



Ape Abundance and Habitat Use in the Goulougo Triangle, Republic of Congo

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Chimpanzee (Pan troglodytes troglodytes) and western gorilla (Gorilla gorilla gorilla) populations in central Africa are rapidly declining as a result of disease epidemics, commercial bushmeat hunting, and habitat destruction. Our main objective was to estimate the absolute abundance and habitat utilization of chimpanzees and gorillas in the intact forests of the Goulougo Triangle in the Republic of Congo, and in an adjacent area in which selective logging will take place in the near future. The estimates provide a unique baseline for apes inhabiting an undisturbed environment. A second objective was to compare estimates of abundance and patterns of habitat utilization generated by different techniques: 1) distance sampling of individual ape nests and nest sites along line transects, 2) direct observations of apes during reconnaissance surveys, and 3) observations of ape traces during reconnaissance surveys. We completed a total of 222 km of line transect surveys in 4 sampling areas, resulting in overall density estimates of 1.53 chimpanzees/km² and 2.34 gorillas/km² from nest sites. We generated a density estimate of 2.23 chimpanzees/km² from direct observations during reconnaissance surveys of a semihabituated community in 1 of the 4 sampling areas. Habitat use profiles that nest surveys depicted on transects differed from those of direct observations and traces we encountered on reconnaissance surveys. We found the highest overall abundance of chimpanzee nests in monodominant Gilbertiodendron forest, whereas our direct observations showed that chimpanzees preferred mixed species forest. Transects that

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traversed the core area of the community range had the highest encounter rates of chimpanzee nests and nest sites. Gorilla nests on transects showed a preference only for mixed species forest with an open canopy, but direct observations and traces on reconnaissance surveys clearly indicated that gorillas use several habitat types. We conclude by evaluating the precision of these nest surveys and our ability to detect future trends in ape densities in the Goulougo Triangle.

KEY WORDS: abundance; ape; chimpanzee; density; direct observation; distance sampling; gorilla; habitat utilization; line transect surveys; reconnaissance surveys.

INTRODUCTION

Chimpanzee (*Pan troglodytes troglodytes*) and western lowland gorilla (*Gorilla gorilla gorilla*) populations in central Africa are rapidly declining as a result of disease epidemics, commercial bushmeat hunting, and habitat destruction (Huijbregts *et al.*, 2003; Leroy *et al.*, 2004; Walsh *et al.*, 2003). We may never know the extent of the declines because precise baseline ape density estimates are not available from most central African forests (Butynski, 2001; Oates, 1996; Teleki, 1989). Even when abundance estimates are available, some have criticized the survey methods as biased, limited in their ability to detect trends, and lacking causal inference (Plumptre, 2000; Walsh *et al.*, *unpubl. ms.*). Researchers must refine the methods and obtain precise ape density estimates to ensure strategic and appropriate conservation planning that would permit the survival of remaining chimpanzee and gorilla populations in central Africa.

The 2 most widely used methods to determine ape densities are the home range and nest count techniques (Plumptre and Reynolds, 1996, 1997). The home range or total count method requires census of all chimpanzees or gorillas in a study area and measurement of their home ranges. Ape density in a given area is calculated by dividing the number of apes by the surface area of their home range. This method is thought to be most accurate because it is based on direct observations of known individuals, but is limited to a relatively small number of sites where apes have been habituated to direct observation. Ape nest counts provide an alternative survey method that involves estimating ape density from indirect evidence. Nest counts along reconnaissance surveys that follow the path of least resistance require less effort than randomly placed line transects, but are biased and less powerful in detecting trends (Buckland *et al.*, 2001; Walsh *et al.*, *unpubl. ms.*). In line transect distance sampling of ape nests, observers traverse a series of transect lines recording perpendicular distances to detected nests. These distances are used to calculate the perpendicular

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distance to the nest site, which is the unit of observation because of the dependence between nests corresponding to a single nest site and the influence of nest site size on the detection of individual nests. Probability of detecting a nest site is modeled as a function of the observed distances and then combined with the nest site encounter rate and estimated nest site size to calculate the density of nests in the study area (Buckland *et al.*, 2001). Most of the concerns with line transect nest survey methods relate to the factors that are used to convert nest densities to absolute chimpanzee or gorilla densities (Plumptre, 2000; Plumptre and Reynolds, 1997; Tutin *et al.*, 1995).

Factors used to calculate ape densities from nest counts include rate of nest creation, identification of the ape species that created the nests, and rate of nest decay. As Plumptre (2000) notes, the variance associated with each of these conversion factors contributes to the variance of the ape density estimate itself. It is important to consider both the potential bias associated with each of these factors and their variance when examining the accuracy and precision of density estimates and their power to detect fluctuations in ape populations.

Nest Creation Rate

Though nest creation rates vary between sites and seasons, the value used in density estimates are often not site specific (Basabose and Yamagiwa, 2002; Plumptre and Reynolds, 1997). Chimpanzee researchers in the Budongo Forest have identified specific behaviors that affect nest creation rates, such as reuse of night nests, proportion of nest building apes, and frequency of day nest building (Plumptre and Reynolds, 1997). In the past, many assumed that apes created 1 nest per day for sleeping, but researchers have observed most chimpanzees and gorilla populations using temporary resting platforms during the day, often referred to as day nests (Fruth and Hohmann, 1996). Day nest building can increase the nest creation rates from 1 nest per day, as shown in Budongo where the actual nest creation rates were 1.09 nests per day after incorporating day nest building (Plumptre and Reynolds, 1997). Some researchers have indicated that gorillas in central African forests frequently sleep on the bare earth, which would reduce their nest creation rates (Mehlman and Doran, 2002; Remis, 2000; but see Brugiere and Sakom, 2001 and Tutin *et al.*, 1995). Not accounting for this behavior could result in a significant underestimation of gorilla density. Gorillas form consistent groups and one can use average group sizes from direct observations in the nest site conversion formula to account for the proportion of individuals that do not build detectable nest

structures. However, it is necessary to obtain specific nest creation rates for the region, requiring direct observations of chimpanzee and gorilla nesting behaviors.

Attribution of Nests to Particular Species

Chimpanzees and gorillas are sympatric within certain regions of east and central Africa. Both construct night nests and it may be impossible to positively identify which species constructed certain nests or sites when verifying signs are not present. Tutin *et al.* (1995) calculated the proportion of gorilla nest sites that one might mistakenly attribute to chimpanzees during one-off surveys if one assumed that chimpanzees created all arboreal nest sites. They suggested that researchers would code 26% of gorilla nest sites erroneously as chimpanzee sites because they consisted of only arboreal nests or would appear as arboreal sites after all ground nests had decayed. This provides a value that has been used to correct for the potential over-estimation of chimpanzees at sites where they are sympatric with gorillas. Furuichi *et al.* (1997) proposed a method for distinguishing nest builders by examining nests with verifying evidence, such as shed hair and feces, and identifying covariates such as nest height and diameter that one could use to distinguish between the nests of the 2 species. Applying their criteria for nest builders, they found only 3 coding errors for the 36 nest groups that could be definitely attributed to either species. The extension of Furuichi *et al.*'s (1997) approach would be to construct a statistical model based on the characteristics of nests with known builders to use to discriminate between unclassified ape nests. Another alternative is to calculate ape densities from only fresh and recent nests, which are more likely to have verifying signs of either ape species. Though this would provide data sets with higher percentages of nests attributable to either species, exclusion of older ape nests dramatically reduces the sample size and increases the required effort of surveys.

Nest Decay Rate

Another obstacle in accurately estimating ape densities is the nest decay rate factor. Reported chimpanzee nest decay rates range from 46 days in the Budongo Forest, Uganda to 114 days in the Lopé Reserve, Gabon (Plumptre and Reynolds, 1996; Tutin and Fernandez, 1984). Rate of decay differs between construction types, habitat types, seasons, tree species, and levels of human disturbance (Marchesi *et al.*, 1995; Tutin and Fernandez, 1984; Tutin *et al.*, 1995). In addition to ecological factors,

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ape nest decay rates calculated at different sites may adopt different operational definitions or employ biased sampling regimes. For example, Tutin and Fernandez (1984) considered a nest completely decayed if it were no longer possible to recognize it, whereas Plumptre and Reynolds (1996) considered a nest to have disappeared if it had lost all its leaves even if the structure remained. It is also necessary to address sampling units, such as the difference in decay rates between individual nests and nest sites, in future decay rate studies. It is ideal to use site-specific decay rates in the ape density equation, but it is often not feasible to establish these values at each survey site (Plumptre, 2000). Researchers frequently borrow decay rates for chimpanzee and gorilla nests from Belinga and Lopé, which are located in Gabon (Tutin and Fernandez, 1984; Tutin *et al.*, 1995).

Although rare, comparisons between home range and nest count surveys at the same sites are important to cross-validate these measures of ape abundance. Chimpanzees live in communities with an exclusive membership that utilizes a specific home range (Boesch and Boesch-Achermann, 2000; Goodall, 1986; Herbinger *et al.*, 2001). Therefore, line transect nest surveys within a chimpanzee community range most likely reflect the density and spatial distribution of a single community. Gorilla home ranges overlap extensively and nest distribution in an area may depict the habitat utilization of several groups, diminishing the comparative potential of direct and indirect survey methods. One cannot use observations of apes and traces on reconnaissance surveys to generate density estimates, but they can provide a general indication of ape abundance and habitat utilization.

Survey methods must be not only accurate in their depiction of immediate ape distribution and abundance, but also precise enough to detect future trends in ape populations. Disturbances associated with mechanized logging present a serious threat to all remaining chimpanzee and gorilla populations including those in Northern Congo, but there are conflicting reports about the specific effects of logging on apes (Carroll, 1988; Hashimoto, 1995; Plumptre and Reynolds, 1994; Skorupa, 1988; Tutin, 2001; Tutin and Fernandez, 1984; Usongo, 1998; White, 1992; White and Tutin, 2001). Chimpanzee densities are generally reported to be lower in logged areas and areas that humans frequent compared to undisturbed areas (Johns and Skorupa, 1987; Marchesi *et al.*, 1995; Plumptre and Reynolds, 1996; Skorupa, 1988; Tutin and Fernandez, 1984; White, 1992; but see Hashimoto, 1995). In contrast, some noted that gorillas preferentially use habitat types with abundant herbaceous vegetation, which often characterizes secondary forests (Carroll, 1988; Fay, 1997; Tutin *et al.*, 1995). It is essential that the impact of timber extraction and associated disturbances on apes be determined as such human influences

expand into the largest remaining tracts of pristine forests in the Congo Basin.

To quantify the effects of the timber extraction process, it is necessary to collect data before and after exploitation in a specific area. Simultaneously collecting control data in adjacent areas in which logging will not take place can further improve the study design. Such an opportunity exists in the Goualougo Triangle located in the remote forests of the Republic of Congo. Chimpanzees and gorillas coexist throughout the study area, some of which was recently annexed to the Nouabalé-Ndoki National Park, while another section remains in the logging concession scheduled for exploitation in the near future. The distribution and abundance of apes we report here reflect their specific adaptations to ecological conditions in an intact central African forest, without the effects of human disturbance or known disease epidemics.

Our main objective was to generate precise density estimates and to document the habitat utilization of apes in the pristine forest of the Goualougo Triangle. We compared great ape abundance and habitat use that we generated from 3 different sampling techniques: line transect nest surveys, direct observations of apes on reconnaissance surveys, and indirect observations of ape traces on reconnaissance surveys. We converted nest site densities from line transect surveys to ape densities with nest creation and decay rates specific to the site. We present several types of nest count analyses to foster comparison among sites and elucidate differences in density estimate calculations. Further, we used discriminant function analysis to construct a statistical model based on nest characteristics that assigned 99% of our nest sample to either chimpanzees or gorillas. We calculated home range density estimates from the social structure and ranging of a semihabituated chimpanzee community contacted on reconnaissance surveys. We discuss the validity of these survey methods and calculate the resolution of transect data to detect future changes in the ape population.

Methods

Study Site

The Goualougo Triangle is located within the Nouabalé-Ndoki National Park (16.51'–16.56'N; 2.05'–3.03'E), Republic of Congo see (Fig. 1). It covers 310 km² of lowland forest with altitudes ranging between 330 and 600 m. The climate is transitional between the Congo-equatorial and sub-equatorial climatic zones (White, 1983). Rainfall is bimodal with a main rainy

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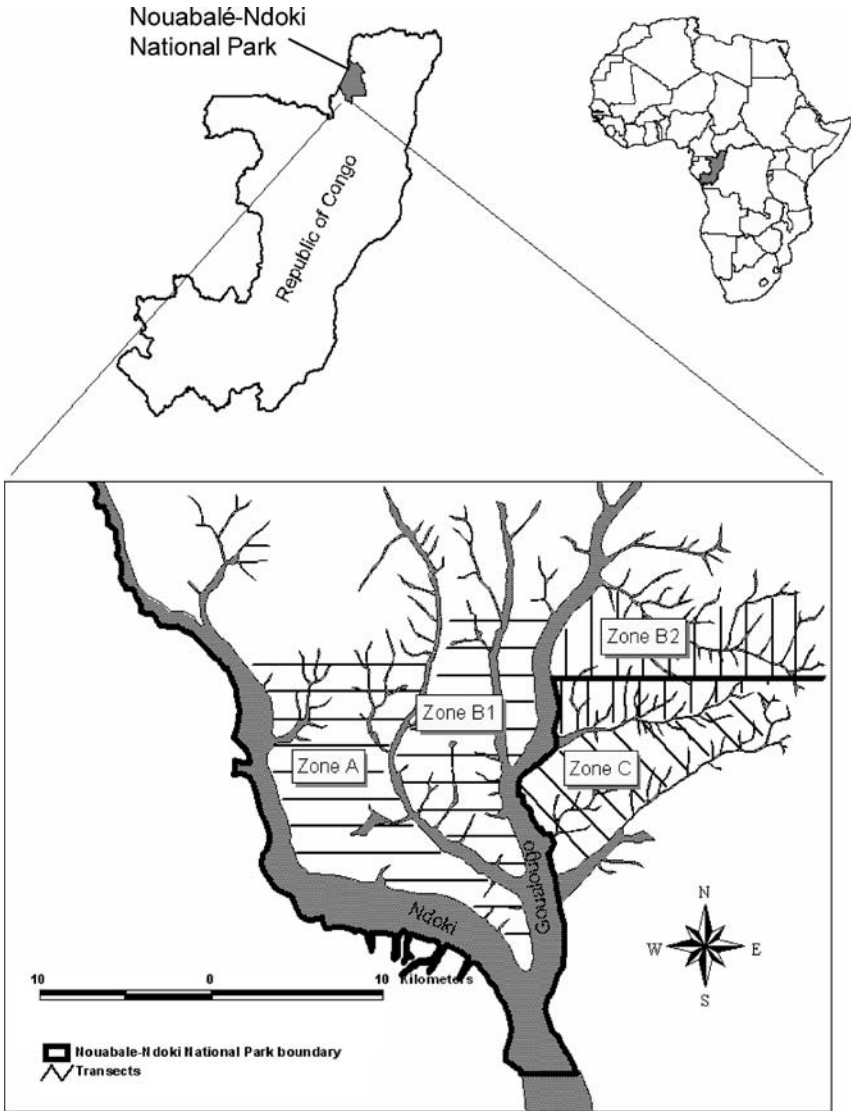


Fig. 1. Map of Republic of Congo with the Nouabalé-Ndoki National Park and detail of line transects conducted in the Goulougo Triangle study area.

season from August through November and a short rainy season in May. E. Stokes recorded average monthly temperatures and rainfall were available for Mbéli Bai base camp, Republic of Congo, 17 km from the study area. The annual rainfall averaged 1728 ± 47 mm between 2000 and 2002

(E. Stokes, *unpubl. data*). The average minimum and maximum temperatures then are 21.1°C and 26.5°C in 2000, 21.5°C and 26.8°C in 2001, and 21.9°C and 26.5°C in 2002, which showed little seasonal variation (E. Stokes, *unpubl. data*).

We recognized 4 habitat types in this study: monodominant *Gilbertiodendron* forest, *Gilbertiodendron* mixed species forest, mixed species forest, and swamp forest. Monodominant *Gilbertiodendron* forest is a single-species formation of *Gilbertiodendron dewevrei* that can have either sparse or dense understory (*Marantaceae* and *Commelinaceae*). It occurs along watercourses as well as on interfluvial plateaus. *Gilbertiodendron* mixed species forest is found between monodominant stands of *Gilbertiodendron dewevrei* and mixed species forest. Mixed species forest has a diverse flora and canopy that is not always continuous. It is semideciduous and occurs on *terra firma* areas. Families typical of this habitat type include *Meliaceae*, *Leguminosae*, *Irvingiaceae*, *Sterculiaceae*, and *Ebenaceae*. Swamp forest consists of diverse flora associated with watercourses in low-lying areas. Dominant families within this habitat type include *Rubiaceae*, *Euphorbiaceae*, and *Annonaceae*.

Though a large portion of the Goulougo Triangle was annexed to the Nouabalé-Ndoki National Park (NNNP) in June 2003, almost a third of the study area remains in a logging concession scheduled for timber extraction. We subdivided the study region into 3 zones by considering the NNNP boundary, future scheduled timber extraction in adjacent regions, and geographic features such as waterways (see Fig. 1). The desire to obtain baseline information that could be used to investigate and quantify future changes in ape density and distribution resulting from planned mechanized logging drove the definition of the zones. Zone A (107 km²) is within the NNNP and serves as a control condition that is geographically removed from future timber extraction. We do not anticipate that future logging or disturbance will affect the ape density and distribution there. Zone B is also within the NNNP, but is located immediately adjacent to logging activities. We expect that logging—noise disturbance, arrival of displaced apes into the protected area—could affect apes in this zone indirectly. We divided zone B (113 km²) into B₁ (60 km²) and B₂ (53 km²) because we expect the postlogging ape abundance and distribution to be affected differently as a result of natural geographic boundaries. Zone C (90 km²) is the experimental zone located within the timber concession where logging will occur, but was still intact at the time of our study. Based on past findings in central African forests, we expect the subsequent changes in ape density and distribution to be the most dramatic in zone C (White, 1992; White and Tutin, 2001).

Line Transect Surveys

Survey Design

Results from a line transect pilot study indicated that a survey design comprised of parallel line transects separated by 1.5 km would provide sufficient survey effort for the desired precision. We used the automated survey design component of the custom DISTANCE 4.0 software to generate systematically spaced transects with a random start in each of the 4 geographic survey strata⁶ (Thomas *et al.*, 2001). This systematic design provided equal coverage probability over the study area, i.e., each location in the study area has the same probability of being sampled, which one assumes during a standard line transect analysis. In each survey stratum we placed transect lines perpendicular to the major watercourses to potentially increase precision by orienting lines parallel to suspected density gradients to maximize variation in encounter rate within transect lines and to minimize variation between them (Buckland *et al.*, 2001).

Field Methods

We used a global positioning system (GPS, Garmin 12XL) to locate the start and end points of each transect. A compass bearer walked in front of the transect observers to mark the path of travel. Rather than clearing wide transect swaths with machetes, we cut all transect lines with hand shears to minimize the ecological impact of the surveys. We continuously recorded habitat type and canopy cover data during surveys to allow poststratification and density estimation by habitat type. Two observers aided a transect team leader in searching for ape sign. We recorded the following data along line transects: direct observations of apes, ape vocalizations, ape signs (feeding signs, feces, nests), species that created the sign (ape, chimpanzee, gorilla), and specific information for individual nests. It was possible to differentiate between chimpanzee and gorilla feces based on form and consistency. We distinguished ape feeding signs from other large mammals by specific foraging techniques, but did not attribute them to either chimpanzees or gorillas unless other verifying signs were present.

We defined nest sites as all nests created by the same ape species and of the same age class created ≤ 50 m of each other. We classified each nest

⁶Used as the technical term in survey design and analysis.

as definitely chimpanzee or gorilla if verifying signs—direct observation of apes, feces, imprints, or hair—were present. As we rarely observed chimpanzees building ground nests, we attributed nests on the ground to gorillas and arboreal nests of the same age class that were associated with nests on the ground to gorillas (Tutin and Fernandez, 1984).

Specific data collected for each nest included topofil distance along the transect, perpendicular distance from the transect, side of transect on which the nest was located, height of the nest, species of vegetation used for nest construction, habitat type associated with the nest, and estimated age of the nest. We used nest age definitions and estimation methods based on Tutin and Fernandez (1984). Fresh nests consisted of fresh green vegetation and intact structure with freshly broken twigs or branches. The nests often had urine, feces, or distinguishable prints and we estimated their age as 1–3 days. Recent nests had an intact nest structure with wilting green vegetation that could be between a few days and 3 weeks old. An intact structure with aged vegetation characterized old nests. Very old nests showed deterioration of both nest material and structure. A large degree of variation in the aging process of different nest types and tree species exists (Onononga *et al.*, *in prep.*), but we estimated old and very old nests to be greater than 3 weeks. Before data collection, training took place to ensure a minimum observer reliability of 90% between observers for designation of ape species that created individual nests, estimation of nest height (within 2 m as verified by a rangefinder device), nest age, and habitat type.

Reconnaissance Surveys

We recorded the location, habitat type, ape species, and age of all ape signs we encountered during daily reconnaissance surveys since initiating the chimpanzee study in February 1999. Sampling efforts and behavioral observations of chimpanzees focused on the Moto community, which consisted of the 43 independent individuals, excluding juveniles and infants (Morgan and Sanz, 2003). We documented community ranging patterns via a GPS to record the initial location of chimpanzee encounters. We used only 1 location point per party encountered each day. We recorded habitat type and canopy coverage at the initial contact location via categories described earlier. Though observers did not directly follow gorilla vocalizations or traces, we often encountered groups during reconnaissance surveys. We recorded location and habitat type at the location of each gorilla encounter.

Data Analysis

Unless otherwise specified, we calculated statistics with MINITAB 13 (Minitab, 2000) and SPSS 11.5 (SPSS Inc., 2002), using a level of significance of 0.01 throughout our study.

Ape Densities Based on Nest Site Line Transect Surveys

We used nest creation rates, identification of the ape species that created the nests, and nest decay rates to convert nest site density estimates to absolute chimpanzee, gorilla, or combined ape densities as follows:

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

wherein the subscript i denotes whether the estimate is for chimpanzees or gorillas; \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 0; $\hat{E}(s_i)$ is the estimated average nest site size; \hat{t}_i is the length of time to nest decay, i.e., the reciprocal of the decay rate; and \hat{r}_i is the estimate of the nest creation rate.

If densities are estimated directly from nests rather than nest sites, this lack of dependence between observations has little effect on the point estimate of density or abundance. Density estimates are then calculated as follows:

$$\hat{D}_i = \frac{\frac{1}{2} \cdot \frac{n_i}{L} \cdot \hat{f}_i(0)}{\hat{r}_i \cdot \hat{t}_i} \quad (2)$$

wherein n_i denotes the number of nests. However, theoretical estimates of sampling variance will be negatively biased, but using empirical estimators or resampling methods for variance estimation can alleviate the problem (Buckland *et al.*, 2001).

We calculated density estimates with their associated coefficients of variation and 95% confidence intervals via the DISTANCE 4.0 software (Thomas *et al.*, 2001). To ensure robust estimation of detection and consequently of the effective strip half-width, we truncated observations made at the furthest distances from the line (Buckland *et al.*, 2001). We considered several different models of detection function (half-normal cosine, uniform cosine, uniform simple polynomial, half-normal hermite polynomial, hazard rate cosine) for each density calculation. We selected models based on the lowest Akaike's Information Criterion (Buckland *et al.*, 2001).

In Sanz *et al.* (*in prep.*), we provide detailed descriptions of how discriminant function analysis to construct a predictive model of nest builder based on characteristics of nests that were definitely attributed to either chimpanzees ($n = 53$) or gorillas ($n = 302$). We used a stepwise variable selection method to identify variables that best discriminated between their nests. The following variables significantly contributed to the model's ability to discriminate between nests: understory closure, type of nest, height, and specific tree species. We based the model on a random sample of 70% of all chimpanzee and gorilla nests. We tested the model separately against this sample and the remaining unselected nest sample to determine its accuracy. The degree of success for accurate nest classification was high: 98.8% of the originally selected nests were correctly classified, 97.9% of original cross-validated⁷ nests were correctly classified, and 98.2% of unselected original nests were correctly classified.

We used survival analysis on a marked-nest data set to estimate nest decay rate for the Goulougo Triangle study area (detailed description reported in Onononga *et al.*, *in prep.*). We monitored the aging of nests detected on initial surveys over subsequent marked-nest circuits. We calculated a logistic regression on start time (fresh nest first detected), stop time (last detected or censused), and status (present, decayed). We also fitted a Cox Proportional Hazard model to age and status, with age standardized to the start of the study. We conducted final survival analysis on nests encountered on the first passage ($n = 92$), of which 50% had completely decayed by the end of our study. We also examined the roles of several covariates—ape species that created the nest, nest structure, nest age, habitat type, canopy, understory, sampling zone—with relation to nest survival by applying a Kaplan-Meier model to the entire data set. Logistic regression resulted in a mean nest decay rate of 91.5 days (SE = 1.67). The Cox Proportional Hazard model resulted in a mean nest decay rate of 90 days (SE = 2.85). We used the same decay rate for both chimpanzee and gorilla density estimation because ape species that created the nest did not significantly affect nest survival according to the Kaplan-Meier results. Though decay rates might differ by habitat type, the data in the sample were insufficient to allow for a separate estimate of decay rate by habitat type (Onononga *et al.*, *in prep.*).

While observing the Moto chimpanzee community, Sanz (2004) recorded all-day nest building events. Day nests were temporary structures constructed as resting and sleeping platforms throughout the day. Based on frequency of day nesting and reuse of nests, Sanz (2004) calculated a nest

⁷Cross-validation refers to a specific technique where each case (nest) is classified with a model derived from all other cases in the sample other than the particular case being assigned.

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creation rate of 1.09 nests per day ($SE = 0.05$) at the site. Gorillas were assumed to create one nest per day. Though this could be an overestimate for the region, we also counted bare earth sleeping sites with no nest construction as nests following methodology of Tutin *et al.* (1995) for recording nest types.

The number of nests in a site is a variable in the conversion of ape nest site density to absolute ape density. Estimations of nest site size can be influenced by the nest aging process, as nests disappear at different rates, and misclassification of ape species, lumping nests of 2 different species into a single site or splitting a single species site into 2 different sites. Therefore, we also estimated ape density estimates with 1) fresh and recent sites that we initially attributed to chimpanzees or gorillas and 2) chimpanzee party sizes and gorilla group sizes from direct observations.

To examine the power to detect future changes in the ape populations, we used Plumptre's (2000) approximate formula:

$$P = 2.77 \left(\frac{CV(\hat{D}_i)}{100} \right) \quad (3)$$

wherein P denotes the proportional change in the population density that can be detected at the 5% significance level with 50% power and $CV(\hat{D}_i)$ denotes the total coefficient of variation for the density estimate. To calculate the proportional change that can be detected with 80% power at the same significance level, one should replace the constant 2.77 with 3.96. We calculated $CV(\hat{D}_i)$ using DISTANCE 4.0 and it already incorporates the standard errors associated with the nest creation and decay rates.

We calculated density estimates for each sampling zone and habitat type. Note that we assumed the nest creation rate to be independent of zone and habitat type. Habitat type varied throughout the study area. We used regression analysis to estimate the linear relationship between nest site frequency and habitat types. We used multiple linear regression to estimate the coefficients of the linear equation that best predicted the frequency of chimpanzee and gorilla nest sites along transects.

We calculated encounter rates for ape signs on transects by dividing the number of signs by the distance surveyed.

Chimpanzee Abundance and Habitat Utilization Based on Direct Observation

Using ARCVIEW 3.2a and the ANIMAL MOVEMENT extension, we calculated home range sizes with the minimum convex polygon (MCP)

and Kernel analysis methods. We identified core areas that had high probabilities (50%, 75%) of encountering chimpanzees in the Moto community by kernel analysis. Peripheral areas that bordered other known chimpanzee communities were located outside of the 95% kernel analysis. We then divided community size—number of nest building individuals—by community range to generate a home range density estimate. We compared encounter rates of chimpanzee nests between line transects that traversed the core and peripheral areas of the Moto community.

Ape Habitat Utilization Based on Direct Observation and Feces

We used χ^2 goodness-of-fit tests to compare observed and expected frequencies of ape direct observations and feces across habitat type categories. We used proportions of habitat types encountered along line transects to calculate expected values for a χ^2 test based on the hypothesis that expected frequencies of habitat use should be proportional to habitat abundance. We then tested observed habitat utilization—direct observations and feces—by chimpanzees and gorillas against these expected values. We also used χ^2 tests to compare habitat use profiles generated by different survey methods.

RESULTS

Line Transect Nest Surveys

Between December 2001 and June 2002, we conducted a total of 222 km of ape nest line transect surveys in the Goualougo Triangle (zone A = 73 km, zone B₁ = 54 km, zone B₂ = 39 km, zone C = 56 km). The general habitat types of the different zones were very similar (Fig. 2). We found mixed species to be the most common habitat throughout the study area (73.5 ± 5.7% of the distance surveyed). Mixed species forest consisted of 54.6 ± 7.6% open canopy and 45.4 ± 7.6% closed canopy. Monodominant stands of *Gilbertiodendron* forest comprised 21.3 ± 4.7%, with 96.5 ± 0.03% having a closed canopy and only 3.5 ± 0.03% an open canopy. Swamp forest accounted for 5.2 ± 0.01% of the surveys, with 26.5 ± 23.2% closed canopy and 73.5 ± 23.2% open canopy.

Overall, the ape traces that we encountered most frequently were individual nests and nest sites, with 7.01 nests/km and 2.76 nest sites/km. We rarely encountered ape feces on transects (0.07 feces/km), encountering direct observations twice as often (0.14 direct observations/km).

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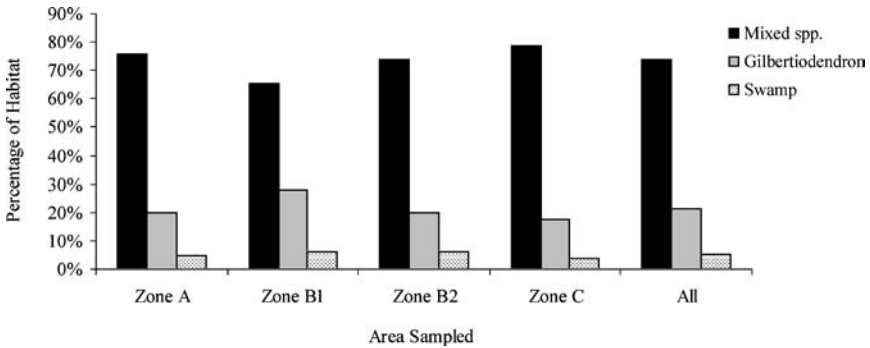


Fig. 2. Proportion of different habitat types in each zone and the entire study area.

As chimpanzee feces decay quickly, it was not surprising that 88% of feces were from gorillas. Though ape feeding traces occurred relatively frequently (0.33 feeding traces/km), it was difficult to attribute them to either chimpanzees or gorillas. Vocalizations occurred relatively rarely (0.10 vocalizations/km) and we attributed 86% of them to chimpanzees.

We encountered a total of 1557 ape nests (53 chimpanzee nests, 302 gorilla nests, 1202 great ape) along transects, comprising 613 nest sites (21 chimpanzee sites, 116 gorilla sites, 476 great ape sites). Discriminant function analysis assigned 919 of them to chimpanzees and 273 to gorillas, with the remaining 10 nests missing values necessary for assignment. Eighty-nine percent of nest sites contained only nests attributed to a single species. Based on the majority of nests in a site, we were able to assign some of the remaining nests to either species. The final sample consisted of 375 chimpanzee sites (972 nests) and 213 gorilla sites (575 nests).

The average nest site size for all chimpanzee nests is 2.75 ± 1.88 ($n = 375$, range: 1, 12) and 2.52 ± 1.99 for gorillas ($n = 213$, range: 1, 11). The average nest site size for fresh and recent chimpanzee nest sites is 2.29 ± 1.40 ($n = 49$, range: 1, 6) and 2.74 ± 2.32 for gorillas ($n = 47$, range: 1, 10).

Table I shows chimpanzee and gorilla density estimates from nest sites in different habitat types. The transect surveys yielded overall density estimates of 1.53 chimpanzees/km² and 2.34 gorillas/km² within the Goulougo Triangle study area (Table II). In Table II we compare Goulougo ape density estimates generated from 1) nests sites, 2) nest sites with decay rates from Gabon, 3) only fresh and recent nest sites, 4) nest sites with site size calculated from only fresh and recent sites, 5) nest sites with site size based on direct observations of chimpanzees in Goulougo and gorillas at Mbeli Bai, 6) individual nest counts, 7) individuals nests with decay rates from

Table I. Ape density estimates from nest sites in different habitat types

| Habitat (distance surveyed) | Nest sites | Density (ind/km ²) | 95% CI ^a (ind/km ²) | % CV ^b |
|--|------------|--------------------------------|--|-------------------|
| Mixed species, open canopy (92 km) | | | | |
| Chimpanzee ^{c,d,e} | 35 | 0.33 | 0.22–0.50 | 20.64 |
| Gorilla ^{d,f,g} | 149 | 4.58 | 3.56–5.89 | 12.80 |
| Mixed species, closed canopy (72 km) | | | | |
| Chimpanzee ^{c,d,e} | 120 | 1.42 | 1.07–1.87 | 13.44 |
| Gorilla ^{d,f,g} | 28 | 1.07 | 0.72–1.58 | 19.87 |
| <i>Gilbertiodendron</i> forest (47 km) | | | | |
| Chimpanzee ^{c,d,e} | 208 | 3.82 | 3.05–4.78 | 11.30 |
| Gorilla ^{d,f,g} | 6 | 0.36 | 0.19–0.68 | 32.93 |
| Swamp forest (11 km) | | | | |
| Chimpanzee ^h | 5 | NA | NA | NA |
| Gorilla ^h | 2 | NA | NA | NA |

^aConfidence interval.

^bCoefficient of variation.

^cNest creation rate of 1.09 (SE = 0.05).

^dNest decay rate of 90.0 days (SE = 2.85) from this site.

^eAverage nest site size for chimpanzees 2.49 (SE = 0.09).

^fNest creation rate of 1.0 (SE = 0).

^gAverage nest site size for gorillas was 2.59 (SE = 0.15).

^hInsufficient sample size to estimate density (Buckland *et al.*, 2001).

Gabon, and 8) only fresh and recent nests. We compare ape nest site density estimates from the Goulougo Triangle to other chimpanzee and gorilla study sites in Tables III and IV.

As shown in Table I, chimpanzee nest site density was highest in monodominant *Gilbertiodendron* forest, giving the impression of high ape density in there. Gorillas showed a preference for nesting in mixed species forest with an open canopy. Multiple regression analysis indicated a predictive relationship between habitat type and chimpanzee nest sites on transects ($R = 0.81$, $n = 50$). We found a similar relationship between habitat type and gorilla nest sites on transects ($R = 0.76$, $n = 50$). Habitat type accounted for most of the variation in nest site frequency for both species ($\text{ANOVA}_{\text{chimp}} = 16.46$, $\text{df} = 49$, $p < 0.01$; $\text{ANOVA}_{\text{gor}} = 11.77$, $\text{df} = 49$, $p < 0.01$).

The total coefficient of variation of the chimpanzee density estimate based on nest sites is 11.78%. Using Plumptre's (2000) formula to calculate resolution, which allows detection of a 32.6% change in the chimpanzee population with 50% power or a 46.6% change with 80% power. The total coefficient of variation for the gorilla density based on nest sites estimate is 12.53%, which allows detection of a 34.7% change in the gorilla population with 50% power or 49.6% change with 80% power.

Chimpanzee Abundance from Direct Observation

The MCP method and 95% kernel methods yielded community ranges of 19.2 km² and 17.3 km². We calculated density estimates of 2.23 chimpanzees/km² and 2.49 chimpanzees/km² using the ranges from the MCP and 95% kernel analysis, respectively. Community ranges, sizes, and density estimates for several chimpanzee study sites are in Table V. At 50% and 75% probabilities, kernel analysis showed chimpanzees in the Moto community preferentially used core areas of 2.80 km² and 6.75 km². Encounter rates of chimpanzee nests and habitat types along transects in the different areas of the home range are shown in Fig. 3. The highest encounter rate of chimpanzee nests was in the core area of the Moto community home range, with fewer nests seen in the other parts of the home range.

Table II. Comparison of ape density estimates generated from different types of nest count analyses, which are defined as following. Nest Site density estimates were calculated from chimpanzee and gorilla nest sites with average nest site size is based on nest sites of all ages. Nest Sites with Decay Rates from Gabon was generated using published chimpanzee and gorilla decay rates from Gabon. Fresh and Recent Nest Sites were used to calculate great ape densities but sample sizes of fresh and recent nest sites were not sufficient to calculate chimpanzee and gorilla densities separately. Nest Sites with Fresh/Recent Site Size was calculated for chimpanzees and gorillas from only the fresh and recent nest sites. These values were used as multipliers, rather than the average size of nest sites of all ages. For Nest Site Size from Direct Observations, we used average chimpanzee party sizes from this site and weighted gorilla group sizes from visitation at Mbeli Bai (17 km from Goulougo) as multipliers, rather than the average size of nest sites. Nest density estimates were generated from individual nests, rather than sites. Density estimates for Nests with Decay Rates from Gabon were generated using published decay rates from Gabon. Only Fresh and Recent Nests were used to calculate chimpanzee and gorilla density estimates

| Density estimate analysis | Sample size ^a | Density (indiv/km ²) | 95% CI ^b (indiv/km ²) | % CV ^c |
|--|--------------------------|----------------------------------|--|-------------------|
| Nest Sites | | | | |
| Chimpanzee ^{d,e,f} | 372 | 1.53 | 1.21–1.93 | 11.78 |
| Gorilla ^{e,g,h} | 185 | 2.34 | 1.83–2.99 | 12.53 |
| Nest Sites with Decay Rates from Gabon | | | | |
| Chimpanzee ^{d,f,i} | 372 | 1.21 | 0.97–1.52 | 11.34 |
| Gorilla ^{g,h,i} | 185 | 2.70 | 2.13–3.43 | 12.12 |
| Fresh and Recent Nest Sites | | | | |
| All Great Apes ^{d,j,k} | 97 | 5.16 | 3.37–7.91 | 21.87 |
| Nest Sites with Fresh/Recent Site Size | | | | |
| Chimpanzee ^{d,e,l} | 372 | 1.41 | 1.06–1.86 | 14.18 |
| Gorilla ^{e,g,m} | 185 | 2.47 | 1.78–3.43 | 16.69 |
| Nest Site Size from Direct Observations | | | | |
| Chimpanzee ^{d,e,n} | 372 | 1.72 | 1.36–2.17 | 11.73 |
| Chimpanzee ^{d,e,o} | 372 | 2.09 | 1.67–2.62 | 11.42 |
| Gorilla ^{e,g,p} | 185 | 4.26 | 3.42–5.32 | 11.17 |
| Nest | | | | |
| Chimpanzee ^{d,e} | 941 | 1.30 | 1.05–1.60 | 10.42 |
| Gorilla ^{e,g} | 559 | 1.96 | 1.56–2.46 | 11.36 |

Table II. Continued

| Density estimate analysis | Sample size ^a | Density (indiv/km ²) | 95% CI ^b (indiv/km ²) | % CV ^c |
|-----------------------------------|--------------------------|----------------------------------|--|-------------------|
| Nests with Decay Rates from Gabon | | | | |
| Chimpanzee ^{d,i} | 941 | 1.03 | 0.84–1.25 | 9.92 |
| Gorilla ^{g,i} | 559 | 2.26 | 1.82–2.81 | 10.91 |
| Fresh and Recent Nests | | | | |
| Chimpanzee ^{d,j} | 102 | 0.96 | 0.62–1.48 | 22.04 |
| Gorilla ^{g,j} | 116 | 3.10 | 2.19–4.40 | 17.65 |

^aSample sizes after truncation.

^bConfidence interval.

^cCoefficient of variation.

^dNest creation rate of 1.09 (SE = 0.05).

^eNest decay rate of 90.0 days (SE = 2.85) from this site.

^fAverage size of chimpanzee nest sites of all ages was 2.49 (SE: 0.09).

^gNest creation rate of 1.0 (SE = 0).

^hAverage size of gorillas nest sites of all ages was 2.59 (SE = 0.15).

ⁱDecay rate of 113.6 days for chimpanzees and 78 days for gorillas (Tutin and Fernandez, 1984; Tutin *et al.*, 1995).

^jDecay rate replaced with time period multiplier during which this sample of nests was created (based on age of new and recent nests, this was estimated to be approximately 15 days).

^kAverage size for fresh and recent ape sites was 2.82 (SE: 0.21).

^lNest site size from only fresh and recent chimpanzee sites (2.29, SE = 0.20).

^mNest site size from only fresh and recent gorilla sites (2.74, SE = 0.34).

ⁿAverage size of initial parties (2.8 chimpanzees, SE = 0.10) substituted for nest site size multiplier.

^oAverage party size from scan observations (3.4 chimpanzees, SE = 0.08) substituted for nest site size multiplier.

^pParnell (2002) reported that 14 groups (average weaned group size of 6.6) and 7 solitaries visited Mbeli Bai. Including solitaries in the nest building population, yields an approximated average group size of 4.73.

Ape Habitat Utilization Based on Direct Observation and Feces

We recorded habitat type for 258 direct observations of chimpanzees (June 2000–June 2001, September 2001–September 2002) and 184 chimpanzee feces encountered on reconnaissance surveys (September 2001–2002). We recorded habitat type for 193 direct observations of gorillas (February 1999–December 1999, June 2000–June 2001, September 2001–September 2002) and 259 gorilla feces encountered on reconnaissance surveys (September 2001–2002). Chimpanzee habitat utilization as depicted by direct observation and feces do not differ significantly from expected values for each habitat type weighted by abundance within the study area ($\chi^2_{\text{Dir Obs}} = 1.72$, $df = 2$, n.s., $\chi^2_{\text{Feces}} = 11.23$, $df = 3$, n.s.). Gorilla habitat utilization as depicted by direct observation and feces differed significantly from expected values ($\chi^2_{\text{Dir Obs}} = 14.06$, $df = 3$, $p < 0.01$, $\chi^2_{\text{Feces}} = 47.73$, $df = 2$, $p < 0.01$), with higher than expected values in mixed species forest with an open canopy.

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Table III. Density estimates of chimpanzees from nest count surveys (95% confidence intervals or ranges are shown in brackets when available)

| Study site | Density (ind/km ²) | Survey (km) | Description | Primary/ secondary | Source |
|--------------------------|-----------------------------------|------------------|----------------------|-----------------------|-------------------------------|
| <i>P. t. verus</i> | | | | | |
| Ivory Coast | | | | | |
| Tai (Nipla.) | 1.06 | 9 | Evergreen Forest | P | Marchesi <i>et al.</i> , 1995 |
| Tai (Audr.) | 1.72 | 15 | Evergreen Forest | P | Marchesi <i>et al.</i> , 1995 |
| Nationwide | 1.64 | — | All Habitats | P | Marchesi <i>et al.</i> , 1995 |
| Nationwide | 0.40 | — | All Habitats | S | Marchesi <i>et al.</i> , 1995 |
| Senegal | | | | | |
| Assirik (Niokolo Koba) | 0.13 | 84 | Savanna | P | Pruetz <i>et al.</i> , 2002 |
| <i>P.t. troglodytes</i> | | | | | |
| Cameroon | | | | | |
| Dja | 0.79 (0.60–1.04) | 95 | Semideciduous forest | P | Williamson and Usongo, 1995 |
| Ntonga | 1.09 | 58 | Semideciduous forest | P, S | Dupain <i>et al.</i> , 2004 |
| Lac Lobeke | 0.15 | 157 | Semideciduous forest | P | Stromayer and Ekobo, 1991 |
| Mongokole | 0.12 | 50 | Semideciduous forest | P | Stromayer and Ekobo, 1991 |
| Boumba Bek | 0.34 | 100 | Semideciduous forest | P | Stromayer and Ekobo, 1991 |
| Campo | 0.63–0.78 | 404 | Semideciduous forest | P, S | Matthews and Matthews, 2004 |
| Ma'an | 0.80–0.10 | 262 | Semideciduous forest | P, S | Matthews and Matthews, 2004 |
| Central African Republic | | | | | |
| Dzangha-Sangha | 0.16 | 100 | Semideciduous forest | P, S | Blom <i>et al.</i> , 2001 |
| Equatorial Guinea | | | | | |
| Rio Muni | 0.31–1.53 | — | — | — | Jones and Sabater Pi, 1971 |
| Gabon | | | | | |
| Nationwide | 0.32 (0.03–0.49) | 783 | Semievergreen forest | P, S | Tutin and Fernandez, 1984 |
| Nationwide | 0.59 | — | Semievergreen forest | P | Tutin and Fernandez, 1984 |
| Nationwide | 0.14, 0.35 | — | Semievergreen forest | S | Tutin and Fernandez, 1984 |
| Lopé Reserve | 0.2–1.1 | 700 ^a | Semievergreen forest | P, S | White, 1992 |
| Petit Loango | 0.97 | 98 | Coastal, interior | P | Furuichi <i>et al.</i> , 1997 |

Table III. Continued

| Study site | Density (ind/km ²) | Survey (km) | Description | Primary/ secondary | Source |
|-----------------------------|-----------------------------------|------------------|------------------------|-----------------------|-------------------------------|
| Petit Loango | 0.52 | 98 | Coastal, interior | S | Furuichi <i>et al.</i> , 1997 |
| Petit Loango | 0.38 | 218 | Coastal, interior | P | Morgan, 2000 |
| Republic of Congo | | | | | |
| Conkouati | 1.09 (0, 2.58) | 19 | Semideciduous forest | P, S | Maisels and Cruikshank, 1996 |
| Conkouati | 2.27 (1.76, 2.78) | 30 | Subtropical | P, S | Maisels and Cruikshank, 1996 |
| Goulougo | 1.53 (1.21, 1.93) | 222 | Semideciduous forest | P | This study |
| Lac Tele | 0.70 (0.4, 1.3) | 234 | All habitats | P | Poulsen and Clark, 2004 |
| Southwest Congo | 0.27 ^a | 265 | Semideciduous forest | P, S | Ihobe, 1995 |
| <i>P. t. schweinfurthii</i> | | | | | |
| Uganda | | | | | |
| Budongo | 1.36 | 514 | Moist semideciduous | P, S | Plumptre <i>et al.</i> , 2003 |
| Kalinzu | 1.55 | 311 | Moist evergreen forest | P, S | Plumptre <i>et al.</i> , 2003 |
| Kalinzu | 1.45, 1.50 | 500 ^a | Moist evergreen forest | P, S | Furuichi <i>et al.</i> , 2001 |
| Kalinzu | 2.0-4.7 | 20 | Moist evergreen forest | P, S | Hashimoto, 1995 |
| Kibale | 1.78-4.81 | 475 ^a | Moist evergreen forest | P | Balcomb <i>et al.</i> , 2000 |
| Kibale | 0.82-1.82 | 475 ^a | Moist evergreen forest | S | Balcomb <i>et al.</i> , 2000 |
| Kibale | 2.32 | 564 | Moist semideciduous | P, S | Plumptre <i>et al.</i> , 2003 |
| Kibale (K-30) | 1.89 (1.04-4.21) | 108 | Moist semideciduous | P | Skorupa, 1988 |
| Kibale (K-15) | 0.65 (0.35-0.98) | 104 | Moist semideciduous | S | Skorupa, 1988 |
| D.R.C. | | | | | |
| Ituri | 0.8 | 268 ^a | Moist semievergreen | P, S | Thomas, 1991 |
| Kahuzi-Biega | 0.13 | — | Montane forest | | Yamagiwa <i>et al.</i> , 1992 |
| Odzala | 2.2 | 68 | All habitats | P | Bermejo, 1999 |

^aSmaller subset of transects were surveyed several times.

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Table IV. Density estimates of western lowland gorillas from nest count surveys (95% confidence intervals or ranges are shown in brackets when available)

| Study site | Density (ind/km ²) | Survey (km) | Description | Primary/secondary | Source |
|---------------------------------|--------------------------------|------------------|----------------------|-------------------|-------------------------------|
| Cameroun | | | | | |
| Dja | 1.71 (1.02–2.86) | 95 | Semideciduous forest | P | Williamson and Usongo, 1995 |
| Ntonga | 3.87 | 58 | Semideciduous forest | P, S | Dupain <i>et al.</i> , 2004 |
| Lac Lobeke | 2.5 | 157 | Semideciduous forest | P | Stromayer and Ekobo, 1991 |
| Mongokole | 1.2 | 50 | Semideciduous forest | P | Stromayer and Ekobo, 1991 |
| Boumba Bek | 1.6 | 100 | Semideciduous forest | P | Stromayer and Ekobo, 1991 |
| Campo | 0.2 | 404 | Semideciduous forest | P, S | Matthews and Matthews, 2004 |
| Central African Republic | | | | | |
| Dzangha-Sangha | 1.52 (0.93–2.50) | 81 | Semideciduous forest | P, S | Remis, 2000 |
| Dzanga-Ndoki | 1.6 (1.1, 2.3) | 100 | Semideciduous forest | P, S | Blom <i>et al.</i> , 2001 |
| Dzangha-Sangha | 0.89–1.45 | 783 | Semideciduous forest | P, S | Carroll, 1986 |
| Ngotto | 0.34–0.40 | 94 | Semideciduous forest | P | Brugiere and Sakom, 2001 |
| Gabon | | | | | |
| Nationwide | 0.18 (0.01–0.44) | 783 | Semievergreen forest | P, S | Tutin and Fernandez, 1984 |
| Nationwide | 0.23 | — | Semievergreen forest | P | Tutin and Fernandez, 1984 |
| Nationwide | 0.19, 0.35 | — | Semievergreen forest | S | Tutin and Fernandez, 1984 |
| Lopé Reserve | 0.3–1.0 | 700 ^a | Semievergreen forest | P, S | White, 1992 |
| Petit Loango | 0.03 | 98 | Coastal, Interior | P | Furuichi <i>et al.</i> , 1997 |
| Petit Loango | 0.59 | 98 | Coastal, Interior | S | Furuichi <i>et al.</i> , 1997 |
| Petit Loango | 0.08 | 218 | Coastal, Interior | P | Morgan, 2000 |
| Republic of Congo | | | | | |
| Conkouati | 3.90 (2.41, 5.39) | 19 | Semideciduous forest | P, S | Maisels and Cruikshank, 1996 |
| Conkouati | 1.62 (1.08, 2.16) | 30 | Subtropical | P, S | Maisels and Cruikshank, 1996 |

Table IV. Continued

| Study site | Density (ind/km ²) | Survey (km) | Description | Primary/ secondary | Source |
|--------------|-----------------------------------|-------------|----------------------|-----------------------|--------------------------|
| Goulougo | 2.34 (1.83, 2.99) | 222 | All habitats | P | This study |
| Lac Tele | 2.91 (1.6, 5.6) | 234 | All habitats | P | Poulsen and Clark, 2004 |
| Motaba | 0.1 | 142 | All habitats | P | Fay and Agnagna, 1992 |
| Ndoki | 0.2 | 101 | All habitats | P | Fay and Agnagna, 1992 |
| Mbomo | 0.6 | 96 | All habitats | P | Fay and Agnagna, 1992 |
| Lake Mboukou | 1.14 | 63 | All habitats | P | Fay <i>et al.</i> , 1989 |
| Ndoki | 1.9–2.6 ^a | — | Semideciduous forest | P | Nishihara, 1994 |
| Odzala | 5.4 | 68 | All habitats | P | Bermejo, 1996, 1999 |

^aSmaller subset of transects were surveyed several times.

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Table V. Density estimates calculated from direct observations of chimpanzee community sizes and home ranges.

| Study Site, Method | Range (km ²) | Community Size | | | Density chimps/km ² | Source |
|---------------------------|--------------------------|-----------------|-------------------|--|--------------------------------|-----------------------------------|
| | | All individuals | Excluding infants | | | |
| Budongo, MCP | 9.7 | 56 | 45 | | 4.6 | Fawcett, 2000 |
| Budongo, Fixed kernel | 9.2 | 56 | 45 | | 4.9 | Fawcett, 2000 |
| Budongo, Adaptive kernel | 18.2 | 56 | 45 | | 2.5 | Fawcett, 2000 |
| Budongo, Centroid cluster | 7.7 | 56 | 45 | | 5.8 | Fawcett, 2000 |
| Gombe, 500 × 500 m grid | 13 | | 23 | | 1.77 ^a | Wrangham and Smuts, 1980 |
| Goulougo, MCP | 19.2 | 54 | 43 | | 2.23 | This study |
| Goulougo, Fixed kernel | 17.3 | 54 | 43 | | 2.49 | This study |
| Kibale, MCP | 14.9 | 41 | 30 | | 2.01 | Chapman and Wrangham, 1993 |
| Kibale, 200 × 200 grid | 8.5 | 41 | 30 | | 3.53 | Chapman and Wrangham, 1993 |
| Kibale, 200 × 200 grid | 7.8 | 41 | 30 | | 3.85 | Chapman and Wrangham, 1993 |
| Kibale, MCP | 15.8 | ~50 | 34 | | 2.15 | Wilson <i>et al.</i> , 2001 |
| Kibale, MCP | 37.8 | ~50 | 34 | | 0.90 | Wilson <i>et al.</i> , 2001 |
| Mahale, 400 × 400 grid | 19.4 | | | | 3.92 | Nishida, 1979 |
| Tai, MCP (1982) | 18.1 | 74 | 56 | | 3.1 | Boesch and Boesch-Achermann, 2000 |
| Tai, Unknown (1988) | 26.0 | 79 | 44 | | 1.7 | Marchesi <i>et al.</i> , 1995 |
| Tai, MCP (1989) | 23.7 | 66 | 51 | | 2.2 | Boesch and Boesch-Achermann, 2000 |
| Tai, MCP (1995) | 15.5 | 29 | 19 | | 1.2 | Boesch and Boesch-Achermann, 2000 |
| Tai, MCP (Northern) | 10.5 | 35 | 32 | | 3.0 | Herbinger <i>et al.</i> , 2001 |
| Tai, MCP (Middle) | 9.0 | 11 | 7 | | 0.8 | Herbinger <i>et al.</i> , 2001 |
| Tai, MCP (Southern) | 13.5 | 63 | 36 | | 2.7 | Herbinger <i>et al.</i> , 2001 |

^aCalculated for this study.

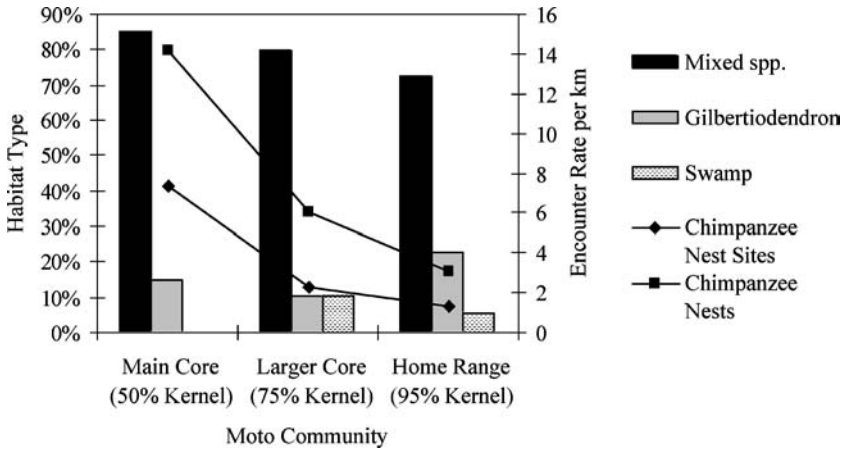


Fig. 3. Habitat composition of core, home range, and peripheral areas in the Moto chimpanzee community compared to the encounter rate of chimpanzee nest sites and nests.

We compare habitat utilization as depicted by different methods in Fig. 4a for chimpanzees and Fig. 4b for gorillas. Habitat use profiles of both species on nest surveys significantly differed from those of direct observations and traces encountered on reconnaissance surveys ($\chi^2_{\text{chimp}} = 302.5$, $df = 4$, $p < 0.01$, $\chi^2_{\text{gor}} = 96.5$, $df = 4$, $p < 0.01$). We found the vast majority of chimpanzee nests in habitat types with closed canopies, which may reflect the constraints of arboreal nesting behavior rather than foraging preferences. Direct observation of gorillas and their fecal traces along reconnaissance surveys showed that they used several habitat types, whereas nest encountered on transects showed only a preference for mixed species forest with an open canopy.

DISCUSSION

Determining the distribution of chimpanzee and gorilla populations is an immediate priority for researchers and conservationists in the Congo Basin. Relatively little is known about their behavior and ecology, but recent surveys showed that $>50\%$ of chimpanzees and gorillas in some regions have already perished (Huijbregts *et al.*, 2003; Leroy *et al.*, 2004; Walsh *et al.*, 2003). A better understanding of the dynamics of the human disturbance, such as habitat destruction and commercial bushmeat hunting, and epidemic diseases that are ravaging their populations can only be gained with accurate baseline information from sites throughout the region. The

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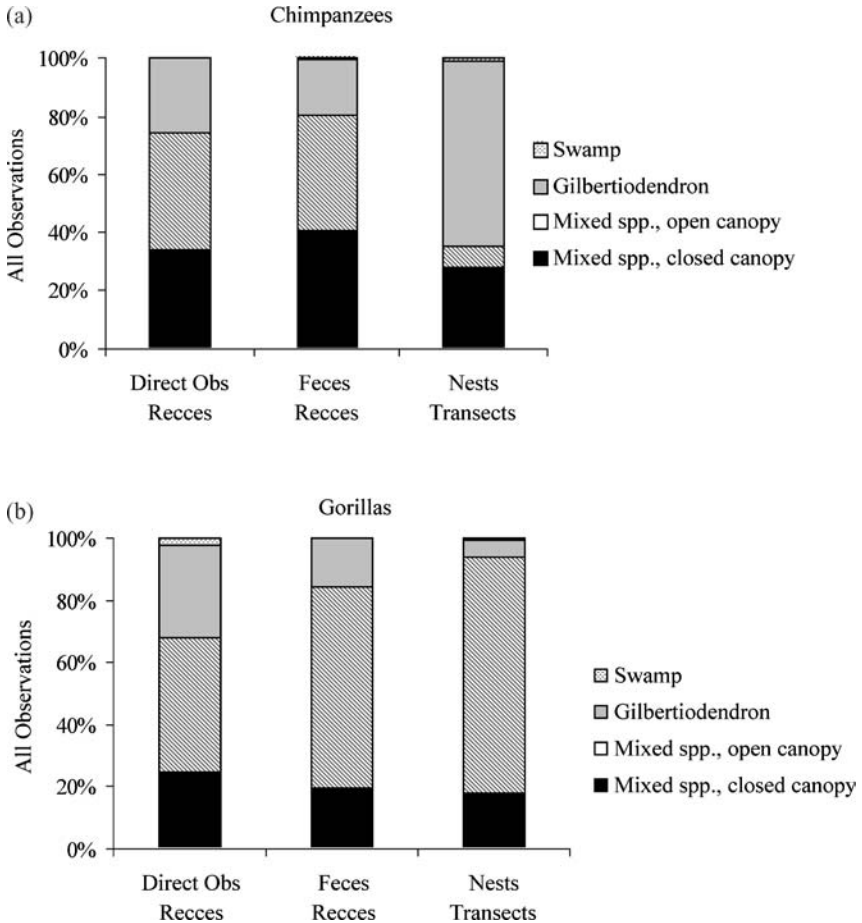


Fig. 4. (a, b) Chimpanzee and gorilla habitat use depicted by direct observation on reconnaissance surveys, feces on reconnaissance surveys, and nests on transect lines.

data also provide a quantitative basis for allocating limited conservation resources and establishing long-term monitoring efforts in stronghold areas that will ensure their preservation.

Estimates of Ape Densities

Though a country-wide survey has not yet been undertaken in the Republic of Congo, previous surveys of ape abundance suggested that the country harbors relatively large chimpanzee and gorilla populations

(Bermejo, 1995, 1999; Blake *et al.*, 1995; Fay and Agnagna, 1992; Maisels and Cruikshank, 1996; Poulsen and Clark, 2004). Using several different techniques to calculate density (Table II), we consistently found a relatively high abundance of both chimpanzees and gorillas in the Goualougo Triangle. The ape density estimates serve as a baseline for the area and comparative data set for similar habitats in the region.

The density of chimpanzees in the Goualougo Triangle is within the range of densities from other sites in the Republic of Congo, but relatively high compared to reports from other central and west African sites (Table III). Gorilla density estimates in Goualougo are relatively high compared to other Central African countries, but do not reach the high densities previously documented in other parts of Congo (Table IV). Based on the potential ape habitat within Nouabalé-Ndoki National Park, it is likely that $\geq 10,000$ apes reside in these forests. With the additional chimpanzees and gorillas residing in the adjacent protected areas (Dzanga-Ndoki National Park and Dzanga-Sangha Special Reserve in the Central African Republic, and the Lac Lobeke National Park in Cameroon), the Sangha River Tri-national Region is one of the largest remaining tracts of continuous ape habitats.

Comparison of Different Survey Methods

Direct observation density estimates (Table V) generally yield higher chimpanzee densities than line transect nest counts (Table III), but few studies have compared the 2 methods at the same site. Marchesi *et al.* (1995) found that the density estimates from observation of a habituated chimpanzee community and nest surveys along transects in the Taï Forest were identical (1.7 chimpanzees/km²). In contrast, researchers have reported direct observation density estimates ranging from 2.5 to 5.8 chimpanzees/km² from Budongo, whereas extensive line transect surveys in the same area resulted in much lower density estimates of 1.36 chimpanzees/km² (Fawcett, 2000; Plumptre *et al.*, 2003). Our results are relatively similar findings between nest counts along transect (1.53 chimpanzees/km²) and direct observations of a single community (2.2–2.5 chimpanzees/km²).

Our results show that chimpanzee nest encounter rates are dependent on the specific area of a community range that is surveyed. Neither nests nor nest sites were randomly distributed within the Moto community and the distribution of nest sites reflected the basic ranging patterns of the chimpanzees. Nest surveys within the community core area resulted in higher encounter rates, relative to more peripheral areas in the community range. Higher density estimates resulting from direct observation methods may

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reflect sampling bias toward frequently used core areas. In contrast, line transects surveys with transects systematically distributed with a random start may more accurately depict ape distribution over a larger landscape than reconnaissance surveys conducted within the range of a single group or community can.

The comparison of habitat utilization in Fig. 4a and b shows that survey methods differed in their depictions of habitat use profiles for each species. For chimpanzees, nests were more often found along transects in monodominant *Gilbertiodendron* forest and mixed species forest with a closed canopy. Direct observation and traces on reconnaissance surveys show that chimpanzees also frequented mixed species forest with an open canopy. Gorilla nests on transects depicted an overwhelming preference for mixed species forest with an open canopy, which we confirmed by direct observations and traces encountered on reconnaissance surveys, but there was also evidence that gorillas used other habitat types. Together, the reconnaissance and transect data sets indicate that chimpanzees and gorillas use the same habitat types to different degrees, with the greatest divergence in sleeping site preferences.

Habitat Type Utilization by Sympatric Apes

We found apes and their traces most frequently in mixed species forest, which comprises 74% of the Goulougo Triangle study area. Estimated chimpanzee density in mixed species forest with a closed canopy was higher than gorilla density there. Marchesi *et al.* (1995) reported a similar preference by chimpanzees in the Taï forest for closed canopy forest and concluded that tree cover played an important role in habitat choice for chimpanzee nesting. Gorilla density estimates from nest surveys are much higher in mixed species forest with an open canopy than in other habitats, which is in agreement with other reports suggesting that it is a preferred habitat for western gorillas (Brugiere and Sakom, 2000; Fay, 1989; Mehlman and Doran, 2002; Tutin *et al.*, 1995).

Chimpanzee nest sites along transects were most frequent in monodominant *Gilbertiodendron* forest. We occasionally encountered gorillas and their traces there, but nest sites were rare. Direct observations of chimpanzees foraging in this habitat type peak in mast fruiting events every few years and are relatively rare during the interim. Based on differences with direct observations and patterns of nest decay, we suggest that the long-lasting arboreal nest sites in *Gilbertiodendron* forest may lead to an overestimation of chimpanzee densities there. Our observations of nest aging patterns indicated that nests may last longer in monodominant *Gilbertiodendron* forest than in other habitat types (Onononga *et al.*, *in prep.*).

Differential nest decay patterns between habitats merits further investigation because this concern extends to ape monitoring efforts in other areas of central Africa with large stands of monodominant *Gilbertiodendron* forests such as the Democratic Republic of Congo, Cameroon, Gabon, and the Central African Republic.

Based on previous surveys in northern Congo, we had anticipated a relatively high abundance of gorilla nests in swamp forests, but apes in the Goulougo study area did not often use swamps (Blake, 1995; Fay and Agnagna, 1992; Fay *et al.*, 1990; Poulsen and Clark, 2004). Although 5% of the study area consists of swamp forests, the low number of observations—direct, feces, nests—there suggests that it is underutilized relative to its occurrence. Researchers generally cite 3 hypotheses to explain gorilla swamp use: ample food sources (Fay *et al.*, 1989), prevalence of nesting materials (Williamson and Usongo, 1995), and refuge provided from human disturbance (Blake, 1993). Our results do not show that gorillas were attracted to food resources or nesting materials in the swamp forests of the Goulougo Triangle, but that they preferred *terra firma* habitat types and more specifically mixed species forests with an open canopy.

Though chimpanzees and gorillas showed specific preferences, we observed both species in all habitats, which reflects a certain degree of overlap in their feeding ecology and ranging patterns. Similar to early reports from northern Congo, we have recorded significant dietary overlap between them in plant items consumed and simultaneous cofeeding on the same fruiting trees (Kuroda *et al.*, 1996; Morgan and Sanz, *in press*). Contrary to reports of mutual avoidance from other sites, we observed neutral interactions between chimpanzees and gorillas at foraging intersections and sleeping sites (Basabose and Yamagiwa, 2002). However, further research is needed to document the niche separation between them in the lowland forests of the Congo Basin.

Conclusions for Monitoring Ape Populations

The necessity of precise density estimates to monitor remaining apes in central Africa has become imperative. We established baseline information to monitor future trends in ape abundance and habitat utilization in the Goulougo Triangle. With the combined coefficient of variation for the chimpanzee density estimate in our study (11.78%), we will be able to detect a change in the population greater than 32.6% with 50% power or a 46.6% change with 80% power. This degree of population fluctuation would represent the type of catastrophic decline like that associated with an Ebola epidemic (Huijbregts *et al.*, 2003; Leroy *et al.*, 2004; Walsh *et al.*, 2003).

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However, resolution of the density estimates would probably not allow us to detect more subtle changes in ranging and social group dynamics associated with selective logging or other human disturbances (Plumptre, 2000; White, 1992; White and Tutin, 2001).

For long-term monitoring, it is necessary to improve the accuracy and precision of estimates and their ability to detect changes in ape populations. Plumptre (2000) showed that to detect a 10% change in a population, the overall coefficient of variation for all factors contributing to the density estimate must be less than 2.4% (with 80% power) or 3.6% (with 50% power). However, the coefficient of variation associated with even a single conversion factor, such as nest decay rate, often exceeds these limits. An alternative is to repeat surveys over time to detect trends. When one monitors the population at regular intervals, TRENDS software (Gerrodette, 1987) can be used to calculate the power to detect trends in specific numbers. For example, if one surveys the population 3 (or 4) times, assuming the population change is linear and that the coefficient of variation is inversely proportional to abundance and equal to 11.78%, then at a 5% significance level, using a 2-tailed test one could detect a 18% (or 11%) decrease in the population with 50% power and a 26% (or 16%) decrease with 80% power. The ability to detect changes in the population numbers continues to improve as the number of times the survey is repeated increases.

Based on our findings, we are able to make several specific suggestions for future studies attempting to estimate ape abundance and depict habitat utilization. Line transect ape nest surveys should encompass the ranges of several social groups and all habitat types within a large landscape. Chimpanzee surveys should encompass both core and peripheral areas of a community range, with both chimpanzee and gorilla surveys stratified by habitat type. Minimizing the number of conversion factors and calculating site-specific factors decreases the associated error and improves ability to detect changes. It is possible to improve the accuracy and potentially the precision of indirect ape surveys by 1) applying discriminant function analysis to assign ape nests to either chimpanzees or gorillas, 2) calculating site-specific ape nest decay rates with associated variance for standing-crop surveys, 3) implementing the marked-nest method (Plumptre and Reynolds, 1996) whenever feasible to completely remove the decay rate conversion factor from the ape density equation, and 4) documenting nest creation rates with variance in survey regions. However, we propose that repeated nest surveys at regular intervals in the same region may be the most effective means to document increasing or decreasing trends in ape populations. One should also record additional relevant variables, i.e., biotic or human disturbance, during repeated surveys to investigate their potential influence on ape densities. Finally, one should validate ape nest survey results with

findings from other methods, such as direct observations, when possible. Only accurate and precise density estimates of existing chimpanzee and gorilla populations in central Africa can effectively inform conservation planning to ensure the preservation of future generations of them.

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