It is important to also mention that repeated surveys can be very time and labor intensive, particularly in remote areas where logistical support is limited.

In addition to the final density estimate, the repeated passages of the marked-nest method provide a potential means to evaluate populations trends in real time. Different trends were evident between the Odzala and Ndoki ape populations. The ape nest encounter rates in Goualougo were relatively stable throughout the study, whereas there was an abrupt decline at Lokoué. During the time that Ebola was confirmed in human and wildlife populations in the southern region of Odzala National Park between 2002 and 2003 [Bermejo et al., 2006; Rouquet et al., 2005], our results showed that the ape population in Lokoué (further north in the park) was seemingly untouched by the epidemic despite being geographically close to the outbreak zone. However, during the last four marked-nest passages in 2004, the encounter rates of ape nests revealed a dramatic decline (more than 80%) relative to previous surveys, which was also confirmed by other reports [Caillaud et al., 2006; Devos et al., accepted]. Although marked-nest surveys are more time consuming and labor intensive than one-off surveys, we have shown that they can be effective tools in monitoring high-risk populations.

In summary, we advocate that density estimates that incorporate detection functions should be used in comparisons between sites rather than encounter rates because of the possibly confounding effects of different habitats on nest visibility. Ape densities can be calculated from either standing-crop or marked-nest surveys when the methods have been appropriately applied to reflect the nesting patterns of the apes. Further research is needed to assess and define the appropriate parameters for implementing the marked-nest method to effectively survey and monitor gorilla populations in western equatorial Africa. Finally, we suggest that encounter rates on repeated transects can be used to monitor ape populations at a site, particularly those known to be at high risk of population decline.

Advantages of Remote Sensing Technology

Remote sensing technology has the advantage of assessing different sites with systematic and spatial techniques. We have demonstrated that a combination of satellite imagery and ground surveys can effectively be used to assess, quantify and interpret large and remote tracts of forest. Differing degrees of canopy coverage and vegetative structures were clearly distinguished between the two sites. Monodominant formations of *G. dewevrei* forests and swamps were particularly well defined by few habitat classifications that directly corresponded to our ground survey data. Remote sensing produced several classes of mixed-species semi-evergreen forest with different degrees of canopy coverage that differed in their prevalence at these two sites. The Ndoki forests showed a high prevalence of mixed-species, semi-evergreen forest with a relatively closed canopy, whereas the mixed-species forests of Odzala were more open. Odzala is typically described as being composed of different types of *Marantaceae* forest, which all have a dense understorey of herbaceous vegetation. Satellite imagery classifies the visible features habitat and therefore focused on the canopy features rather than understorey vegetation of these forests. In their habitat classification of Landsat imagery in Democratic Republic of Congo, Hashimoto et al. [1998] reported that it was impossible to reliably distinguish between primary and old secondary forests or between cultivated fields and young secondary forest. This demonstrates why it is necessary to interpret satellite classifications with conventional ground surveys of vegetation, particularly in mixed-species habitats that may harbor different ape densities [Morgan et al., 2006; Tutin & Fernandez, 1984].

Conservation Implications

We have shown that ape habitats, densities, and population trends differ dramatically over relatively small spatial and temporal scales. Our findings also confirm previous reports that previously large ape populations in this region were declining due to emerging diseases [Caillaud et al., 2006; Huijbregts et al., 2003; Walsh et al., 2003] and that this can be documented through ape nest surveys. The extent of such declines over the entire region may never be known because of lack of baseline survey information from many remote areas; the low precision of existing ape density estimates to evaluate trends and the lack of continued ape population monitoring.

Accurate assessments of the conservation status of these apes will require that these issues are rectified.

It is imperative that researchers and conservation managers take a proactive approach to ape population surveys and monitoring. Standing-crop and marked-nest surveys provide the means to assess and monitor ape populations, but will require further methodological improvements to increase the precision and accuracy of their resulting density estimates. Technological resources exist to use satellite imagery to classify all remaining ape habitats, which can facilitate strategic planning to survey these habitats and assess the status of remaining ape populations. Furthermore, collaborative research between sites can provide methodological insights and contextual information to identify regional trends. It is only through such immediate and innovative approaches that conservation initiatives will be developed within the time frame that is necessary to ensure the long-term preservation of chimpanzee and gorilla populations in the Congo Basin.

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