RESEARCH ARTICLE

Estimating Chimpanzee Population Size with Nest Counts: Validating Methods in Taï National Park

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Successful conservation and management of wild animals require reliable estimates of their population size. Ape surveys almost always rely on counts of sleeping nests, as the animals occur at low densities and visibility is low in tropical forests. The reliability of standing-crop nest counts and marked-nest counts, the most widely used methods, has not been tested on populations of known size. Therefore, the answer to the question of which method is more appropriate for surveying chimpanzee population remains problematic and comparisons among sites are difficult.

This study aimed to test the validity of these two methods by comparing their estimates to the known population size of three habituated chimpanzee communities in Taï National Park [Boesch et al., Am J Phys Anthropol 130:103–115, 2006; Boesch et al., Am J Primatol 70:519–532, 2008]. In addition to transect surveys, we made observations on nest production rate and nest lifetime. Taï chimpanzees built 1.143 nests per day. The mean nest lifetime of 141 fresh nests was 91.22 days. Estimate precision for the two methods did not differ considerably (difference of coefficient of variation $<5\%$). The estimate of mean nest decay time was more precise ($CV = 6.46\%$) when we used covariates (tree species, rainfall, nest height and age) to model nest decay rate, than when we took a simple mean of nest decay times ($CV = 9.17\%$). The two survey methods produced point estimates of chimpanzee abundance that were similar and reliable: i.e. for both methods the true chimpanzee abundance was included within the 95% estimate confidence interval. We recommend further research on covariate modeling of nest decay times as one way to improve the precision and to reduce the costs of conducting nest surveys. Am. J. Primatol. 71:447–457, 2009. © 2009 Wiley-Liss, Inc.

Key words: *Pan troglodytes*; methods validation; modeling decay; production rate

INTRODUCTION

Ecologists and wildlife managers generally agree that reliable estimates of population size are vital for conservation and successful management of wild animals [McKechnie et al., 2007; Plumptre & Cox, 2006; van Schaik et al., 2005]. Indeed, predicting exactly the extent of the decline of large mammals that are increasingly threatened in tropical forests is difficult if a reliable baseline of their distribution and abundance are not available [Oates, 1996; Teleki, 1989].

Surveying populations of great ape and other large mammals is a challenging task, as they occur at low densities and visibility is low in their forested habitat. Censusing by taking total counts of individuals within an approximated home range size is often impracticable over large areas [Reynolds & Reynolds, 1965]. Therefore, in order to get sample sizes large enough and (consequently) estimate standard errors small enough to allow detection of population trends [Plumptre, 2000], large forest

mammals are often surveyed using indirect signs. Dung may be the most often used sign [Barnes, 2001], but great ape populations' size estimates have almost always relied on counts of sleeping nests built by weaned individuals [Ghiglieri, 1984; Hall et al., 1998; Johnson et al., 2005; Sanz et al., 2007].

A major problem with the use of indirect signs is that some basic assumptions made to estimate population size can be violated. For example, for

nest counts, each individual typically tends to build more than one nest per day [Plumptre & Reynolds, 1997]. Furthermore, the number of nests being built at a given time is not always equal to the number of nests that decay (the steady-state assumption is violated) because the decay process is not constant through time [Kuehl et al., 2007; Plumptre & Harris, 1995; Walsh & White, 2005]. This raises important questions about the validity of such approaches to surveying wild ape populations.

Two methods based on line-transect distance sampling [Buckland et al., 2001], are currently widely used to estimate chimpanzee population sizes: the standing-crop nest counts (SCNC) [Tutin & Fernandez, 1984] and the marked-nest counts (MNC) [Hashimoto, 1995; Plumptre & Reynolds, 1996].

The SCNC uses a count of all nests detected during a single visit to each transect and is by far the most common approach to estimating chimpanzee density [Ghiglieri, 1984; Marchesi et al., 1995]. But, in order to be unbiased, this method requires site-specific estimates of nest production rate and the mean age of nests (conversion factors). Nest production rate estimates require the study of habituated animals, and estimation of the lifetime of nests necessitates nest decay studies that are time consuming and problematic because of spatial and temporal heterogeneity in decay rates [Kuehl et al., 2007]. Several studies have used conversion factors based on data collected at other sites. However, sampling errors associated with the estimates of these factors have not always been integrated into animal's density estimates [Plumptre, 2000]. This results in questionable population size estimates even though the high variability in decay rates was known to result in wide estimate confidence limits for the SCNC method [Tutin & Fernandez, 1984]. Given that decay rates depend on many factors (e.g. season, habitat), Laing et al. [2003] proposed a retrospective approach to reliably estimate the mean lifetime of signs present at the time of the survey. It consists of locating freshly built nests on several dates regularly spaced in the lead up to the transect survey and then revisiting them at the beginning of the counts to establish whether they have decayed. This method integrates over decay rate heterogeneity in the period preceding the survey. Another alternative is the modeling of variation in decay time using data on the factors that affect the decay process. Such an approach has the advantage of reducing uncertainty in the estimate of decay time, if powerful predictors of decay can be identified [Barnes & Dunn, 2002]. Unfortunately, neither the factors that determine chimpanzee nest decay rates nor their relative importance are well documented (but for gorilla nests see [Walsh & White, 2005]).

As a way of avoiding the problems inherent in nest decay studies, the MNC was proposed [Hashimoto, 1995; Plumptre & Reynolds, 1996]. This method involves repeated counts of fresh nests on transects during a short period and is meant to reduce the temporal bias of the density estimate by eliminating the steady-state assumption [Furuichi et al., 2001; Kuehl et al., 2007]. However, this method requires higher transect sampling effort and its precision remains unclear, especially in West African forests where chimpanzee densities are generally lower in comparison to the East African subspecies [Plumptre, 2004].

Differences in survey methods among studies complicate the comparisons of chimpanzee abundance and density. Evaluation of the reliability of survey methods, as well as their relative costs is needed to determine which method is the most appropriate for surveying chimpanzees. However, no prior attempt has been made to validate the reliability of nest counts methods by comparing their estimates to those derived from counting habituated animals inhabiting a known home range.

The aim of our study was to validate two survey methods based on nest counts of a well-known population of chimpanzees of Taï National Park's [Boesch & Boesch-Achermann, 2000]. We first estimated the site-specific nest production rate and mean nest lifetime. We investigated whether chimpanzee nest decay probability could be predicted using the variables: rainfall, nesting tree species, height of nest above the ground and nest age. Nest lifespan at our site was previously estimated in the studies of Marchesi et al. [1995], but we wanted to take into account the temporal heterogeneity of decay rate and to identify the main factors affecting nest survival. Second, we estimated the density of chimpanzee nest-builders using each method (SCNC and MNC) and compared the precision and accuracy of both methods with the real population size. Precision refers to the variability around the survey mean estimate, and a low precision is represented by a high coefficient of variation. Accuracy refers to how close the survey estimate is to the true population size.

Once conversion factors (nest production rate and decay time) were accurately known, we predicted that the true number of chimpanzees would be included in the confidence limits of estimates from both nest counts methods. Regardless of the survey method used, the density estimate must be multiplied by the study area size to obtain the abundance of animals. Thus, for rigorous comparison of abundance estimates derived from the two survey methods, we used both the minimum convex polygon (MCP) method [Mohr, 1947] and the kernel method [Worton, 1989] to estimate the area size of the territories of habituated chimpanzees. We hypothesized that there was a systematic variation in the

density of nests across the territories. Therefore, we predicted that nest encounter rates were higher within the territories' core areas than in peripheral areas; and thus poststratification would lead to greater precision of the overall chimpanzee abundance estimate.

METHODS

Study Sites

We conducted the study from June 2004 to May 2006 in Taï National Park, in southwestern Côte d'Ivoire (Fig. 1). This park is one of the last major
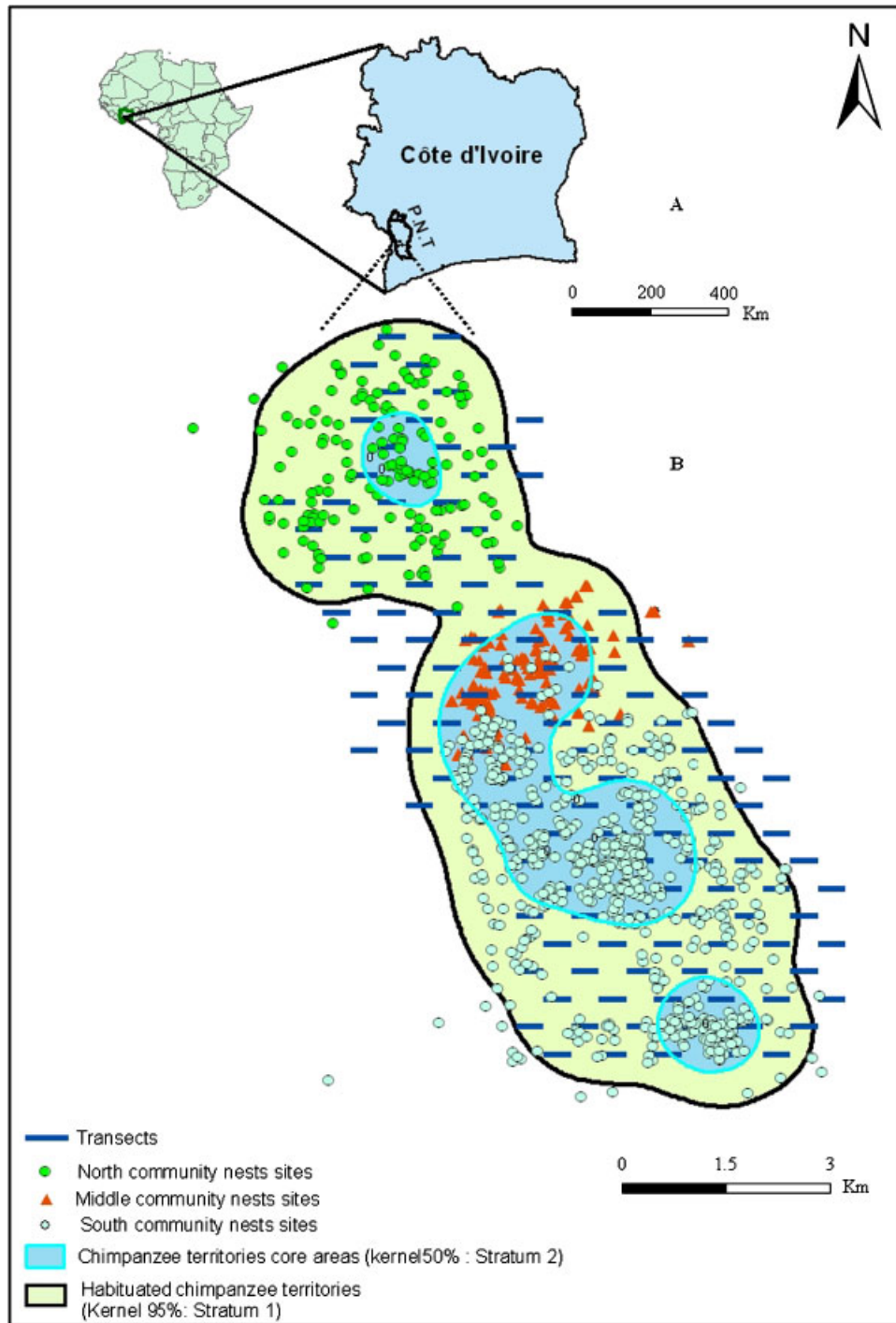

Fig. 1. Map of the study area showing survey design and chimpanzees territories estimates with the kernel method **A:** Location of Tai National Park (PNT) in Cote d'Ivoire; **B**: Territories of three communities of habituated chimpanzee based only on nests sites for each community.

remnants of the primary tropical forest of West Africa spreading from 5°08′N to 6°07′N and 6°47′W to 7°25′W. The annual average temperature in the study area is between 24 and 30°C and the annual average rainfall is approximately 1800 mm [Anderson et al., 2005]. We collected data in the territories of three communities of chimpanzees (North, Middle and South) that have been habituated to human presence for several years [Boesch et al., 2006, 2008]. The communities had in total 40 weaned individuals from November 2004 to May 2006.

Data Collection

Territory size estimate based on nest site locations

Our protocol did not violate any ethics rules for conducting research on endangered wild animals; thus we obtained all official approvals for the study from local officials. The daily nest site locations of habituated chimpanzees were recorded by field assistants using a Global Positioning System (GPS, Garmin 60, GARMIN International and GARMIN Corporation, State of Kansas) or plotted on grid maps of 500 m × 500 m cells with X/Y coordinates referring to individual cells when a GPS was not available [Lehmann & Boesch, 2003]. This data collection started 1 year before the survey in each community and finished at the end of the survey.

Nest production rate and nest decay studies

We followed methods of Plumptre and Reynolds [1997] to estimate the number of nests built per individual per day. Thus, 26 habituated chimpanzees comprising seven males and 19 females were observed during nest-to-nest follows in the three communities during 145 days. This sample, with roughly one male for every three females, reflected the sex ratio of Taï chimpanzees [Boesch & Boesch-Achermann, 2000].

For the decay study, we followed the decay of 141 nests in nine groups from the first day of construction, with 66 nests built in September and November 2005 during the rainy season. In the dry season, we located 75 nests built in January and February 2006. Transect counts started after last nest-group was found in each of these periods. We visited each group of nests weekly until at least 80% of nests had decayed. We defined a nest as decayed when it was no longer possible to recognize it as a nest [Tutin & Fernandez, 1984]. Thus, nests were supposed to have disappeared when no twigs were visible or twigs present did not seem to have been broken or bent by chimpanzees; and we used the same definition during the counts along transects. To investigate which factors affect nest decay, we recorded for each nest: nest age (time period between nest construction and visit date), nesting tree species, and height of nest above ground estimated with a range finder. We also collected daily rainfall data from March 2005 until May 2006, using an All-Weather Rain Gauge.

Survey design and nest counts on line transects

We used the Geographic Information System (GIS) package ARCVIEW 3.2 to randomly determine a start point in positioning transects in the survey area. We generated systematically spaced transects of 400 m in length to ensure that each location in the area had the same probability of being sampled (Fig. 1).

In the field, we used a GPS and a compass to locate transects that were marked by putting beige color paint, at breast height, on the nearest tree on the line each 100 m and at the start and end points of transects. We were three experienced surveyors who walked each transect with a mean speed of 0.6 km/hr to ensure detection of all chimpanzee nests. We did not cut the vegetation, and thus largely avoided any impact on the habitat, although we bent some branches when necessary, to mark our path. Each transect was walked once during the first visit for SCNC survey and three subsequent times every 2 weeks during the MNC survey. We marked all nests during each visit and assumed that all fresh nests were built between subsequent time periods [Plumptre & Reynolds, 1996]. For each nest encountered, we recorded: nest-group size, perpendicular distances to transect, nesting tree species, nest height, and age class. Nests with the same age class and within 20 m from each other were designated to belong to the same group. Following Tutin and Fernandez [1984], we defined nest age classes: (1) Fresh: all leaves in the nest were green and generally feces or urine odors were underneath the nest; (2) Recent: drying leaves of different colors; (3) Old: nest structure still intact with the majority of leaves brown; (4) Very old: nest with holes showing few or no leaves, but still identifiable by bent twigs. When no twigs were visible or twigs present did not seem to have been broken or bent by chimpanzees, objects were not identified as nests during transect surveys.

Data Analysis

Habitat utilization by chimpanzees for estimation of territories size

We pooled nesting site locations data ($n = 719$) from the three communities and used the extension Hawths Tools in ARC GIS 9.2 to estimate the area size using two methods. The fixed kernel was the first method consisting of placing a probability density over each data point [Worton, 1989], and we chose a fixed smoothing parameter (1200) that gave a better fit to nest site distributions. This method excludes unused areas and creates isopleths of intensity of utilization, thus leading to more accurate depiction of areas [Seaman & Powell,

1996]. In Figure 1, we used the isopleths 50% kernel (core areas) and 95% kernel, suggestive of the amount of time spent by chimpanzees in these contours to define two strata (poststratification), and used this to calculate chimpanzee density with relatively homogeneous variance within each stratum [Buckland et al., 2001]. The stratum 1 or peripheral areas was the areas within the territories external to the core areas.

We secondly estimated the area size with the MCP method by joining the outer limits of nest site locations [Mohr, 1947]. This simple technique generally overestimates area size by including nonused areas into the estimate. We reduced this bias by excluding 5% of the most distant nest sites of each community and we estimated the area size with 95% MCP [Herbinger et al., 2001].

Conversion Factors

Nest production rate

We pooled nest-building data from the three communities to estimate nest production rate. Sex differences in nesting behavior were tested via the software SPSS 13.0 using a nonparametric test (Mann–Whitney exact U test) because the data did not meet the assumption of normality and sample size was low ($n = 26$).

Modeling nest decay: factors affecting nest decay and lifetime estimation

We were interested in whether chimpanzee nest decay probability was dependent on nest age, height above the ground, rainfall and nesting tree species; and whether they could be used to predict nest decay time. We dummy coded the variable tree species and used a multimodel selection approach [Johnson & Omland, 2004], thus we built a set of alternative hypotheses based on all the variables and a constant. The constant model was similar to the exponential decay described in fecal decay rate studies in which time is treated as continuous [Barnes & Barnes, 1992. But, we treated decay as a first-order Markov process with discrete daily steps [Walsh & White, 2005].

We defined the response variable CD (Code Decay) to be 1 if a nest i was judged not to have decayed at the revisit or 0 otherwise, and $p(t_i)$ the probability that the nest remains detectable t days after construction was assumed to follow the logistic function:

$$p(t_i) = \frac{1}{1 + \exp{-\left(a_0 + \sum_j a_j x_{ij}\right)}} \quad (1)$$

Where x_{ij} is the value of covariate j for nest i at day t, and a_0 and a_j are the coefficients to be estimated. The survival probability of a nest over any time interval t was the product of the discrete daily survival

probabilities [Kuehl et al., 2007]. To fit models to the data, we used the function "optim" (applying the method BFGS) provided by the software R [Team, 2007] to estimate the maximum likelihood values of the coefficients of each variable in the different models. For nests that did not decay during the study, the likelihood was the survival probability at the last visit.

The logistic function initially did not fit well the observed data, thus we chose the reciprocal transformation (1/age) of the age variable in all models for a best fit to the data. We computed Akaike's information Criterion (AIC) values and used them to generate a 95% confidence set [Burnham & Anderson, 2002]. The reciprocal transformation fitted very well the data and AIC for the best model was 716.1 (about ten units less than the best model using the logistic function). Models in the confidence set were used to estimate mean lifetime of nests, by multiplying the probability of nests decayed on each day with the time after construction and then summing values over time. We then derived confidence intervals of nests' mean lifespan by bootstrapping [Efron & Tibshirani, 1986] using 1,000 resamples.

Nest counts on line transects data analysis

We calculated nest encounter rates within each stratum by dividing the number of nests encountered by the total length of transects in the given stratum. We used conversion factors with their associated errors estimated during this study and from Marchesi et al. [1995], Plumptre and Reynolds [1996] to compare density estimates. We calculated chimpanzee densities using the package DISTANCE with the equation:

$$\widehat{Dc} = \frac{\widehat{Dn}}{r.t} = \frac{Ng.f(0).\widehat{E}(s)}{2.L.r.t} \quad (2)$$

where $\widehat{Dc}$ is the estimated chimpanzee density, $\widehat{Dn}$ is the estimated nest density, r is the nest production rate, t nest mean lifetime, Ng is the number of nest-group, L is the total length of transect lines or survey effort, $f(0)$ represents the value of the probability density function of perpendicular distance evaluated at zero distance from the transect, $E(s)$ is the average nest-group size.

We used only fresh nests for the marked-nest counts (MNC) data analysis in which nest lifetime t was replaced by the time period elapsed between transects visits [Plumptre & Reynolds, 1996]. MNC analysis were based on individual nests because nest-groups detected (Ng = 23) during that survey were lower than the minimum sample size required (Ng = 60) for a reliable estimate. However, to overcome the problem of clumped distribution, we used empirical estimators of variance [Buckland et al., 2001]. We grouped perpendicular distances and we

discarded the largest 5–9% of these observations in all analyses to facilitate model-fitting to the data. We tested several models of detection function and we selected the model with the lowest AIC [Buckland et al., 2001]. We used the area size estimated from the kernel and MCP methods to calculate via DISTANCE, chimpanzee abundance with the associated coefficient of variation (CV) for methods precision comparison. Furthermore nests found out of the communities range (Fig. 1) during transect surveys were attributed to neighbor groups and discarded in the analysis.

RESULTS

Nest Production per Individual per Day (*r*)

A total of 165 nests were constructed by the 26 individuals from both sex during 145 days. Females built on average 1.17 nests per day per individual, whereas each male built 1.07 nests per day. However, we found no statistical difference in nesting behavior between both sex ($Z = -1.448$; two tailed $P = 0.166$). The overall mean nest production rate (r) of chimpanzees at Taïwas ($r = 1.143$ nests per day; SE = 0.04) and the associated coefficient of variation (CV) was 3.51 % (with CV (%) = SE/$r \cdot 100$).

Factors Affecting Nest Decay and Mean Nest Life Span

We monitored 141 fresh nests observed being made from dawn to dusk follows of chimpanzees. Among them 119 nests (84.4%) were each effectively monitored until it had completely decayed. The simple mean decay times of these 119 nests was 62.92 days (SD = 51.79; CV = 9.17%). Only six nests decayed between 238 days and 247 days, which was the longest period of monitoring the duration of nests. To avoid bias in the estimation of nest lifespan, we predicted decay time of all nests with the models in the 95% confidence set shown in Table I. Based on AIC values, the best-fitting model included nest age, height, tree species and rainfall; and accounted for 61% of the Akaike weight (0.61

was the probability of being the best). The two other models in the confidence set accounted for only 30 and 6% of the Akaike weight. The constant model with a relatively high value of AIC ranked 14 out of 16 models tested in total, and it was unlikely to be useful in predicting nest decay rates. The three models in the 95% confidence set included age and tree species, and the first two models included rainfall. Therefore, these three variables are the most important factors explaining nest decay. Nest height had less explanatory power because adding this variable to the second model did not substantially increase AIC (less than two units). The coefficient of effect of nest age variable was positive, implying that chimpanzee nests decay more slowly with increasing nest age. Figure 2 shows that the observed data and our predictions fit quite well, especially for the first model in the confidence set, and also confirmed that nest decay rate is slower during relatively late nest age stages (approximately 100 days after construction) than during the first 3 months. The coefficient of effect of rainfall was negative implying that increasing rainfall intensity increased the probability of decay (Table I). We believe that rainfall intensity for the first month preceding nest construction may play an important role. We did not present the decay time of different
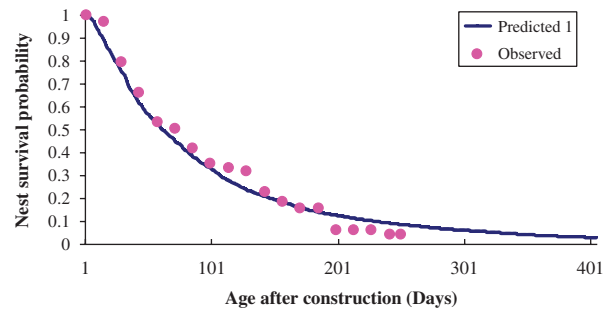

Fig. 2. Observed and predicted cumulative probability of chimpanzee nest survival over time. The solid curve (Predicted 1) shows nest survival probability with the best model in the confidence set that include the constant and the variables age, rain, height and tree species. The dots show the observed survival probability of nests.

TABLE I. Factor Affecting Nests Decay and Relative Importance of Models in the Taï Forest

Rank and models	Parameters	Intercept	AIC	W_i	Age (α)	Rain (β)	Height (λ)	μTar	μCal	μSac	μDial
1. $C+\alpha$/Age$+\beta$Rain$+\lambda$Height$+\mu_i$Tree$_i$	13	3.309	716.1	0.61	3.535	−0.052	0.032	1.202	0.021	0.843	−1.074
2. $C+\alpha$/Age$+\beta$Rain$+\mu_i$Tree$_i$	12	4.079	717.5	0.30	3.253	−0.051		1.356	0.170	0.819	−0.849
3. $C+\alpha$/Age$+\lambda$Height$+\mu_i$Tree$_i$	12	3.059	720.8	0.06	4.157		0.031	1.161	0.024	0.775	−0.985
14. Constant	1	4.567	744.0	10^{-5}							

The 95% Akaike weight confidence set we generated contained the three models with rank shown in boldface type. AIC: Akaike information criterion; W_i: Akaike Weight. α, β, λ are the respective coefficients of effect of nest age, rain fall and nest height. μ: Coefficient of effect of tree species with four examples for easy representation; μTar: Coefficient for *Tarrietia utilis* (Sterculiaceae); μCal: Coefficient for *Calpocalyx brevibracteatus* (Mimosaceae) and *C. aubrevillei* (Mimosaceae); μSac: Coefficient for *Sacoglottis gabonensis* (Himiriaceae); μDial: Coefficient for *Dialium aubrevillei* (Caesalpiniaceae).

tree species, but our results suggest that chimpanzee nest survival probability differs between tree species. Indeed, the coefficient of effect differs between tree species. Relatively higher coefficient of effect (for example, for *Tarrietia utilis* and *Sacoglottis gabonensis*), imply that chimpanzee nests on these trees had a higher survival probability at Taï. Nests that completely decayed during the study confirm those results: e.g. the observed mean decay time of 14 nests built on *S. gabonensis* trees was 59.04 days, 104.53 days for 19 nests built on *T. utilis* trees, whereas it was 30.82 days for 14 nests on *Dialium aubrevillei* trees.

The overall mean decay time of nests estimated using the models in the confidence set was 91.22 days (SE = 5.89) and relatively higher than 62.92 days, because in addition to completely decayed nests, those which did not decay during the study were considered in the estimation derived from models. The 95% confidence interval based on 1,000 bootstraps resamples ranges from 78.27 to 104.82 with CV = 6.46%.

Chimpanzee Population Size Estimate Using the MNC and the SCNC Methods

In Table II, we compare chimpanzee density and abundance estimates from the two nests counts methods. The area size of the three territories of chimpanzee was 44.79 km^2 using the kernel method and 48.26 km^2 using the 95% MCP.

During the SCNC, survey effort was 45.30 km considering only transects within the territories limits described with the kernel method and 48.57 km for the 95% MCP. Nest encounter rates were 15.70 nests/km in the territories' core areas, whereas in the peripheral areas they were 1.15 nests/km, and we counted in total 295 nests from 66 groups of nest. Chimpanzee density in the core areas was 2.19 individuals/km^2, whereas it was 0.15 individuals/km^2 elsewhere in the communities range. During the MNC we walked about 145.71 km, and we counted 84 nests from 23 groups.

The precision and accuracy of all estimates derived from the SCNC vary with the conversion factors used but also depend on the area size estimate method (Table II). As we defined it, the lower the coefficient of variation (CV), the more precise was the method [Buckland et al., 2001]. The closer the point estimate was to the true abundance (40 weaned chimpanzees), the more accurate was the method. Applying correct conversion factors has an important effect on density and abundance estimation of a population (Table II, Fig. 3): ranging from 50 to 200% of overestimation. In a range of decay time (roughly 80–100 days for this study), the accuracy of chimpanzee density estimate may not be affected considerably. But, this density estimate was biased and different from the true density using conversion factors from other site at Taï. Although stratification increased precision as expected, it did not increase accuracy (Table II). The SCNC estimates using nest decay time and nest production rate derived from this study were more precise and more accurate than estimates using conversion factors from other studies. Moreover, and regardless of the area size estimate method and the survey method used, these results indicated that the known chimpanzee abundance was included in the 95% confidence interval of the estimates. Using the 95% MCP, chimpanzee abundance was overestimated in all results derived from SCNC. In particular, the true abundance was not included in the confidence limits of estimates using another site nest lifetime and nest production rate (example Budongo forest from [Plumptre & Reynolds, 1996]). Although our results

TABLE II. Comparison of Estimates from the Standing Crop and the Marked Nest Count Methods Applied in the Territories of Three Habituated Chimpanzee Communities with 40 Weaned Individuals

Area size estimate method	Nest count methods analysis	Density estimate (indiv/km2)	Abundance point estimate (indiv)	95% CL abundance estimate (indiv)		Abundance estimate CV (%)
				Low	Upper	
MCP	Marked-nest counts	0.690	33	19	59	29.34
	Standing-crop nest counts[K]	0.842	41	25	67	25.37
	Standing-crop nest counts[M]	1.198	58	34	99	27.72
	Standing-crop nest counts[P]	1.756	85	51	140	25.94
Kernel	Marked-nest counts	0.836	37	22	64	27.40
	Standing-crop nest counts[K]	0.778 (0.691)	35 (31)	20 (18)	60 (52)	27.85 (26.51)
	Standing-crop nest counts[M]	1.107	50	30	83	26.52
	Standing-crop nest counts[P]	1.622	73	42	126	28.37

95% CL: 95% confidence limits; CV (%): coefficient of variation in percentage.
[K]Nest mean lifetime of 91.22 days (SE = 5.89 days) and nest production rate of 1.143 (SE = 0.04) estimated from this study. Values in brackets indicate estimation with stratification of the surveyed area.
[M]Nest mean lifetime of days 73.3 (SE = 9.77) from [Marchesi et al., 1995] and nest production rate of 1 (SE = 0.0) from the general assumption.
[P]Nest mean lifetime of 45.9 days (SE = 3.6) and creation rate of 1.09 (SE = 0.05) both from [Plumptre & Reynolds, 1996].
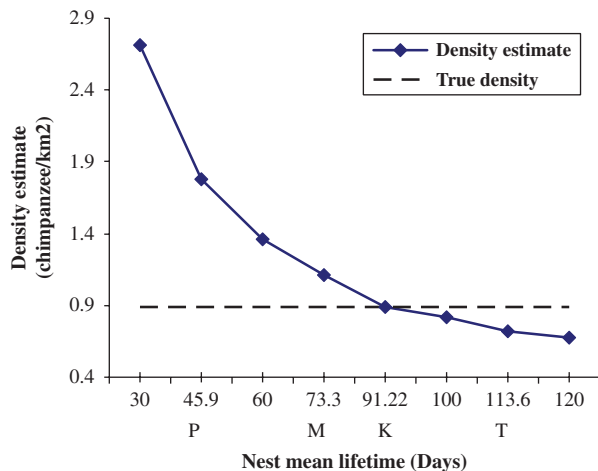
Fig. 3. Deviation from chimpanzee true density using different nest mean lifetime estimate. [K] nest mean lifetime of 91.22 days estimated from this study. [M] nest mean lifetime of 73.3 days estimated from [Marchesi et al., 1995]. [P] nest mean lifetime of 45.9 days estimated from [Plumptre & Reynolds, 1996]. [T] nest mean lifetime of 113.6 days estimated from [Tutin & Fernandez, 1984].

indicated that the MNC underestimate the abundance of chimpanzee, both survey methods produced approximately the same level of precision (difference between CV less than 5%) and similar accuracy, especially when the area size was estimated using the kernel method. Therefore, the true ape density estimated using the kernel method and conversion factors from this study was 0.89 chimpanzee/km^2.

In summary the conversion factors we estimated were sufficiently precise; consequently both survey methods were reliable in estimating chimpanzee densities.

DISCUSSION

The validation of two widely used survey methods is one important step in the continuing efforts of researchers to precisely document animal population size. The primary finding of this study was that nest counts on line transects produce reasonable ape density estimates as long as precise and unbiased conversion factors are used, and the survey is conducted in a way that fulfills the basic assumptions of distance sampling methodology [Buckland et al., 2001]. Indeed, we have shown that the true number of weaned chimpanzees lies between the 95% confidence limits of all estimates from both the MNC and the SCNC using site-specific estimates of nest production rate and nest decay time.

Conversion Factors

Second, using correct nest production rate increased our precision. We have shown that in Taï National Park each weaned chimpanzee produce 1.143 nests per day. These results confirm that

individuals do not build a single nest per day as revealed by Plumptre and Reynolds [1997] in Budongo forest, where nest production rate was 1.09. Furthermore, these two studies differed by 5% $(1.143–1.09)/1.09 = 0.048$. Thus, using the same estimate everywhere may induce a bias on the order of 5% or more.

Third, nest decay rates are more difficult to estimate. Traditionally, they were estimated by monitoring fresh nests until complete disappearance. Thus, the decay study was very time consuming and mean lifetime was derived from a relatively small sample size, as an exact decay time of each long-lived nest of chimpanzee had to be known (Examples, $n = 26$ for [Marchesi et al., 1995] and $n = 96$ for [Plumptre & Reynolds, 1996]). Our approach is an alternative methodology that estimates the functional relationship between environmental factors and the decay time of animal signs. The mean decay time is then estimated by integrating the estimated decay function rather than taking the average of sampled nests [Kuehl et al., 2007; Laing et al., 2003]. This approach does not require monitoring all nests until they decay completely and, thus, allows higher sample sizes. This gives a more representative sampling of nests in the survey area. Indeed, Hiby and Lovell [1991] showed that the contribution of decay rate estimation to overall variability in the animal abundance estimate is small if the number of monitored signs in the study area is on the order of 100.

In implementing this approach we faced the constraint that the relationships between ape nest survival and environmental covariates are not clearly understood [Mathewson et al., 2008]. We found that chimpanzee nest decay rate was related to nesting tree species, rainfall intensity, nest age, and nest height. Using a covariate modeling approach allowed us to estimate mean nest lifetime time (t) with precision ($t = 91.22$ days; CV = 6.46%) higher than in other chimpanzee nest decay studies for which errors around estimation where provided ($t = 73.3$ days; CV = 13.3% for [Marchesi et al., 1995] and $t = 45.9$ days; CV = 7.8% for [Plumptre & Reynolds, 1996]).

Nest age and rainfall have been previously used to predict gorilla nest survival [Walsh & White, 2005]. But unlike gorillas, chimpanzees commonly build nest in trees and ground nesting is rare, e.g. in the Nimba Mountains in Guinea [Koops et al., 2007]. Therefore, we think that nest decay rates may depend mainly on whether branches in the nest are completely broken or just bent. Consequently, we chose tree species as a predictor because the ability of apes to bend or to break branches for nesting might be related to wood density or other specific characteristics of each tree type [van Schaik et al., 1995]. Moreover, we used rainfall data from 3 months preceding the transect nest survey as an alternative to the retrospective method proposed by Laing et al.

[2003]. And, we repeatedly marked fresh nests so that the time to decay was estimated from nests built at different times of the year to overcome the problem of temporal heterogeneity in decay rate. Indeed, chimpanzee nest decay was not constant over time and these results confirmed the violation of the steady-state assumption [Plumptre & Harris, 1995; Walsh & White, 2005].

None of the variables alone (especially height) was a good predictor of decay (Table I). However, the results of chimpanzee density estimates (Table II) confirmed that the overall decay time we estimated was reliable. On the other hand the definition of when a nest has decayed is crucial and borrowing conversion factors from other sites (especially nest lifetime) without knowing this and using the same definition will cause errors in ape population estimates. Thus, although extrapolation of decay rate estimates from other studies provides rapid results, conclusions emerging from such studies might, unfortunately, have very little value for the management of apes.

In addition to the challenge of precisely estimating conversion factors, careful attentions to the survey design and field protocol were taken into account in order to obtain reliable estimate of chimpanzee density. We used three experienced observers searching for nests on and near the transect line, we carefully measured perpendicular distances using a tape measure, and transects line were randomly distributed in the study area. Therefore, the basic assumptions of distance sampling were likely to be met [Buckland et al., 2001].

Comparison of the SCNC and the MNC Methods: Implications for Management

Evaluation of survey methods is important in assessing the reliability of results used to make management and conservation decisions [Rusk et al., 2007]. Both nest counts methods have not been tested on chimpanzee communities of known size. This makes previous comparisons of both methods questionable [Devos et al., 2008; Hashimoto, 1995; Plumptre & Reynolds, 1996].

We found that the two methods did not differ considerably in terms of accuracy and precision, subject to the conditions we mentioned earlier in this discussion. The MNC showed the same level of estimate variation as the SCNC using the nest lifetime estimate derived from this study (Table I). We showed that the MNC method slightly underestimated ape densities. The 2-week time interval between transect visits was probably effective in not allowing nests to decay between visits. But all fresh nests on transect line may be not have been detected. However, for gorillas, which build nests with shorter lifetime, nests may decay during this period [Devos et al., 2008].

Although we did not evaluate the financial cost of each method during this study, it is indisputable that the SCNC are cheaper than the MNC, if one is able to shorten the decay study because only one passage of each transect is required for the former method. Indeed, in this study, survey effort during the MNC was 135.9 km, whereas only 45.3 km were walked for the SCNC. Therefore with the same amount of money, the SCNC count has the advantage of increasing survey coverage. For both survey methods, the optimal sampling effort necessary to return density estimates with acceptable precision should be estimated by carrying out a pilot study.

The decision regarding a choice of method may also be guided by other purposes of the survey. Illegal logging, deforestation and hunting pressure continue to occur in several tropical forests [Chapman & Lambert, 2000; Refisch & Kone, 2005]. Indirect survey methods may aim to examine the impacts of these activities on wildlife and the habitat in order to monitor population trends [Köndgen et al., 2008]. The MNC may be considered more appropriate in answering these questions because repeated visits to a site may provide more detailed observations of habitat quality. However, in the light of our results, we recommend to use the SCNC method by modeling nest decay that with equal accuracy is cheaper and allows surveying a large area of the protected zone. We agree with Laing et al. [2003] that it may be possible to predict nest lifespan in other sites using the modeling approach. But we recommend further research using this approach because of the probable differences in chimpanzee nesting tree species between sites. Models including other variables, for example, altitude, wood density and soil pH, should be investigated [Buij et al., 2003; van Schaik et al., 1995].

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