Range Occupation and Population Estimates of Bonobos in the Salonga National Park: Application to Large-scale Surveys of Bonobos in the Democratic Republic of Congo

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Introduction

Conservation of the bonobo, Congo's endemic ape, is one of the most important conservation priorities in the Democratic Republic of Congo (DRC). Bonobos are classified as endangered by both the IUCN (1996) and CITES (2001). In determining where bonobos occur, their population numbers and the threats to them are critical for development of a range-wide conservation strategy for the species. The need for information on the bonobo's status is all the more urgent given the imminent opening of their range to logging and other extractive activities following the end of DRC's conflict.

The potential bonobo range, variably estimated from 341,000 – 472,000 km^2, is restricted to DRC's central cuvette; however, occupation of this area by bonobos is not contiguous (Butynski 2001, Meyers Thompson 1997). Large areas of forest contain few or no bonobos, while the species occurs in relatively high numbers in other areas. Most studies of bonobos have been conducted in very small study areas, widely dispersed within the range. Even at this scale, researchers report wide variability in occurrence and population size. Speculative estimates of the bonobo's global population range from 13,500 – 100,000, though figures from 20,000 – 50,000 are the most widely cited (Butynski 2001). Some authors suggested that 50% of the bonobo's range might have been lost over the past several decades (Dupain and Van Elsacker 2001, Thompson-Handler et al. 1995), though early records of bonobos suggest that there were major discontinuities in their distribution over 80 years ago (Kortland 1995).

Until recently, much of the bonobo's range was isolated from major settlements and had historically low human population density. This has likely ensured the protection of many bonobo populations. Passive protection, however, may no

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longer be adequate. A decade of conflict and political instability (1996 – 2006) has weakened the national parks service (Institut Congolais pour la Conservation de la Nature, ICCN) and favored widespread access to firearms. Artisanal scale extraction of natural resources, including bushmeat, increased in many areas in the bonobo's range during the period of conflict (Draulans and van Krunkelsven 2002, Dupain et al. 2000). As Congo's human population and economy grow, even the most remote forests occupied by bonobos will be opened to exploitation. Threats to bonobos and other wildlife will intensify. Active protection and conservation will become increasingly more important.

Mobilizing the financial resources and creating the political will to protect bonobos and conserve key areas of their range will require strategies that are well-informed and focused if they are to have any chance of success. This will require updated information on the distribution and abundance of bonobos, and a well-founded evaluation of the impact of the threats they face. Developing conservation priorities and monitoring the status of bonobos will require large-scale surveys over important areas of their range (Mohneke and Fruth 2008, Reinartz et al. 2008, Thompson-Handler et al. 1995). An important question is how these surveys should be completed?

The Salonga National Park and its Bonobos

The Salonga National Park is the largest, and until recently the only, protected area within the bonobo's range. The park was established in 1970 and enrolled as a World Heritage Site in 1984. The park is composed of two sectors, a northern and a southern, separated by a corridor buffer zone between them (Fig. 10.1). It covers ca. 33,346 km^2, about 10% of the bonobo's range, and represents one of the most intact blocks of tropical forest in DRC (Siegert 2003, Sanderson et al. 2002). Closed mixed tropical forests cover > 90% of the park and ca. one third are permanently or seasonally inundated. Recent clearings, regenerating forests, and natural savannas represent a small percentage of the park area (Siegert 2003).

Current human occupation averages less than 3 inhabitants per km^2 over the area within 15 km of the park limits. About 215 villages are within 15 km of the park borders. Most of them are small with < 500 individuals. There are nine villages within the park. Under current legislation they are all illegal. Kitawala, located just inside the park border in the northern sector, has a total population of 5,000 – 7,000 people, many of whom belong to a syncretic religious sect of the same name that retreated into what was to become the park in the1960s to avoid contact with other groups. Eight settlements of the Iyaelima people, with a total population of ca. 2500 and comprising the entire population of this ethnic group, are located along a major footpath bisecting the southern sector of the park (Thompson et al. 2008). Almost half of the park area is located > 15 km from a permanent human settlement (Fig. 10.2).

Despite a low level of permanent human occupation and distance from major settlements, the park remains relatively accessible along a network of rivers that can be navigated by dugout canoe. Less than one-third of the park area is located more

Fig. 10.1 The Salonga National Park (*See Color Plates*).

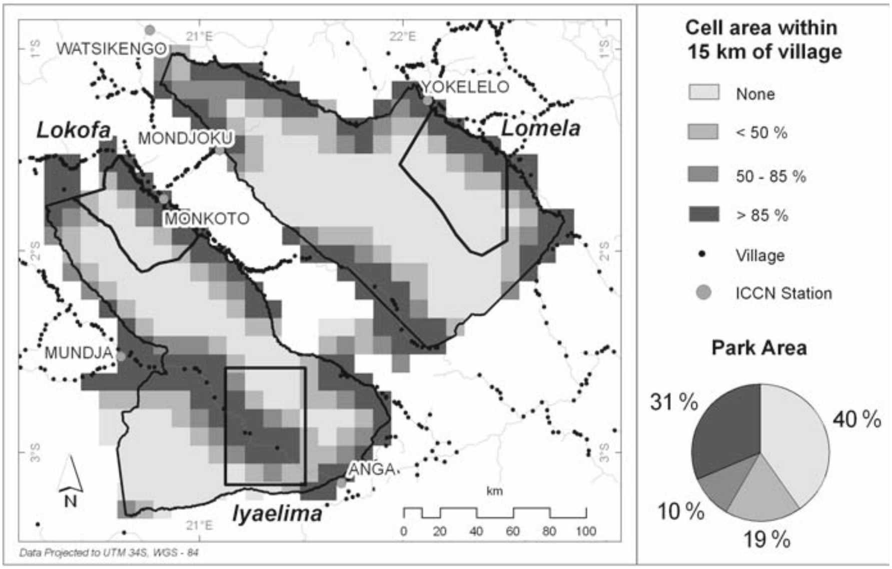

Fig. 10.2 Human settlement in the Salonga National Park and vicinity. Bonobo population inventory blocks are indicated in outline.

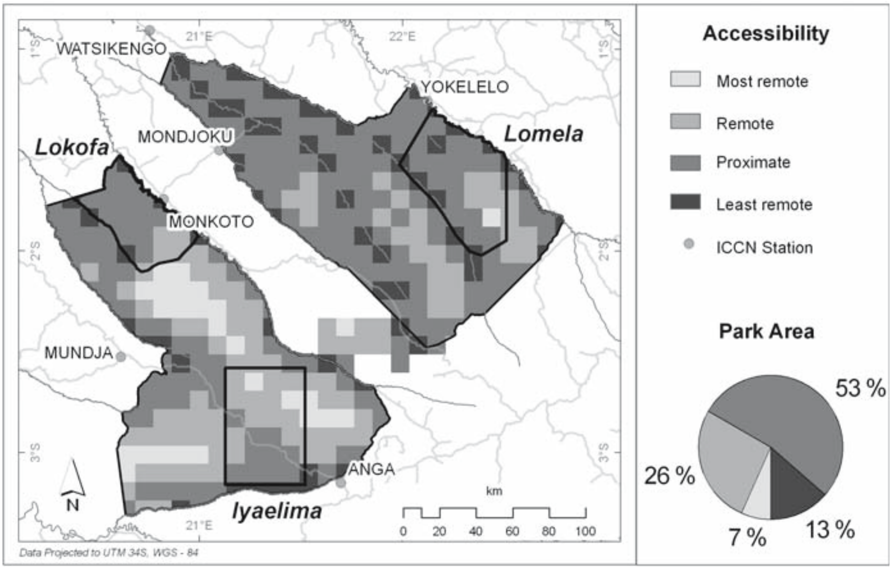

Fig. 10.3 Accessibility of the Salonga National Park and eastern corridor survey zone is calculated as the percentage of each 10 × 10 km quadrat that is within 15 km of human access (roads and rivers accessible by dugout canoe). Percentage quadrat area > 15 km from access: Most remote, 100; remote, 75 – 99; proximate, 50 – 74; least remote < 50. Bonobo population inventory blocks are indicated in outline.

than 15 km from a navigable river. Nearly 85% of the northern sector of the park is within 15 km of a river navigable by dugout canoe (Fig. 10.3).

The status of bonobos in the Salonga National Park was poorly known throughout the early years of the park's history. As recently as the 1980s, it was uncertain whether the park even contained bonobos (Susman et al. 1981). Van Krunkelsven (2001) and van Krunkelsven et al. (2000) reported the first population surveys of bonobos in the Salonga National Park in the late 1990s. Other surveys followed, including Lui Kotal, just outside the park (Mohneke and Fruth 2008, Mohneke 2004) and at a number of sites in both the northern and southern sectors (Reinartz et al. 2008, 2006). Intensive studies of semi-habituated bonobos were initiated at Lui Kotal in 2000 (Hohmann and Fruth 2003) and Etate in 2004 (Reinartz et al. 2008).

Taken as a whole, these surveys confirmed that at least some areas of the Salonga National Park contained important numbers of bonobos and provided a useful comparison of the abundance of different bonobo communities. However, most of the survey sites covered relatively small areas, < 300 km^2, and often much smaller. Direct extrapolation of the results to larger areas is problematical because there is little basis to determine how representative these study areas are of communities and populations elsewhere. A comprehensive picture of the park's bonobos and factors affecting them was lacking.

In the late 1990s, following the outbreak of conflict, ICCN patrols were reduced leaving the park mostly untended for much of the past decade. Just how badly the park and its bonobos were threatened by the conflict remained uncertain (Draulans and van Krunkelsven 2002). Surveys were urgently needed to provide an up-to-date status of bonobos and to identify needs for protection.

Objectives

The current chapter and Chapter 12 in this volume present the results of a multiphase, spatially nested survey to develop the first park-wide estimate of the distribution and abundance of bonobos and an evaluation of the impact of human activities, in particular hunting, in the largest protected area within their range. We first present the design and results of the surveys, which at the largest spatial extent cover an area >30,000 km^2. We then integrate the results of the different survey phases to provide an estimate of the population of bonobos in the park. The paper concludes with recommendations for the use of multiphase surveys to determine the occurrence and abundance of bonobos in other areas of their range.

Survey Design and Data Collection

Two major challenges face large-scale surveys of bonobos. First, is the impossibility of using direct counts for the census. Bonobos are shy, and visibility in the forests they occupy is limited. Thus, inventories depend upon counts of their sign, in particular nests, and their conversion to estimates of bonobo density. The second challenge is to develop a survey design that will provide a representative sample of observations of bonobos and their sign, the habitats they occupy, and human activity in the forest at an appropriate degree of spatial resolution.

Field data for forest surveys, including those reported here, are generally collected over relatively small areas and at a fine spatial resolution, with observations made from line transects and reconnaissance walks usually at distances of a few tens of meters or less from the observer and line of travel. Yet the total extent of the area to be surveyed is much larger, and in the case of landscape-scale surveys, such as the Salonga National Park, tens of thousands of square kilometers must be evaluated. Costs and logistical difficulties preclude covering all areas of the landscape with the same degree of survey resolution. Determining what will be measured for each observation and where observations will be made (allocation of survey effort) are questions of major concern.

To resolve these problems we used a multiphase survey design. In multiphase designs, an initial area is surveyed for readily measured, coarse-resolution variables. In subsequent phases, subsets of the overall survey area are selected based on the results of the initial survey and resurveyed for the same and new variables at a finer spatial resolution (Urban 2002). Multiphase designs provide a means to allocate survey effort efficiently and optimally across a range of spatial scales. They also provide a statistically sound framework for the extrapolation of the results of smaller scale surveys to larger areas.

The Salonga survey program used a three-phase design spanning a twenty-fold range of spatial resolution. The largest survey zone was > 2500 times the area of the smallest. The surveys shared the same overall goals. However, the objectives of each survey phase were specific to the spatial scale of the design. Figure 10.4 provides an overview of the survey objectives and associated spatial design and data collection of each phase.

In Phase I, at the largest spatial extent, the survey area covered most of the park and portions of the immediate buffer zone and corridor between the two park sectors. We made field observations from compass-directed reconnaissance walks, termed "recces," placed systematically at a spatial grain of ca. 10 × 10 km (quadrats of 100 km^2). In Phase II, we surveyed three subsets of the landscape covered in Phase I, termed inventory blocks, which cover 2000–3000 km^2 each, using quadrats of ca. 5 × 5 km (25 km^2) to allocate survey effort. We collected field data from both recces and formal line transects, allocated spatially using the DISTANCE software (Thomas et al. 2001a) and using data collection methods and analytical protocols described in Buckland et al. (2001). In Phase III surveys, we evaluated the persistence of bonobo nest site use in spatial units termed monitoring zones covering ca. 12.5 km^2 each. We collected Phase III data from line transects at a spatial grain of 0.5 × 0.5 km (0.25 km^2). Phase III surveys were repeated in a sample of 8 monitoring zones at intervals of 5 – 7 months.

At the outset of the surveys we had very little information on the distribution and abundance of bonobos across the park. We used a nonstratified, systematic placement of recces and transects. This is recommended to ensure unbiased and representative samples of observations where little antecedent information is available to stratify or otherwise model survey design (Thomas et al. 2001b).

A. Survey objectives specific to spatial scale.

GOALS:	Determine bonobo occurrence	Identify key habitats	Assess impact hunting
OBJECTIVES			
Phase I	Occupancy	Geographic clines	Landscape-scale patterns
Phase II	Density	Nesting habitats	Relationship with bonobo density
Phase III	Nesting site use over time	Characteristics of intensively used nesting sites	Impact on nesting site use

B. Survey effort and data collection specific to spatial scale.

Phase	Spatial class (sample size)	Survey unit area (km^2)	Survey grid (km)	Data collection	Sampling placement
I. Exploratory	Landscape (n=1)	33,000	10 x 10	Recces	Systematic
II. Inventory	Block (n = 3)	2,000 - 2,750	5 x 5	Recces, transects	Systematic
III. Monitoring	Zone (n = 8)	12.5	0.5 x 0.5	Transects	Systematic

Fig. 10.4 Objectives and design of the Salonga National Park multiphase survey. A) Survey objectives are based on the same survey goals but are specific to each survey phase determined by the spatial scale and resolution of the data collection. B) Survey zone area, the spatial grain and placement of survey effort and data collection methods are specific to each survey phase. Phase I results inform design and data collection of Phase II inventories. Phase I and Phase II results are used to design Phase III monitoring data collection. Phase I and Phase II are single data collection designs. Phase III data collection is repeated over intervals of 4–6 months.

We conducted Phase I field work from 2003 – 2005. Field teams covered the southern sector and about half the northern sector of the park from 2003–2004 during the CITES-MIKE project (Blake 2005). They completed the remaining half of the northern sector and the eastern corridor in 2005. We conducted Phase II surveys in the Lokofa, Iyaelima and Lomela blocks from 2005 – 2006. We initiated Phase III surveys in 2005 in eight monitoring zones in the Lokofa block. Six monitoring zones covered bonobo nesting areas discovered during Phase I and Phase II surveys. Two monitoring zones covered areas where nests were not previously encountered. We resurveyed the monitoring zones two to three additional times each from 2005 – 2006.

We used GIS to determine geographic coordinates of line transects (start and end points) and to plot quadrat centroids used to orient recces. We used GPS units and compasses to locate recce and transect positions in the field and to orient in the forest. We measured distances along line transects with topofils.

Teams composed of a team leader, assistant leader, compass man, two observers, and supported by 6 – 8 porters and local guides collected the field data. We used GPS track logs to document the geographic position of survey teams as they moved across the survey zone. Field teams recorded geographic coordinates (waypoints) for all observations, and measured perpendicular distances from the line of travel to the center of the observed object (bonobo nest, snare, etc) on line transects (but not on recces).

Indicators of bonobo occurrence recorded in the field include direct observations of subjects (seen, heard, or both), feeding signs, and nests. We recorded tree species containing nests, nest height, nest age class (fresh, recent, old, disappearing) based on criteria established for this study and photographed each nest. After completing nest measures from the recce or line transect, field teams located additional nests not seen from the line of travel and produced a field map of each nest aggregation showing nest locations.

Habitat indicators recorded in the field include substrate and vegetation type and under-story class. We classified the habitat for all observations at every 100 m along line transects. Substrate types were: permanently inundated, seasonally inundated, and *terra firma* (non-inundated). Vegetation types included permanently flooded forest, seasonally inundated forest, mixed *terra firma* forest, monodominant *terra firma* forest, open canopy Marantaceae forest, recent regeneration, secondary forest, and savanna. Understory classes included: open shrub, closed liana/shrub and herbaceous dominated. Observers classified habitats as the dominant types covering a circle of ca. 10m surrounding their position or the position of the observation.

Indicators of human hunting included encounters with hunters, snares (classed as active or inactive and by the size of the sapling anchor) and hunting camps. We recorded hunting camp activity (occupied, recently abandoned, long-abandoned), the number of shelters and beds, and the presence and size of meat drying racks. We also recorded fishing camps and other fishing signs, trail crossings, machete cuts, and evidence of other extractive activities. We photographed most of the illegal hunting and fishing camps encountered in the park.

We recorded field observations with associated geo-referencing data (GPS waypoints and tracklogs) on Excel spread sheets for data analyses. We used DISTANCE software (Thomas et al. 2001a, Southwell and Weaver 1993) to determine nest densities based on line transect nest counts. We mapped encounter rates (number of observations per km surveyed) of bonobo and human activity indicators to each survey quadrat using ARC GIS and conducted further spatial analyses via ESRI statistical packages (Mitchell 2005) and other sources. Table 10.1 is a summary of data collection and analytical methods for the three survey phases.

Table 10.1 Data collection and analysis of the multiphase bonobo surveys in the Salonga National Park

Survey phase	Dates	Location	Survey units	Indicators	Analysis
I. Landscape exploration	2003 – 2005	Southern and northern sectors of park; eastern corridor	Pilot transects (1 km each) linked by recces for MIKE surveys. Recces linking centroids of 10 × 10 km quadrats for northern sector and corridor surveys.	• Bonobo: direct observation, nest count, feeding sign. • Habitat: substrate, vegetation type, sub-canopy • Hunting: snares, camps, encounters with hunter	Spatial analysis of indicator encounters.
II. Inventory block	2005 – 2006	Lokofa, Iyaelima, Lomela	Systematically placed line transects (1.4 km each) linked by recces.	• Bonobo: nest count, direct observation • Habitat: substrate, vegetation type, sub-canopy • Hunting: snares, camps, encounters with hunter	DISTANCE estimates of nest density from line transect encounters. Spatial analysis of indicator encounters.
III. Monitoring zone	2005 – 2006	Lokofa	Five Systematically placed line transects; 500 m, each, separated by 500 m, linked by recces.	• Bonobo: nest count, direct observation • Habitat: substrate, vegetation type, sub-canopy • Hunting: snares, camps, encounters with hunter	Spatial analysis of i ndicator encounters.

Estimating Bonobo Densities

We used standing crop nest counts (Mohneke and Fruth 2008, Mohneke 2004) to estimate bonobo density as follows:

Bonobo density (number/km^2) = [Density of bonobo nests (number/km^2) / mean decay rate of nests (day)] / daily nest production per individual (number/day).

This estimate of the population of bonobos is actually an estimate of nest building individuals. Infant bonobos nest with their mothers, and even older individuals may share nests (Fruth 1995). Hashimoto and Furuichi (2001) estimated that two-thirds of nest-building individuals built nests at Wamba. We have no basis to estimate the proportion of the population that does not build its own nests. Our estimates of nest building individuals are conservative and underestimate total population.

To convert estimates of standing crop nest density to bonobo density requires estimates of two additional parameters: daily nest production rates and nest decay rates. We used an estimate of daily nest production per individual of 1.37 nests/day based on observations in the Lomako forest (Fruth 1995). We used mean nest decay estimates of 78 days with a 95% confidence interval upper and lower range of 68 and 83 days, based on nest decay studies at Lui Kotal (Mohneke and Fruth 2008, Mohneke 2004).

Phase I: Bonobo Occurrence in the Salonga Park

Phase I: Coverage

Field teams conducted 2,900 km of reconnaissance during the Phase I survey, covering an area of 33,000 km^2, including 2,100 km^2 of the eastern corridor between the two park sectors. We did not survey the eastern limits of the northern and southern sectors, as these areas were thought to be occupied by rebels and not safe when the survey was designed. The excluded areas represent < 8% and < 15% of the southern and northern sectors respectively.

Survey teams sampled 325, 10 × 10 km quadrats, of which 233 quadrats had ≥ 5 km reconnaissance coverage. We considered cells with < 5 km reconnaissance coverage insufficiently sampled and excluded them from statistical analyses. Figure 10.5 shows the Phase I survey coverage.

Phase I: Results

Figure 10-6 shows the distribution of all 10 × 10 km grid cells wherein we observed bonobo indicators. We also include locations of historic records provided by Kortland (1995). We recorded evidence of bonobos in 173 (53%) of the 325 quadrats

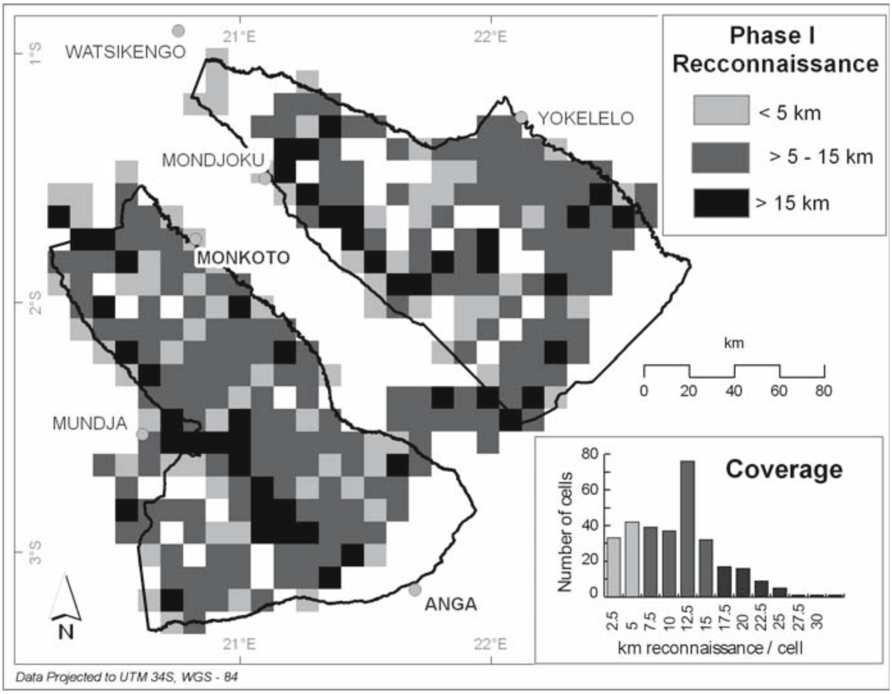

Fig. 10.5 Phase I survey coverage. Survey coverage classes determined by the distance of reconnaissance (recce) track traversed within each 10 × 10 km quadrat. Grid cells with < 5 km of recce are not included in the statistical analyses.

sampled. This included 31 direct encounters with bonobos in 25 quadrats. Bonobo nests were present in 93 quadrats.

We integrated the field indicators of bonobos into a composite index of occurrence for each grid cell by summing the encounter rates of each indicator weighted by a score based on the indicator's probability of detection, the certainty of its identity, possible time lapse between the detection of the indicator and the occurrence of bonobos, and the production and decay rates of the indicator. The criteria for the scoring are in Table 10.2. The weighting scores of the indicators are in Table 10.3.

Bonobo occurrence indices have a log normal distribution. We log transformed and classed them on an ordinal scale as low, average and high with the mean +/− one standard deviation of the log transform values classed as average. We classed the quadrats with the highest 12 occurrence values as very high.

The distribution of bonobo occurrence for 233 quadrats with ≥ 5 km of survey effort is illustrated in Fig. 10.7. We grouped the sampled survey quadrats into larger contiguous areas, termed population extrapolation blocks, to be used for developing a park-wide estimation of bonobo numbers. Bonobo occurrence increases significantly in a cline from west to east across the park using Rosenberg's (2000) bearing correlogram. The spatial trend is correlated with the geography of the hydrological network and relative elevation of the park. Bonobos are less abundant and more

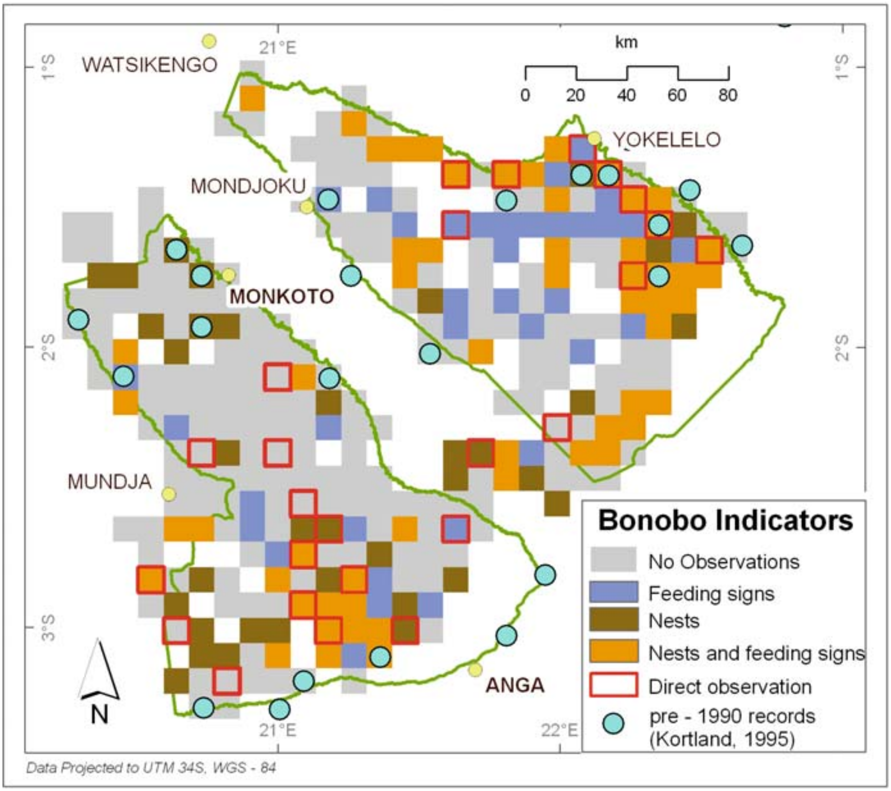

Fig. 10.6 Distribution of bonobos and indicators of their presence observed during Phase I survey in the Salonga National Park. Locations of bonobo records predating creation of the park in 1970 are shown (*See Color Plates*).

localized in the western area of the park, a lower-lying region of river confluences. They are more abundant and widespread in the eastern area of the park, a region of higher-lying plateau forests and river headwaters.

Bonobos are not adverse to proximity of human settlement. They are consistently associated with areas that are accessible to and used by humans (Fig. 10.8). Some of the highest bonobo indices were found near villages in the Iyaelima and Lomela inventory blocks.

Phase II: Population Estimation in Inventory Blocks

Phase II: Coverage

Two of the inventory blocks – Iyaelima and Lomela – had high mean Phase I bonobo occurrence indices, while the Lokofa block had one of the lowest mean index values. We allocated line transects of 1.4 km systematically across each inventory block at

Table 10.2 Criteria for determining field indicator weighting score used to calculate composite indices of faunal occurrence and human activity for survey girds

	Criteria				
Score	Certainty	Detection	Time lapse	Production rate	Decay rate
0	*Ambiguous association.* Indicator may be confused with more than one faunal species or human activity.	*Difficult.* Unpredictable and not consistent; uncertain classification by age or category.	*Large time lapse.* Long delay possible between the observation of the indicator and the occurrence of the fauna or human activity producing it.	*Unpredictable.* Rarely produced, highly variable by season or habitat or variable for unknown reasons.	*Unpredictable.* Rapid decay, highly variable by season or habitat or variable for unknown reasons.
1	*Indirect evidence.* Dung, feeding remains, constructions, evidence of tool use or other sign produced by animals or humans.	*Seasonally variable.* Observation and classification affected by habitat, season or other external factors.	*Small time lapse.* Small delay between the observation of the indicator and the occurrence of the fauna or human activity producing it.	*Known variability.* Consistent known relationship between occurrence of indicator and fauna or activity.	*Known variability.* Consistent known relationship with habitat and season.
2	*Direct observation.* Fauna or human activity observed directly (seen or heard).	*Consistent.* Limited variability; classification based on well defined criteria.	*Immediate.* Indicator immediately associated with the fauna or human activity producing it.	*Stable.* Consistent relationship between indicator and occurrence of fauna or human activity.	*Stable.* Consistent across habitat and season; variability associated with known factors.

Table 10.3 Weighting values for indicators of bonobo occurrence

Indicator	Criteria: Certainty	Detection	Time lapse	Production rate	Decay rate	Total score
Feeding sign	0	1	1	0	0	2
Nest	1	2	0	1	1	5
Bonobo encounter	2	0	2	0	0	4

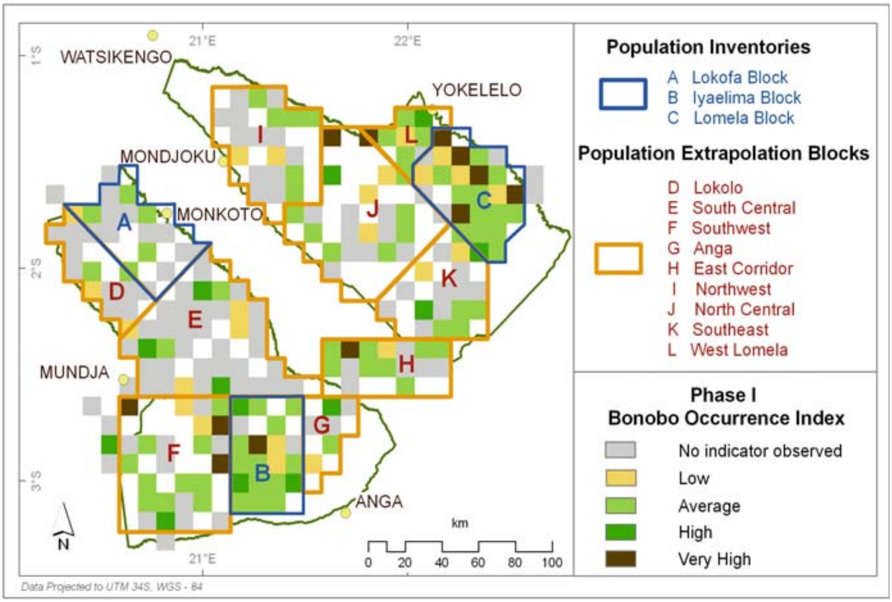

Fig. 10.7 Bonobo occurrence indices integrate Phase I encounter rates of weighted field indicators for 10 × 10 km quadrats with ≥ 5 km reconnaissance coverage. Contiguous quadrats are combined into 12 population extrapolation blocks to calculate an estimate of bonobo populations for the total park area. Three extrapolation blocks cover the Phase II population inventory blocks (*See Color Plates*).

a rate of about one transect per 6 km^2. In addition, we conducted between 511 and 583 km of recce in each block. We completed full surveys for the Lokofa and Iyaelima blocks; however, 11 transects and ca. 400 km^2 of the planned Lomela block were truncated when field teams were threatened by residents of the Kitawala village. In total, we inventoried 7,250 km^2 for standing crop nest counts in all three blocks, using 186 transects totaling 260 km and an additional 1,609 km of recce.

Phase II: Results

Table 10.4 is a summary of survey effort and nest encounter rates for the three inventory blocks. Figure 10.9 presents the spatial distribution of the line transect nest encounter rates within each block. The spatial distribution of Phase II nest

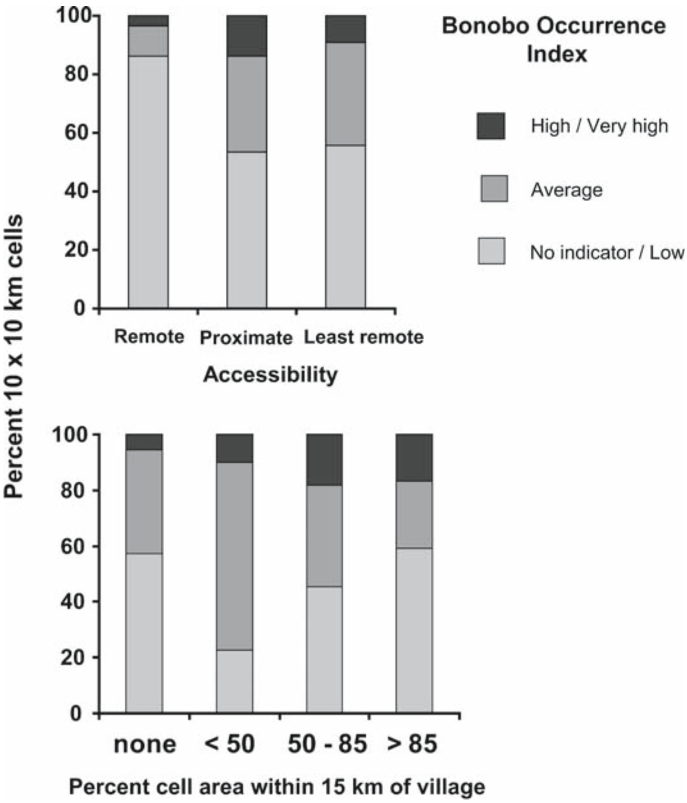

Fig. 10.8 Bonobo occurrence in relation to (A) human settlement and (B) accessibility. Bonobo occurrence varied significantly between classes for both human settlement and accessibility (Chi Square probability = 0.0002 and 0.0194 respectively). Bonobos consistently occur in accessible areas and in proximity to human settlement in the park.

encounters reflects the distribution of bonobo occurrence determined during Phase I surveys in all three inventory blocks. Mean transect nest encounter rates varied from 1.15 to 2.29 nests per km for the three blocks. Nest encounter rates on recces averaged 82% of encounter rates recorded on transects. In total, we recorded 2,941 nests in 1,032 nest aggregations on the three inventories.

Table 10.5 is a summary of nest density estimates for each inventory block calculated via the DISTANCE software. Nest detections exhibited a strong shoulder at distances near the transect line for all three inventories, thus facilitating the fit of the detection curves. Effective strip width varied from 14.9 to 16.2 m across the three blocks.

Mean nest densities ranged from 29.9 – 90.2 nests per km^2 for the three blocks. These are equivalent to 0.27 – 0.84 nest-building bonobos/km^2, via a mean nest decay value of 78 days and nest production rate of 1.37 nests per day per bonobo. We estimated upper and lower densities using 95% confidence limits generated by

Table 10.4 Survey effort and nest count data for Phase II inventory blocks in Salonga National Park

		Line Transects						Recces				Total survey		
Block	Area (km^2)	Transects	Effort (km)	Nests observed	Transects with nests	Nest aggre-gations	Nest encounter (per km)	Effort (km)	Nests observed	Nest aggre-gations	Nest encounter (per km)	Effort (km)	Nests observed	Nest aggre-gations
Lokofa	2000	55	76.6	88	11	23	1.15	583	542	156	0.93	660	630	179
Iyaelima	2500	63	88.2	194	34	67	2.20	511	974	378	1.91	599	1168	445
Lomela	2750	68	95.2	218	31	49	2.29	515	925	359	1.80	610	1143	408
TOTAL	7250	186	260	500	79	139	1.93	1609	2441	893	1.52	1869	2941	1032

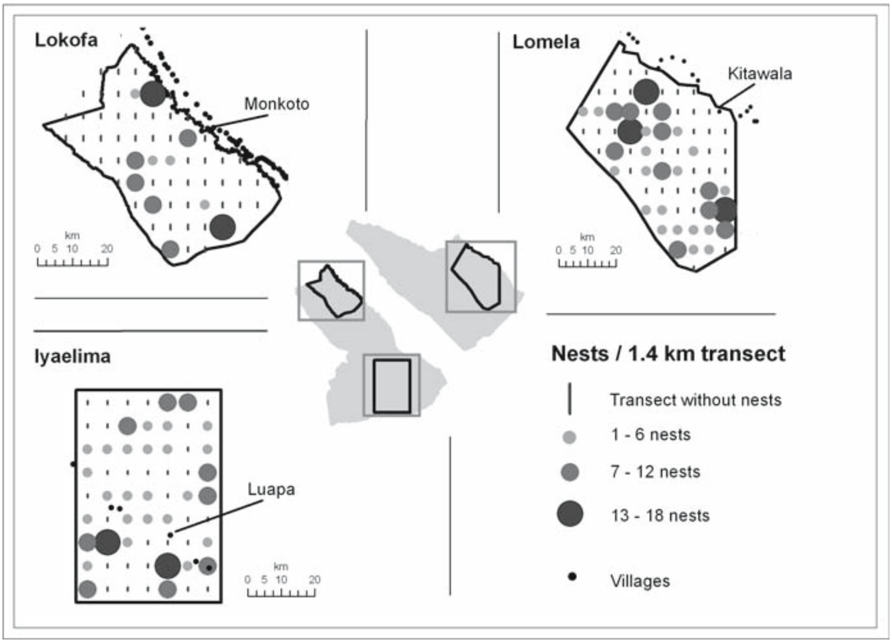

Fig. 10.9 Encounter rates of the standing crop of bonobo nests recorded on line transects in Phase II inventories.

Table 10.5 Estimates of bonobo numbers in Phase II inventory blocks

	Nest density (per km^2)					Nest building bonobos		
				(95% CI)			Population in block [a]	
Block	Mean	Standard error	Coefficient of variation (percent)	Low	High	Mean density (per km^2)	Mean	Range
Lokofa	28.9	8.74	30.3	16.0	52.1	0.27	541	281 – 1119
Iyaelima	54.8	15.41	28.1	31.8	94.4	0.51	1282	699 – 2533
Lomela	90.2	17.2	19.1	61.9	131.3	0.84	2321	1497 – 3876
Mean or total	Mean 58.0					Mean 0.54	Total 4144	2477 – 7528

[a] Parameters used to estimate bonobo populations in blocks:
Mean estimate: mean nest density from DISTANCE, nest decay 78 days, nest production 1.37 nests / day.
Low estimate: lower 95 % confidence interval nest density from DISTANCE, nest decay 83 days, nest production 1.37 nests / day.
High estimate: upper 95 % confidence interval nest density from DISTANCE, nest decay 68 days, nest production 1.37 nests / day.

DISTANCE, with lower and upper nest decay estimates used in the conversion of nest densities to bonobo densities. Together, the three inventory blocks, covering 7,250 km^2, contain an estimated 4,144 (2,477 – 7,528) nest building bonobos, an average density of 0.54 individuals/km^2.

Phase III: Spatial-Temporal Use of Nesting Zones

Phase III: Coverage

We selected the Lokofa block for Phase III surveys since it had the longest survey history (dating to 2003), and the low bonobo indices were typical of many other areas in the park. We delimited 8 circular monitoring zones (2 km radius each) following completion of the Phase II inventories in April 2005. We centered 6 zones on areas that contained bonobo nests during the Phase I or Phase II surveys. We centered 2 zones on areas where no nests had been detected. In each zone we laid out 5 transects, 2.5 km each separated by 500 m (12.5 km total) (Fig. 10-10). We visited each zone and conducted a standard line transect nest count once or twice over the subsequent 14 months. The average interval separating visits was 5 months (range

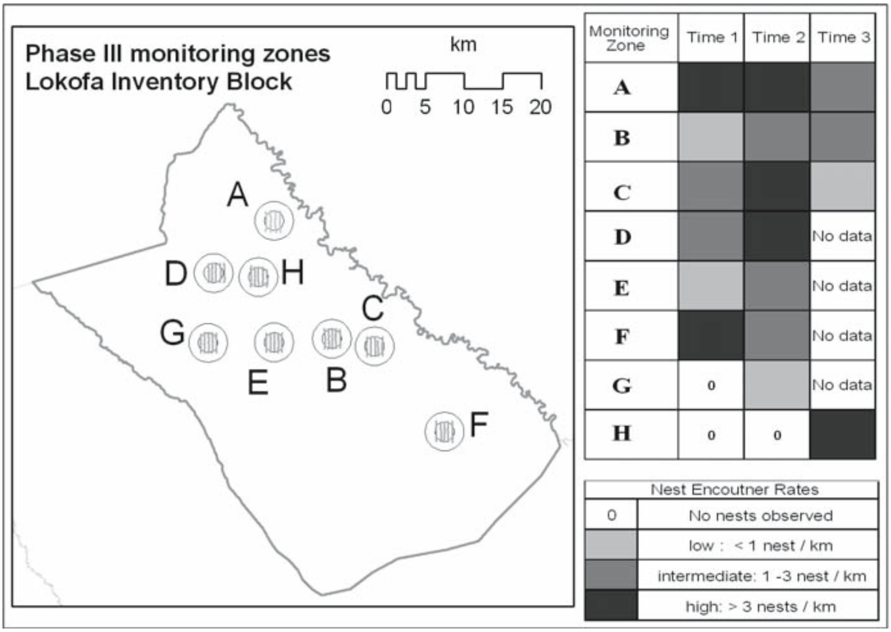

Fig. 10.10 Phase III encounter rates of bonobo nests in 12.5 km^2 monitoring zones in the Lokofa block.

4 – 7 months). This interval ensured that nests counted at one period would have a low probability of persisting to the next period.

Phase III: Results

Nest counts in individual monitoring zones were often too low to estimate nest density. Thus, we used nest encounter rates for comparisons. Following each visit we classed nest encounter rates in four relative abundance classes from no nest to high nest encounter rates (Fig. 10.10).

Six of the eight monitoring zones had nests initially. We inspected 3 zones three times and 3 zones twice. All 6 monitoring zones had nests on all inspection visits. Nest encounter rates varied within monitoring zones over time, but most changes were not large. Two zones did not have nests initially, but eventually contained them. One zone that was empty on the first and second visit had high nest encounter rates on the third visit. Of the nine pair-wise comparisons from one inspection visit to the next, encounter rates remained in the same frequency class only twice. However, 6 changes were relatively small, shifting one frequency class. Only one change was of a large magnitude. Zone C dropped from a high nest encounter rate at inspection 2 to a low rate at inspection 3, 5 months later.

Estimating the Bonobo Poulation of Salonga National Park

We regressed Phase I bonobo occurrence indices with nest densities determined in Phase II inventories to estimate bonobo populations for 12 extrapolation blocks covering the park and eastern corridor using the following equation:

$$y = ax + b$$

wherein y = mean nest density for the block, × = mean bonobo occurrence for the block, a = slope, and b = intercept value, both determined from the regression equation. We calculated mean and upper and lower estimator equations separately using the mean, and the upper and lower 95 percent confidence interval nest density values produced by the DISTANCE analysis of the Phase II surveys (Fig. 10.11).

We delimited 3 extrapolation blocks to cover the inventory blocks surveyed in Phase II. These represent ca. 20% of the total park area and span the range of bonobo occurrence from lowest to highest. We delimited 9 blocks to include contiguous areas of comparable extent to the Phase II blocks and with relatively homogenous bonobo occurrence indices for the 10 × 10 km grid cells within their limits. We calculated a mean occurrence index for each block. Most blocks had > 75% Phase I coverage, and all blocks had ≥ 50% Phase I coverage (Fig. 10.7).

Estimates of bonobo populations for the 12 blocks are in Table 10.6. We used the mean nest decay period of 78 days to convert mean nest densities to an estimate

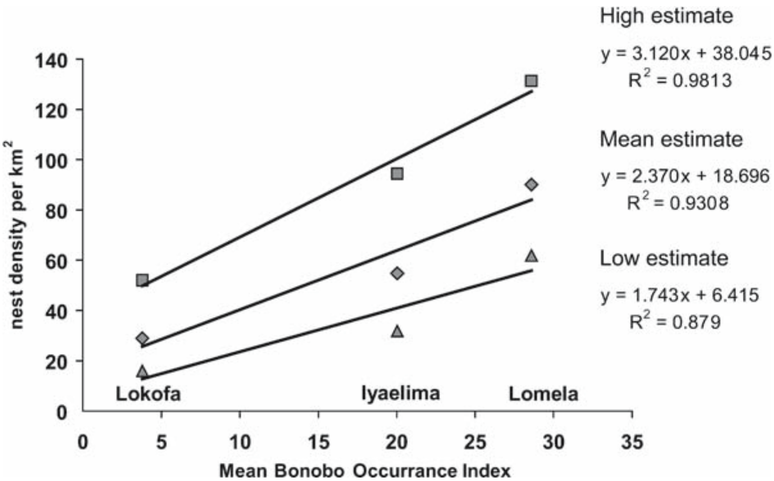

Fig. 10.11 Equations for estimating bonobo nest densities in the Salonga National Park based on the relationship between nest densities determined in Phase II inventories and mean Phase I occurrence indices for population extrapolation blocks. Mean, low and high estimating equations are based on mean and 95% confidence interval values for nest densities determined by the DISTANCE analysis of the Phase II nest encounters for the three inventory blocks.

of nest-building bonobos for each estimator block. We used the lower nest decay value of 68 days to estimate the upper population values and the upper nest decay value of 83 days to estimate the lower population values.

Via these parameters, we estimated 14,883 nest-building bonobos in the park (0.42/km^2), with lower and upper estimates of 7,119 (0.20/km^2) and 20,434 (0.57/km^2) respectively. Estimates of mean bonobo density for the different blocks within the park range from 0.26 to 0.84 nest building individuals/km^2. We estimated the eastern corridor block, covering 2,100 km^2, to contain 809 nest building bonobos (377 – 1,128) with a mean density of 0.39/km^2.

Discussion

The results of the surveys confirm that the Salonga National Park contains a globally significant population of bonobos. They are numerous and widespread within the park, and there are important populations in at least some areas of the corridor linking the northern and southern sectors of the park. Our estimates of mean bonobo densities are lower than density estimates of 0.72/km^2 and 1.15/km^2 given in two earlier limited surveys of the park (Reinartz et al. 2006, van Krunklesven 2001). They are lower than the densities of 0.83 – 1.04/km^2 for bonobos in the forest-savanna ecotone at Lukuru (Meyrs Thompson 1997) and less than one third the estimate of 1.3 – 1.4/km^2 for the Lomako (Eriksson, 1999). They are consistent

Table 10.6 Population estimates of nest building bonobos in the Salonga National Park

Sector	Population extrapolation block[a]	Area (km^2)	Mean occurrence index	Low estimate			Mean estimate			High estimate		
				nest density	bonobo density	bonobo population	nest density	bonobo density	bonobo population	nest density	bonobo density	bonobo population
Southern	A. Lokofa	2300	3.79	13.0	0.106	243	27.7	0.266	611	49.9	0.404	930
	B. Iyaelima	2400	20.04	41.3	0.335	805	66.2	0.636	1526	100.6	0.816	1958
	D. Lokolo	1550	3.87	13.2	0.107	165	27.9	0.268	415	50.1	0.406	630
	E. South Central	4750	3.33	12.2	0.099	471	26.6	0.255	1213	48.4	0.393	1866
	F. Southwest	4200	15.25	33.0	0.268	1124	54.8	0.527	2212	85.6	0.694	2917
	G. Anga	1100	8.57	21.4	0.173	190	39.0	0.375	412	64.8	0.525	578
	Unsampled zone	1800	8.40	21.1	0.171	307	38.6	0.371	667	64.3	0.521	938
	TOTAL	18100				3306			7057			9816
Northern	C. Lomela	2700	28.59	56.2	0.456	1232	86.5	0.830	2242	127.2	1.032	2786
	I. Northwest	3100	7.19	18.9	0.154	476	35.7	0.343	1064	60.5	0.490	1521
	J. North Central	4700	5.11	15.3	0.124	584	30.8	0.296	1391	54.0	0.438	2058
	K. Southeast	2500	11.55	26.5	0.215	538	46.1	0.442	1106	74.1	0.601	1502
	L. West Lomela	900	23.51	47.4	0.384	346	74.4	0.715	643	111.4	0.903	813
	Unsampled zone	3700	8.50	21.2	0.172	637	38.8	0.373	1380	64.6	0.524	1937
	TOTAL	17600				3813			7826			10618
Park	**Block Totals**	**35700**			**0.199**	**7119**		**0.417**	**14883**		**0.572**	**20434**
Corridor	H. East Corridor	2100	9.03	22.2	0.180	**377**	40.1	0.385	**809**	66.2	0.537	**1128**

[a] See Fig. 10-7 for delimitation of blocks.

with densities of 0.54/km^2 reported from the northern sector of the Luo Reserve (Hashimoto and Furuichi 2001) and 0.52/km^2 for the Lui-Kotal study area, using the same standing crop nest count methods as this study (Mohneke and Fruth 2008). They are similar to an estimate of 0.4/km^2 presented more than 20 years ago by Kano (1984) for the overall bonobo range. All of the high estimates cited above are based on survey areas that are considerably smaller than the 3 inventory blocks we surveyed, and they can not be extrapolated to larger areas.

We have no evidence of major population declines of bonobos in the Salonga National Park in the recent past. Historic records mapped by Kortland (1995) are mostly located in areas where we found bonobos. Of the 21 bonobo records before 1990, 11 were located in Phase I quadrats with ≥ 5 km reconnaissance coverage. We confirmed occurrence of bonobos in 9 of the 11 sites (Fig. 10.5). We recorded no evidence that the bonobos in the Salonga National Park have been reduced by recent widespread epidemic diseases, as has occurred in some populations of western gorilla (*gorilla gorilla*) and chimpanzees (*Pan troglodytes*) (Lahm et al., 2006; Formenty et al.,1999), though we can not eliminate the possibility. A further analysis of the impact of human hunting on bonobos is presented in Hart et al. (2008).

At a landscape scale, bonobos increase in abundance and occurrence from west to east across the park. Extensive areas of the western Salonga landscape are covered by black water swamp forests not favored by bonobos, and the entire region is underlain by highly leached white sand soils. White sand soils often have reduced primary productivity and are dominated by chemically protected plants less palatable to many primary consumers, including primates (Oates et al. 1990, Freeland and Janzen 1974). The bonobo's localized distribution in some areas of Salonga National Park may be determined by the limited availability of areas of marginally higher productivity suitable for their needs. The repeated use of the same nesting areas observed in the Lokofa block, an area of extensive white sand substrate, indicates intensive use of limited areas by bonobos there. A further investigation of the relationship of habitat productivity and bonobo socioecology may provide a useful basis for developing conservation programs appropriate to their varied ecological context.

Reinartz et al. (2008, 2006) report that bonobos avoid areas of human settlement and activity in the Salonga landscape. We did not confirm their conclusion. While bonobos occur in remote areas of the park, we found some of the highest concentrations of bonobo nests near villages, particularly in the Iyaelima block. The Iyaelima people traditionally avoid contact with bonobos, which they consider to be highly capable fighters (Thompson et al. 2008). Bonobos and humans coexist in other areas as well, such as Wamba, Yasa and Lilungu, (Thompson et al. 2008, Kano et al. 1996). Our surveys show that the relationship between humans and bonobos must be evaluated in a site-specific context and that the relationship is dynamic (Hart et al. 2008). The possibility that humans and bonobos selectively occupy the same localized areas of marginally higher productivity within an overall nutrient constrained environment needs to be evaluated. Human modification of the forest may also attract bonobos. A better understanding of the relationship between human settlement and use of the forest and bonobo occurrence is important as human populations grow and disperse within the bonobo's range.

The Use of Nest Counts to Estimate Bonobo Occurrence and Density

All great apes make nests, and nest counts can be used to estimate populations where animals are difficult to detect, and where large areas must be covered. Researchers have used nest counts to develop landscape estimates of chimpanzees and gorillas, including nation-wide surveys of apes in Gabon (Tutin and Fernandez 1984), Cote d'Ivoire (Marchesi et al. 1995) and Uganda (Plumptre et al. 2003). We also confirm their utility for large-scale bonobo surveys.

Apes live in groups and often nest together, so many nest counts use nest groups as the observational unit with line transect measures to the center of the group. Counts of nest groups assume that each one represents a single nesting event, that separate nest groups can be distinguished, and that all nests in a group are constructed at the same time. Early in the Salonga survey, we found that some aggregations of bonobo nests observed in the field represented different nesting events in close spatial proximity. As nests aged, it was impossible to distinguish one nesting event from another, especially if different nesting events were separated by short periods of time. We opted to use the individual nests instead of nest groups as the observational unit.

The Phase III surveys confirmed that bonobos consistently use at least some nesting zones over time, and that nest site fidelity can be very specific. In 9 of 15 pair-wise comparisons from one time period to the next, bonobo nesting events occurred on the same transect within the monitoring zone and in all but two cases, within the same 250m of transect line. Mohneke (2004), Fruth (1995) and Fruth and Hohmann (1993) observed in Lomako and Lui Kotal that nesting is concentrated in selected areas of a bonobo community's home range, and that nesting events accumulate in the same locations. They also opted to count individual nests instead of nest groups in population surveys. Len Thomas (personal communication, 2005) reports that the potential bias due to non-independence of observations in counting individual nests from clusters is small, and also recommends counts of nests rather than nest groups on line transects where there is inability to distinguish the groups.

The phenomenon of repeated nesting in limited areas is not restricted to bonobos. Furuichi et al. (2001) compared counts of individual nests versus nest groups for chimpanzees in Uganda and justified the use of individual nests counts. While it has rarely been evaluated, it is likely that at least some of the large aggregations of nests reported for bonobos, and possibly chimpanzees, represent multiple nesting events in the same location instead of a large single nesting event (Kuroda 1979).

We observed that bonobos sometimes refurbished and reused older nests, especially in repeatedly used nesting areas. Therefore, estimates of daily nest production rates should be given with estimates of percentage reuse of old nests. This allows for the calculation of a correction factor in estimating bonobo densities from nests estimates (Plumptre and Reynolds 1997). If nest production rates are not corrected for reuse, estimates of bonobo density from nest counts might be biased downward.

Our surveys used standing crop nest counts. A second nest count method, using marked nests, requires repeated visits of the same transects. This has the advantage that it does not require independent estimates of nest decay (Plumptre and Reynolds 1996). However, the method is not feasible for large surveys where each sampling unit is visited once. It may not be feasible where nest accumulation rates are very low. In one study comparing marked and standing crop nest counts, the marked nest methods led to a higher density estimate (Mohneke 2004). It is not known if this is likely to be a consistent trend.

Evaluation of Multiphase Design and Recommendations for Large-Scale Surveys

Bonobo populations can be surveyed at a range of spatial scales; however, the spatial resolution and the spatial extent of survey effort will determine the precision of the results and how representative they are of larger areas. No single spatial scale will be appropriate for all questions concerning bonobo distribution and abundance. Thus, it is important to know at the outset what questions to ask and what conclusions to seek for surveys at different spatial scales. In the Salonga design, we identified patterns of bonobo occurrence over a large area and coarse spatial resolution, and correlated these with results of population inventories at a finer spatial resolution in subsequent survey phases to provide a basis for extrapolation of population estimates over large areas.

Our large scale surveys used direct encounters with bonobos, and observations of nests and feeding signs to confirm their presence. We integrated observations of field indicators into a composite index of occurrence that weighted each indicator by its relative utility, based on five criteria, and its frequency calculated by its encounter rate along recces and transects within each mapped grid cell. The composite index permits comparisons of bonobo occurrence across the landscape and is correlated with estimates of population density when averaged over contiguous blocks of grid cells. We recommend a similar approach to evaluating the occurrence of bonobos in other large scale surveys where different indicators are likely to be encountered and comparisons made between different sites and seasons. We also recommend that Phase II population inventories include blocks that span the range of bonobo occurrence from low to high when used to estimate population abundance over larger Phase I landscapes.

The single biggest challenge to large scale surveys is to ensure that the allocation of survey effort provides a representative sample of the spatial variation in bonobo occurrence across the survey zone. This is especially important in the Phase I surveys where results covering a large spatial extent inform finer resolution surveys over smaller areas. It is generally better to increase the number of sample sites rather than increasing sample coverage per site when allocating limited survey effort. Large scale spatial variation is generally the largest component of survey variance and the most important factor in determining survey design (Thomas et al. 2001b). We recommend non-stratified, systematic placement of reconnaissance walks and transects. This ensures that the results are unbiased and is the most efficient survey design where bonobo occurrence is variable or poorly known, and where factors contributing to differences in occurrence are likely to vary spatially in their importance. Stratification may increase survey efficiency; however, this is most likely to be the case at smaller spatial scales, as shown by Reinartz et al. (2008). We stratified survey effort in allocating bonobo nest monitoring sites in Phase III of this study.

We recommend line transect standing crop nest counts to estimate bonobo populations over large survey areas and counts of individual nests, as opposed to nest groups. This is especially recommended in areas where bonobos are likely to re-use the same nesting areas intensively and where nest clusters can not be separated into discrete nesting events with certainty. Differences in nest decay rates and, to an unknown extent, nest production rates can have a major impact on the conversions of standing crop nest densities to estimates of bonobo densities (Monheke and Fruth 2008). These parameters are often not measured directly, and their range of variability is often poorly known (Monheke 2004). We recommend that other large scale surveys gather further data on nest construction and decay rates when possible.

Nest encounter rates and estimates of nest densities are the most reliable indicators of relative bonobo abundance for standing crop nest counts covering large areas and where survey locations are visited only once. We recommend that all surveys present geo-referenced survey efforts and results separately for line transects and reconnaissance walks, and provide encounter rates of individual nests recorded, even if information on nest groups is also provided. This will facilitate comparisons across sites and between different surveys within the same site. It will also permit estimates of bonobo populations to be revised as new data on nest decay and nest production become available (Plumptre 2000).

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References

Blake S (2005) Forêts d'afrique centrale: rapport final sur les relevés démographiques d'éléphants (2003–2004). CITES–MIKE, Nairobi

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers, DL, Thomas L (2001) Introduction to distance sampling: estimating abundance of biological populations (2nd edn). Chapman & Hall, London

Butynski TM (2001) Africa's great apes. In: Beck B, Stoinski TS, Hutchins M, Maple TL, Norton, B, Rowan A, Stevens EF, Arluke A (eds) Great apes and humans: the ethics of coexistence. Smithsonian Institution Press, Washington DC, pp 3–56

CITES (2001) Database of listed species. *http://www.cites.org/CITES/common/dbase/fauna/index.shtml*

Draulans D, Van Krunkelsven E (2002) The impact on war on forest areas in the Democratic Republic of Congo. Oryx 36(1):35–40

Dupain J, Van Elsacker L (2001) The status of the bonobo in the Democratic Republic of Congo. In: Galdikas BMF, Briggs NE, Sheeran LK, Shapiro GL, Goodall J (eds) All apes great and small, vol. 1: African apes. Kluwer Academic / Plenum, New York, pp 57–74

Dupain J, Van Krunkelsven E, Van Elsacker L, Verheyen RF (2000) Current status of the bonobo (*Pan paniscus*) in the proposed Lomako Reserve (Democratic Republic of Congo). Biological Conservation 94:265–272

Eriksson J (1999) A survey of the forest and census of the bonobo (*Pan paniscus*) population between the Lomako and the Yekokora rivers in the Equateur province, D R Congo. MSc Thesis, University of Uppsala

Formenty P, Boesch C, Wyers M, Steiner C, Donati F, Dind F, Walker F, Le Guenno B (1999) Ebola virus outbreak among wild chimpanzees living in a rain forest of Côte d'Ivoire. Journal of Infectious Disease 179 (Suppl 1): S120—S126

Freeland WJ, Janzen DH (1974) Strategies in herbivory by mammals: the role of plant secondary compounds. American Naturalist 108:269–289

Fruth B (1995) Nests and nest groups in wild bonobos (*Pan paniscus*) ecological and behavioral correlates. Shaker-Verlag, Aachen

Fruth B, Hohmann G (1993) Ecological and behavioral aspects of nest building in wild bonobos (*Pan paniscus*). Ethology 94: 113–126

Furuichi T, Hashimoto C, Tashiro Y (2001) Extended application of a marked–nest census method to examine seasonal changes in habitat use by chimpanzees. Int J Primatol 22: 913–928

Hart J, Grossmann F, Vosper A, Ilanga, J (2008) Human hunting and its impact on bonobos in the Salonga National Park, D.R. Congo. In: Furuichi T, Thompson J (eds) The bonobos: ecology, behavior, and conservation, Springer, New York, pp 245–271

Hashimoto C, Furuichi T (2001) Current situation of bonobos in the Luo Reserve, Equateur, Democratic Republic of Congo. In: Galdikas BMF, Briggs NE, Sheeran LK, Shapiro GL, Goodall, J (eds) All apes great and small, vol. 1: African apes. Kruwer, Academic/Plenum, New York, pp 83–93

Hohmann G, Fruth B (2003) Lui Kotal: a new site for field research on bonobos in the Salonga National Park. Pan Africa News 10:25–27

IUCN (1996) IUCN red list of threatened snimals. IUCN, Gland, Switzerland

Kano T (1984) Distribution of pygmy chimpanzees (*Pan paniscus*) in the Central Zaire Basin. Folia Primatologica 43:36–52

Kano T, Lingomo B, Idani G, Hashimoto C (1996) The challenge of Wamba. In: Cavalieri P (ed) The great spe project, Ecta and Animali 96/8, Milano, pp 68–74

Kortlandt A (1995) A survey of the geographical range, habitats and conservation of the pygmy chimpanzee (*Pan paniscus*): An ecological perspective. Primate Conservation 16:21–36.

van Krunkelsven E (2001) Density estimation of bonobos (*Pan paniscus*) in Salonga National Park, Congo. Biological Conservation 99:387–391 van Krunkelsven E, Inogwabini B, Draulans D (2000) A survey of bonobos and other large mammals in the Salonga National Park, Democratic Republic of Congo. Oryx 34:180–187

Kuroda S (1979) Grouping of pygmy chimpanzees. Primates 20:161–183

Lahm S, Kombila M, Swanepoel M, Barnes R (2006) Morbidity and mortality of wild animals in relation to outbreaks of Ebola haemorrhagic fever in Gabon, 1994—2003, Transactions of the Royal Society of Tropical Medicine and Hygiene, doi:10.1016/j.trstmh.2006.07.002

Marchesi P, Marchesi N, Fruth B, Boesch C (1995) Census and distribution of chimpanzees in Côte D'Ivoire. Primates 36: 91–607

Mitchell A (2005) The ESRI guide to GIS analysis, vol 2: Spatial measurements and statistics, ESRI Redlands, California

Mohneke M (2004) Ecological approach and comparative methodology of density estimates of the bonobo (*Pan paniscus*) population of Lui Kotal, in the Salonga National Park, Democratic Republic of Congo. Diploma thesis, Rheinische Friedrich Wilhelms University, Bonn

Mohneke M, Fruth B (2008) Bonobo (*Pan paniscus*) density estimation in the SW-Salonga National Park, DRC: common methodology revisited. In: Furuichi T, Thompson J (eds) The bonobos: ecology, behavior, and conservation. Springer, New York, pp 151–166

Myers Thompson JA (1997) The history, taxonomy and ecology of the bonobo (*Pan paniscus*) with a first description of a wild population living in a forest/savanna mosaic habitat. Ph-D dissertation, University of Oxford, England. 358 pgs

Oates JF, Whiteside GH, Davies AG, Waterman PG, Green SM, Dasilva GL, Mole S (1990) Determinants of variation in tropical forest primate biomass: New evidence from West Africa. Ecology 71:328–343

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

Plumptre AJ, Reynolds V (1997) Nesting behavior of chimpanzees: implications for censuses. Int J Primatol 18:475–485

Plumptre AJ (2000) Monitoring mammal populations with line transect techniques in African forests. J Applied Ecol, 37:356–368

Plumptre AJ, Cox D, Mugume S (2003) The status of chimpanzees in Uganda. Albertine Rift Technical Report Series No. 2, Wildlife Conservation Society, Kampala

Reinartz GE, Inogwabini BI, Ngamankosi M, Wema LW (2006) Effects of forest type and human presence on bonobo (*Pan paniscus*) density in the Salonga National Park. Int J Primatol 27:603–634

Reinartz, GE, Guislain, P, Mboyo, B, Isomana, E, Inogwabini, BI, Ndouzo B, Mafuta N, WemaWL (2008) Ecological factors influencing bonobo density and distribution in the Salonga National Park: applications for population assessment. In: Furuichi T, Thompson J (eds) The bonobos: ecology, behavior, and conservation. Springer, New York, pp 167–188

Rosenberg MS (2000) The bearing correlogram: a new method of analyzing directional spatial autocorrelation. Geographical Analysis 32:267–278

Sanderson EW, Malanding J, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The human footprint and the last of the wild. BioScience 52: 891–904

Siegert F (2003) Assessment of land cover and land use in the Salonga National Park based on satellite imagery. Remote Sensing Solutions GmbH Spatial data applications, GTZ, Kinshasa 16 pages unpublished report

Southwell C, Weaver K (1993) Evaluation of analytical procedures for density estimation from line-transect data: data grouping, data truncation and the unit of analysis. Wildlife Research 20: 433–444

Susman RL, Badrian NL, Badrian A, Handler NT (1981) Pygmy chimpanzees in peril. Oryx 16: 179–183

Thomas L, Laake JL, Strindberg S, Marques F, Borchers DL, Buckland ST, Anderson DR, Burnham KP, Hedley SL, and Pollard JH (2001a) Distance 4.0, Beta 1. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK, *http://www.ruwpa.st-and.ac.uk/distance/*

Thomas L, Beyers R, Hart J, Buckland ST (2001b) Recommendations for a survey design for the Central African Forest Region. MIKE Central African Pilot Project, Technical Report N° 1, CITES-MIKE

Thompson J Myers, Lubuta, N. Kabanda RB (2008) Traditional land-use practices for bonobo conservation. In: Furuichi T, Thompson J (eds) The bonobos revisited: ecology, behavior, and conservation. Springer, New York, pp 227–244

Thompson-Handler N, Malenky RK, Reinartz GE (1995) Action plan for *Pan paniscus*: Report on free-ranging populations and proposals for their preservation. Zoological Society of Milwaukee County, Milwaukee

Tutin CEG, Fernandez M (1984) Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. American Journal of Primatology 6:313–336

Urban DL (2002) Tactical monitoring of landscapes. In: Liu J, Taylor WW (eds) Integrating landscape ecology into natural resource management. Cambridge University Press, pp 294–311