

# Distinguishing between the nests of sympatric chimpanzees and gorillas

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## Summary

**1.** Our current inability to estimate precisely the population sizes of chimpanzees and gorillas across much of the Congo Basin has been detrimental to the development of conservation strategies for the preservation of these endangered apes. Systematic counts of nests are currently the most commonly used method to estimate ape abundance, but distinguishing between the nests of sympatric chimpanzees and gorillas has proven to be an enduring obstacle to estimating species-specific abundance. In general, the builder of more than 75% of nests recorded during surveys is undetermined. We hypothesized that sleeping habits and nest building patterns would allow us to differentiate between the nests of these apes.

**2.** We constructed a predictive model using stepwise discriminant function analysis to determine characteristics that accurately distinguished between chimpanzee and gorilla nests. We analysed 13 variables associated with 3425 ape nests from three independent surveys conducted in the Goulougo Triangle of the Nouabalé-Ndoki National Park, Republic of Congo.

**3.** The model correctly classified more than 90% of nests in our validation subsample. Nest height, nest type, forest type and understorey closure were identified as important variables for distinguishing between chimpanzee and gorilla nests at this site. Attributing nests to either species increased the precision of resulting density estimates, which enhanced the statistical power to detect trends in population fluctuation.

**4.** Although specific variables may differ between study sites, we have demonstrated that predictive models to distinguish between the nests of sympatric chimpanzee and gorillas provide a promising approach to improving the quality of ape survey data.

**5. *Synthesis and applications.*** Our study introduces an innovative solution to the dilemma of discriminating between the nests of sympatric chimpanzees and gorillas, which increases the specificity and precision of resulting ape abundance estimates. There is an urgent need to improve methods to evaluate and monitor remaining ape populations across western and central Africa that are experiencing the imminent threats of emergent diseases, poaching and expanding human development. Increasing the quality of density estimates from field survey data will aid in the development of local conservation initiatives, national strategies and international policies on behalf of remaining ape populations.

*Key-words:* density estimate, discriminant function analysis, *Gorilla gorilla*, *Pan troglodytes*, precision, sympatric ape, transect survey

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### Introduction

With the rapid advancement of human development and the threat of emerging diseases, including Ebola hemorrhagic fever, it has become imperative to determine precisely the abundance of remaining ape populations in the Congo Basin. Despite more than 9000 km of cumulative survey effort in the range of the central subspecies of chimpanzee *Pan troglodytes troglodytes* and western lowland gorilla *Gorilla gorilla gorilla*, the numbers and distribution of apes in this region remain largely speculative (Tutin *et al.* 2005). Oates (2006) has shown that even largely unsubstantiated and unreliable population estimates may be cited in assessments of the international conservation status of these apes. Some of the problems in accurately assessing ape density estimates are associated with the fact that the most commonly employed methods involve counts of ape nests, rather than surveys of the apes themselves, who are elusive and often reside in dense forest habitats (Tutin *et al.* 1995; Plumptre & Reynolds 1997; Plumptre 2000; Morgan *et al.* 2006).

All great apes build nests that serve as resting or sleeping platforms. These nests are fashioned from herbs, twigs and/or branches that are bent or broken to form a cushion of vegetation that provides comfort, thermoregulation, protection from the elements and a

potential means of avoiding predators (Anderson 1984). The physical structure of the nests may persist for several months and provides a means of surveying ape populations over large spatial scales (Tutin & Fernandez 1984). Prior to Tutin *et al.*'s (1995) report that gorillas in Gabon frequently build nests in trees, it had been common practice in nest surveys of sympatric apes to attribute all arboreal nests to chimpanzees. However, this results in overestimation of chimpanzee abundance and underestimation of gorillas where their nesting behaviour intersects.

Improving methods to distinguish between the nests of sympatric chimpanzees and gorillas is important for estimating population sizes and implementing conservation strategies throughout their overlapping ranges, which encompass large areas of west and central Africa (Fig. 1). The aim of this study was to apply multivariate analysis to several explanatory variables describing nesting behaviours in order to distinguish between the nests of these sympatric apes. We then examined whether attribution of nests to species level improves the precision of resulting density estimates, which has implications for large-scale long-term population monitoring.

Although differences in the nest building behaviour of chimpanzee and gorillas have been described in the literature, confidently distinguishing between the nests

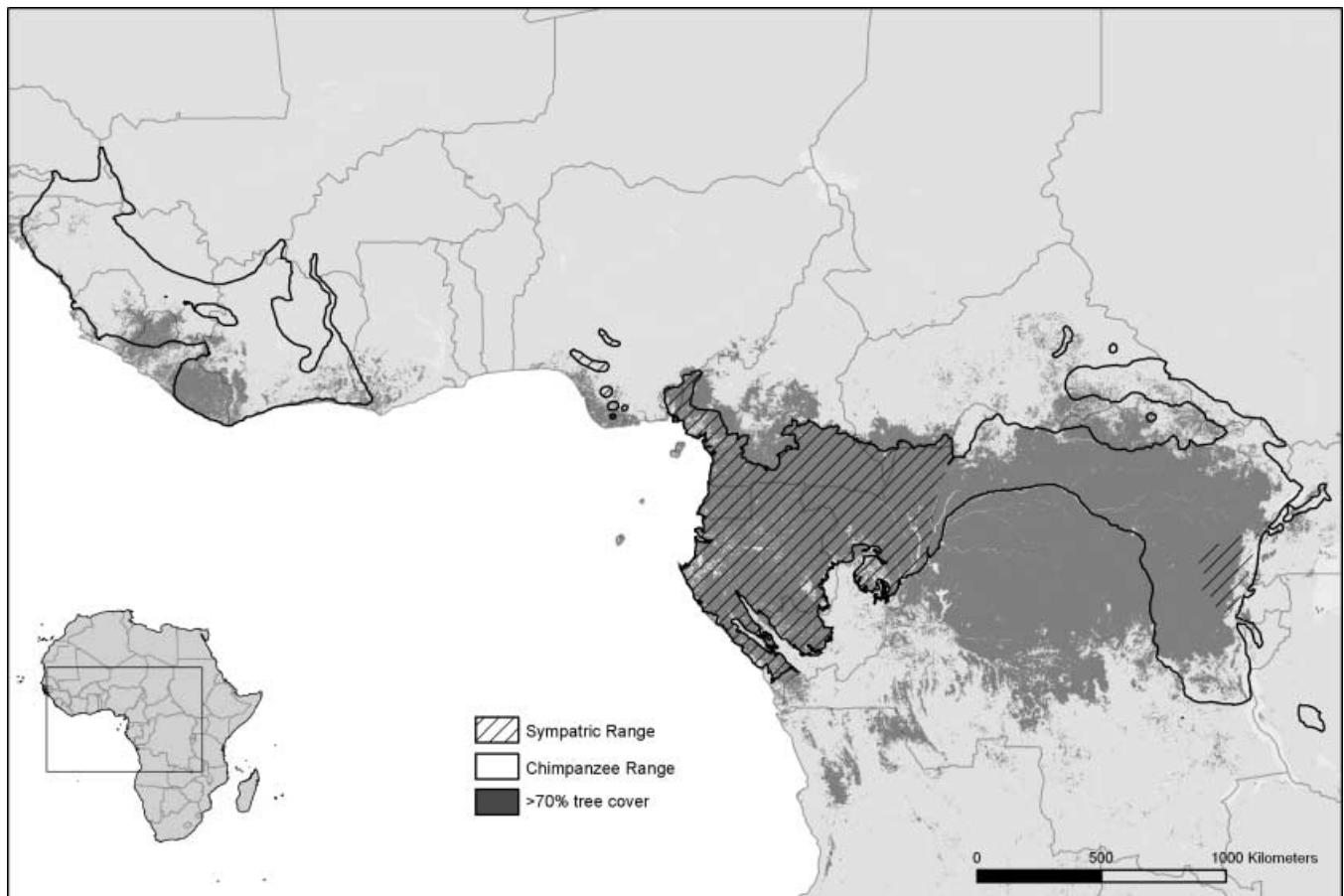


Fig. 1. Forest cover across Africa in relation to the distribution of wild chimpanzees and extent of overlap with sympatric gorillas.

of these species has proven difficult when verifying signs are not present. Associated ape signs (such as faeces, hair and knuckle prints) disappear much more rapidly than the actual nest structure, which may persist for several months (Tutin & Fernandez 1984). To attribute nests encountered on line transect surveys to either chimpanzee or gorillas, many researchers have adopted the definitions of Tutin & Fernandez (1984). These criteria include: (i) all nests on the ground are attributed to gorillas; (ii) all nests in trees closely associated with and the same age as nearby nests on the ground are attributed to gorillas; (iii) all nests above the height of 2 m in trees and not associated with ground nests are attributed to chimpanzees (Tutin & Fernandez 1984). Only nine nests (which represented 0.3% of their entire data set) were ambiguous and excluded from analysis, but they acknowledged that a proportion of arboreal gorilla nests was likely to be mistakenly attributed to chimpanzees during surveys (Tutin *et al.* 1995). Tutin *et al.* (1995) proposed a 26% correction factor based on the proportion of gorilla nest sites that consisted of arboreal nests only or would appear as arboreal sites after all ground nests had decayed. This correction factor has been widely applied to address the potential overestimation of chimpanzees at sites where they are sympatric with gorillas, but is based on a small sample size from a single study area and does not provide a means to distinguish individual ape nests.

Within the same context of distinguishing nests of sympatric apes in central Africa, Furuichi, Inagaki & Angoue-Ovono (1997) proposed a method for identifying nest builders by the physical characteristics of individual nests. They recorded the height and diameter of all nests encountered and examined the frequency distribution of values for identified chimpanzee and gorilla nests. Ape nests were assigned to a species using a composite method that involved evaluating whether the nest height and diameter were within the distributions characterizing known chimpanzee and gorilla nests. To examine the accuracy of their classification, shed hairs were collected from a subsample of accessible ape nests and differentiated using a scanning electron microscope. Only 8.3% of the validation subsample consisting of 36 nest sites (representing 140 individual nests) was misclassified by the composite method, which indicated the potential of using nest characteristics to identify nest builders.

We report the results of our efforts to develop, validate and apply a model using discriminant function analysis to distinguish between the nests of sympatric chimpanzees and gorillas encountered during surveys in the northern Republic of Congo. Our analysis was more comprehensive and rigorous than previous attempts to address this issue because we used a suite of variables associated with known chimpanzee and gorilla nests to construct a model to predict group membership of unassigned nests. Although specific variables may differ between habitats with different vegetative composition and structure, we show that using a statistical model to distinguish nest

builders provides a promising approach to improving ape survey methods. These results have direct implications for improving the precision of monitoring methods and sensitivity of trend detection, which are critical tools for ensuring the long-term survival of wild ape populations throughout much of equatorial Africa.

## Methods

### STUDY SITE

The Goualougo Triangle is located within the Nouabalé-Ndoki National Park (16°51'–16°56'N; 2°05'–3°03'E), Republic of Congo. It encompasses 380 km<sup>2</sup> of lowland forest, with altitudes ranging between 330 and 600 m. The climate can be described as transitional between the Congo equatorial and subequatorial climatic zones. Rainfall is bimodal, with a main rainy season from August to November and a short rainy season in May. Four habitat types were recognized in this study: mixed species forest, monodominant *Gilbertiodendron dewevrei* forest, *Gilbertiodendron* mixed species forest and swamp forest.

### DATA COLLECTION

All surveys consisted of distance sampling along systematically spaced line transects with a random start (Buckland *et al.* 2001; Thomas *et al.* 2005). Between November 2001 and July 2002, a standing crop (SC-2002) survey was conducted that consisted of 50 transects and 222 km of survey effort. Between September 2002 and July 2003, a marked nest study (MN-2003) was conducted that consisted of 38 transects and totalled 57 km. Between March and May 2004, another standing crop (SC-2004) survey was conducted that consisted of 29 transects totalling 106 km. The standing crop method requires that all nests are inventoried during a single passage, whereas the marked nest method involves initially marking all nests and then conducting repeated surveys to count new nests (Plumptre & Reynolds 1996; Furuichi, Hashimoto & Tashiro 2001).

Specific data recorded for each nest included: distance along transect; perpendicular distance from the transect line to the nest; height; forest type; understorey closure; tree species; and nest type (adopted from Tutin *et al.* 1995). In addition, each nest encountered was designated as built by chimpanzee or gorilla based on the presence of faeces, shed hair, odour and other signs associated with the nest that allowed us to attribute a subsample of nests to either ape species with certainty. Nests without verifying sign were classified as great ape. Nest sites were defined as all nests of the same age class within 50 m of one another.

### MODEL CONSTRUCTION

We used discriminant function analysis to construct a predictive model of nest builder identity based on a

combination of explanatory variables that best discriminated between chimpanzee and gorilla nests. Logistic regression is an alternative analysis method that can be used if the assumptions underlying discriminant function analysis are violated. Logistic regression requires larger data sets but deals better with unequal group sizes. We chose to use discriminant function analysis because of its efficiency and increased power, but also advocate the use of a well-fitted regression model as another option in this application. We performed forward stepwise canonical discriminant analysis on 13 variables and two groups. Models were based on a random sample of 70% of identified chimpanzee and gorilla nests. The remaining 30% of the original data set was used for model validation. Unless otherwise specified, statistics were calculated with SPSS 11.5 (SPSS Inc. 2002).

#### SELECTION OF PREDICTOR VARIABLES

Several candidate predictor or discriminating variables were included in the analysis. These included nest height, nest type, understorey closure, mixed species forest type and several tree species. Categorical variables were coded as dummy variables. A stepwise variable selection method was used to identify variables that best discriminated between nests of sympatric apes. Standardized canonical discriminant function coefficients were examined to determine the relative importance of each explanatory variable. These values indicated the order of importance by unique contribution of each explanatory variable.

#### DEFINITION OF CLASSIFICATION FUNCTION

The following classification function was used to calculate classification scores for ape nests:

$$S_i = w_{i1}x_1 + w_{i2}x_2 + \dots + w_{im}x_m + c_i$$

The subscript  $i$  denotes the group, either chimpanzee or gorilla. The subscripts 1, 2 ...  $m$  denote predictor variables and  $c_i$  is a constant for the  $i$ th group. Ape nests were assigned to either chimpanzees or gorillas based on Wilks' lambda. The probability of nest membership to either chimpanzees or gorillas was calculated for each nest site and the average scores for nests assigned to either species were greater than 90% for all surveys.

#### CLASSIFICATION EFFICIENCY AND MODEL STABILITY

Evaluation of the model's performance was based on the proportion of nests with known builders that were correctly assigned using the defined classification function. The efficiency of the model could be overestimated by using the same observations to construct and test the model, so we also tested the model separately against the validation subset (30% of original data set)

to determine its accuracy. In addition, a cross-validation jack-knife procedure was used to assess the stability of our model. This required classifying each case (nest) with a model derived from all other cases in the sample other than the particular case being assigned. The resulting coefficient of variation was used as an index of stability.

#### APE DENSITY ESTIMATION

Density estimates with their associated coefficients of variation and 95% confidence intervals were calculated using the DISTANCE 5 software (Thomas *et al.* 2005). Nest construction rates, identification of the ape species that built the nests and nest decay rates were used to convert standing-crop nest density estimates to absolute chimpanzee and gorilla densities, as described in Morgan *et al.* (2006). Calculating density estimates from marked nest surveys involved excluding nests encountered on the first passage and combining nest counts from all subsequent passages to calculate one density estimate (Plumptre & Reynolds 1996; Furuichi, Hashimoto & Tashiro 2001).

#### Results

During three surveys in the Goulougo Triangle study area conducted between 2001 and 2004, we encountered a total of 3425 individual ape nests comprising 1314 nest sites. Ape nests were frequently encountered along line transects throughout the study area, with an average encounter rate of  $7.79 \pm 2.49$  nests  $\text{km}^{-1}$ . However, nests attributable to either species with certainty were rare and more common for gorillas (0.71–2.33 nests  $\text{km}^{-1}$ ) than chimpanzees (0.22–0.42 nests  $\text{km}^{-1}$ ). The majority of nests in each of these data sets consisted of great ape nests (77.2% in SC-2002, 74.0% in the first passage of MN-2003, 83.9% in SC-2004) that were not attributable specifically to chimpanzees or gorillas. The repeated passages of the marked nest data set yielded a lower percentage of great ape nests (47.0%), which was expected as this type of survey is designed to encounter only fresh and recent nests. These new nests were more likely to be associated with species-specific verifying signs than the standing nests of all ages encountered in a one-off standing crop survey.

#### NEST TYPE

All chimpanzee nests were tree nests, whereas gorillas constructed more diverse nest types. Twenty-six per cent of gorilla nests were arboreal, and the rest were ground sleeping sites, with or without nest construction. The most common type of ground nest built by gorillas was herbaceous (45%), followed by woody nests (13%) and mixed nests (7%). Nests with minimum construction and bare earth sleeping sites each accounted for less than 5% of all individual gorilla nests.

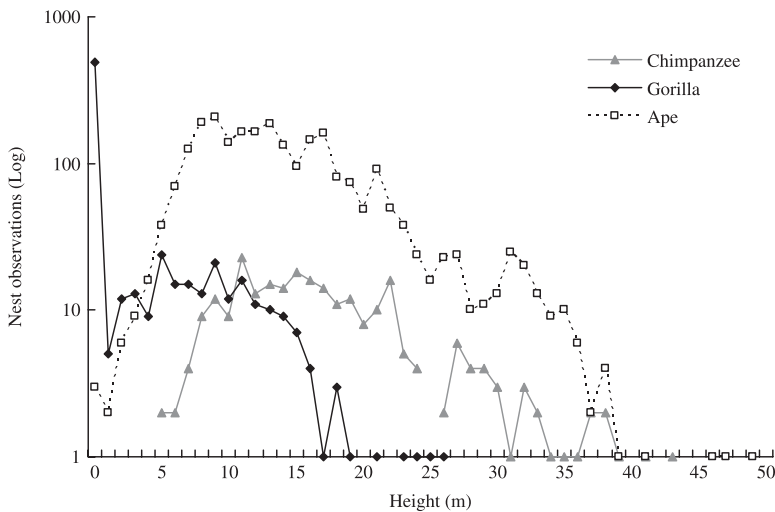


Fig. 2. Different height distributions of chimpanzee, gorilla and ape nests.

### NEST HEIGHT

Seventy-four per cent of gorilla nests were located on the ground, whereas all chimpanzee nests were arboreal. The average height for arboreal gorilla nests ( $9.6 \pm 4.6$  m,  $n = 175$ ) was significantly lower than the average height of chimpanzee nests ( $17.3 \pm 7.4$  m,  $n = 247$ ) ( $t = 12.3$ , d.f. = 420,  $P < 0.01$ ). Although the distributions of chimpanzee and gorilla nest heights diverged as shown in Fig. 2, there was a significant overlap in the nest heights of these species.

### HABITAT TYPE

Gorilla nests were found most often in mixed species forest (96% in SC-2002, 89% in MN-2003, 92% in SC-2004). Very few gorilla nests were located in *Gilbertiodendron* (1–9%) and flooded (1–7%) forest types. Chimpanzees frequently nested in both mixed species (49% in SC-2002, 58% in MN-2003, 58% in SC-2004) and *Gilbertiodendron* habitats (51% in SC-2002, 39% in MN-2003, 38% in SC-2004). Few

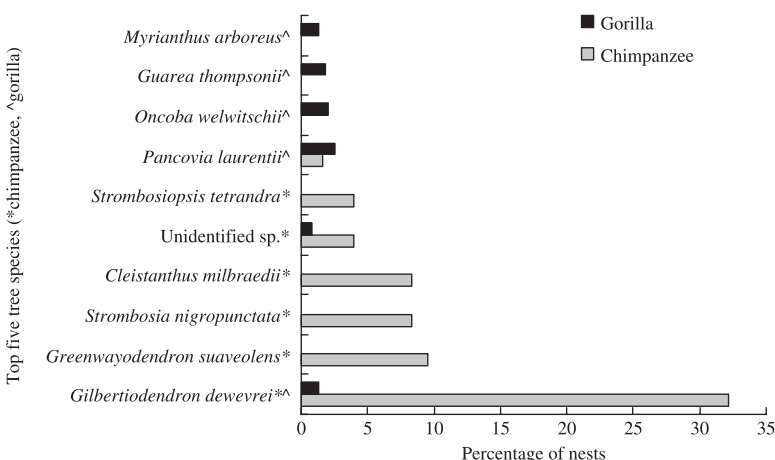


Fig. 4. Utilization of different tree species by chimpanzees and gorillas.

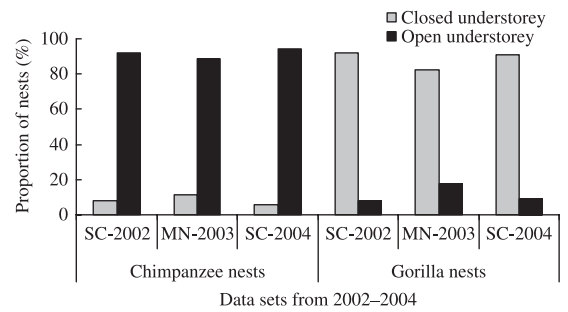


Fig. 3. Chimpanzee and gorilla nests located in closed and open understorey habitats during three transect studies.

chimpanzee nests were found in flooded forests (less than 4% of nests).

### FOREST UNDERSTOREY

There was a significant difference in nesting preferences for understorey closure by these sympatric apes (Mann–Whitney  $U = 0.0$ ,  $P < 0.05$ ). Gorillas consistently preferred nesting in closed understorey habitats, with 80–90% of their nests located in this habitat during each of the three surveys (Fig. 3). Less than 10% of chimpanzee nests were found in closed understorey habitats.

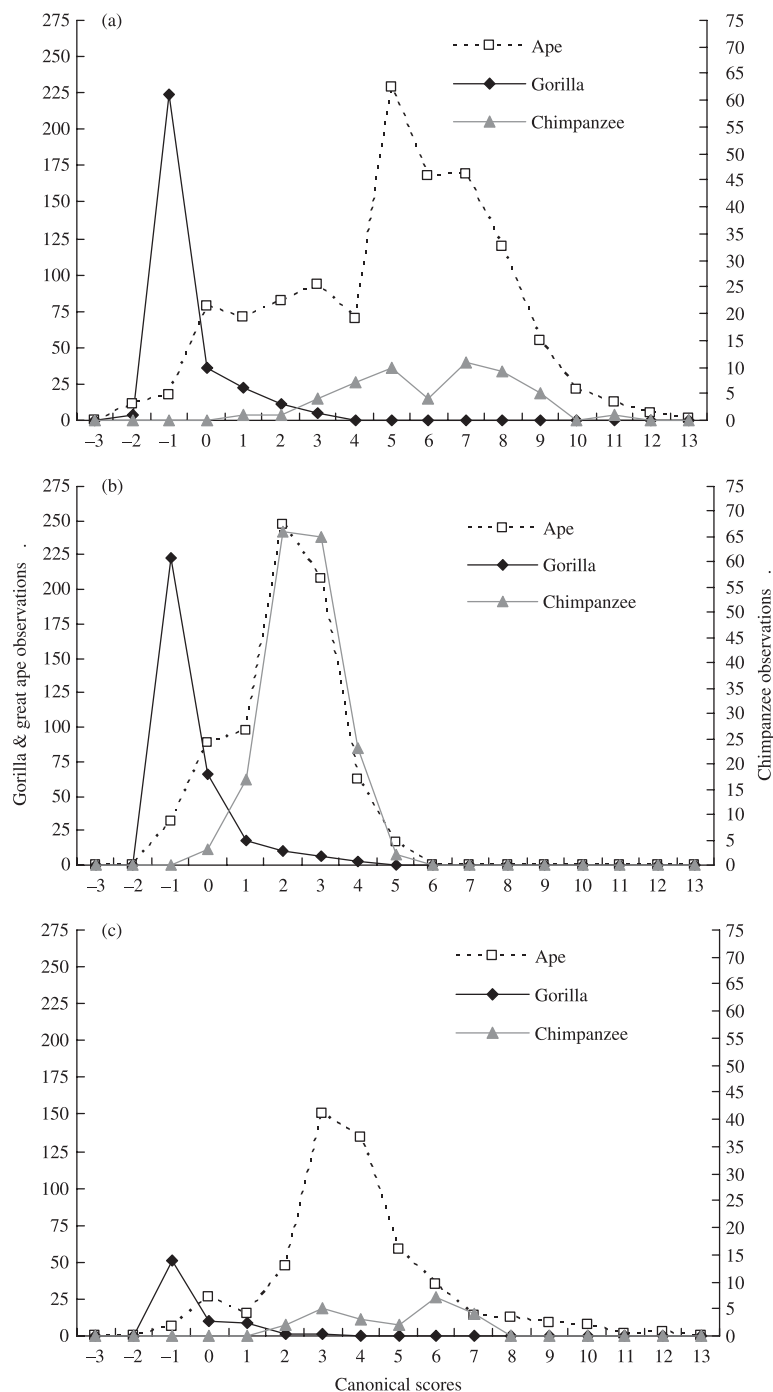
### TREE SPECIES

Chimpanzees and gorillas showed distinct preferences in their top five tree species used for nesting (Fig. 4). The top five tree species preferred by chimpanzees accounted for 62% of their nests, and the top 10 tree species harboured 76% of all chimpanzee nests. Gorillas were less consistent in their selection of arboreal nesting sites, with the top five tree species accounting for 9% of their nests and the top 10 for 13%.

### DISCRIMINANT FUNCTION ANALYSIS

Nest height, nest type, forest type and understorey were important variables for distinguishing chimpanzee and gorilla nests in the Goulougo Triangle. Figure 5 shows the distribution of canonical classification scores for known chimpanzee and gorilla nests, compared with unclassified great ape nests. Identified chimpanzee and gorilla nests in each data set produced distinct nest characteristic profiles that were used to assign great ape nests to either species. Although the SC-2004 data set had few chimpanzee nest observations, distinct species-specific nest distributions were still evident.

Results of the discriminant function analysis are shown in Table 1. The degree of success for accurate nest classification was high in each survey (Table 2). Each method of model evaluation yielded classification efficiency scores higher than 80%, with most exceeding 95%. As one would expect, classification scores were highest within the subset of data that was used to build the predictive model. However, the validation subset



**Fig. 5.** Canonical discriminant function results for (a) SC-2002, (b) MN-2003, and (c) SC-2004 data sets.

yielded only slightly lower scores for each survey, with overall accuracy above 90% for all three data sets. All cross-validation scores were above 90%, which indicated model stability. The detection functions for chimpanzee and gorilla nests were distinct (Fig. 6a,c), with gorilla nests being detected more often near the transect line. Comparison of the detection functions from nests attributed to either species with certainty and those classified from the discriminant function analysis were very similar (Fig. 6a,b for chimpanzees, Fig. 6c,d for gorillas).

Assignment of nests to either chimpanzees or gorillas using discriminant function analysis provided more specific and precise ape density estimates than unclassified data (Table 1). Confidence intervals were narrower for ape density estimates calculated from assigned nests. Ape densities calculated from raw data consistently produced very low chimpanzee-specific density estimates (0.1–0.6 chimpanzees  $\text{km}^{-2}$ ), with associated variation up to 63%, and seemingly underestimated gorilla densities (0.7–1.6 gorillas  $\text{km}^{-2}$ ). Unclassified raw data also produced a relatively high density of nests with an unknown builder (1.0–2.4 apes  $\text{km}^{-2}$ ). Application of discriminant function analysis to each data set yielded more specific density estimates (1.3–1.7 chimpanzees  $\text{km}^{-2}$ ; 1.1–2.4 gorillas  $\text{km}^{-2}$ ), with lower associated coefficients of variation.

## Discussion

There is an urgent need to increase the accuracy and precision of ape survey methods as a result of the myriad of threats facing wild chimpanzee and gorilla populations. To aid in addressing this situation, we have presented a new approach to distinguish between the nests of sympatric chimpanzees and gorillas which results in increased accuracy and precision of resulting ape abundance estimates. Discriminant function analysis was used to synthesize information about nest characteristics and build a predictive model to distinguish between the constructed nests of sympatric apes in the lowland forests of northern Congo. All classification efficiency measures indicated that this model was very accurate in correctly attributing nests to either chimpanzees or gorillas. Further, our results clearly indicated that density estimates calculated from data assigned to either species were more informative and had lower coefficients of variation than unclassified raw data sets. Post-hoc correction factors should be replaced by similar classification approaches such as discriminant function analysis and logistic regression. We advocate further refinements of methods to estimate mammal densities, as such innovations and improvements in survey methodology are essential for effective population monitoring (Walsh & White 1999; Plumptre 2000; Walsh *et al.* 2001).

Tutin *et al.* (1995) reported that the nesting behaviour of western lowland gorillas was more diverse than nest types built by sympatric chimpanzees. Chimpanzees built exclusively ‘tree’ nests that were located in the forest canopy, whereas gorillas built six different nest types that were stratified from the ground to the high canopy. We also found a strong contrast between the diverse nest types of gorillas and consistent arboreal nesting behaviour of chimpanzees. Gorillas in the Goulougo Triangle exhibited all six different types of nest construction defined by Tutin *et al.* (1995), with combinations of nest types found within a single nesting group. The majority of gorilla nests encountered on these transect surveys were constructed ground nests (72%), with less than 5% consisting of bare earth sleeping sites. However,

**Table 1.** Comparison of ape density estimates and associated variance calculated from raw data and data sets resulting from application of discriminant function analysis (DFA) to distinguish nests of sympatric chimpanzees and gorillas

Survey	Analysis	Ape species	Nests	Density (95% CI*) individuals km <sup>-2</sup>	CV† (%)
SC-2002		Chimpanzee‡¶	53	0.08 (0.05, 0.15)	30.6
		Gorilla§¶	302	1.28 (0.99, 1.65)	12.8
		Ape‡¶	1202	1.71 (1.44, 2.04)	8.8
	DFA	Chimpanzee‡¶	972	1.26 (1.03, 1.55)	10.2
		Gorilla§¶	576	1.75 (1.41, 2.15)	10.5
SC-2004		Chimpanzee‡¶	24	0.10 (0.03, 0.34)	62.6
		Gorilla§¶	75	0.66 (0.47, 0.93)	17.1
		Ape‡¶	515	1.62 (1.28, 2.06)	11.7
	DFA	Chimpanzee‡¶	447	1.32 (1.03, 1.68)	12.2
		Gorilla§¶	166	1.10 (0.81, 1.48)	15.2
MN-2003 first passage		Chimpanzee‡¶	24	0.08 (0.04, 0.16)	38.5
		Gorilla§¶	133	1.56 (0.89, 2.73)	28.4
		Ape‡¶	446	2.38 (1.80, 3.13)	13.8
	DFA	Chimpanzee‡¶	387	1.72 (1.31, 2.26)	13.7
		Gorilla§¶	210	2.44 (1.61, 3.70)	20.9
MN-2003 subsequent passages		Chimpanzee‡***	152	0.60 (0.39, 0.93)	21.9
		Gorilla§***	193	1.34 (0.86, 2.11)	22.6
		Ape‡***	306	1.04 (0.75, 1.45)	16.6
	DFA	Chimpanzee‡***	400	1.43 (1.05, 1.95)	15.4
		Gorilla§***	248	1.52 (1.02, 2.26)	19.9

\*Confidence interval; †coefficient of variation; ‡nest construction rate of 1.09 (SE = 0.05); §nest construction rate of 1.0; ¶nest decay rate of 90.0 days (SE = 2.85) from this site; \*\*\*nest decay rate conversion factor was replaced in marked nest density estimates by total time elapsed between the first and last passage.

**Table 2.** Classification efficiency score as depicted by percentage of sample correctly classified by discriminant function analysis

	Model sample (validation sample)			Model subset*			Validation subset†			Cross-validation‡		
	Chimp.	Gorilla	Variables	Overall	Chimp.	Gorilla	Overall	Chimp.	Gorilla	Overall	Chimp.	Gorilla
SC-2002	33 (20)	209 (92)	U, N, H, T	98.8	90.9	100	98.2	100	97.8	97.9	90.9	99.0
MN-2003	131 (45)	224 (102)	U, H, T	92.7	96.9	90.2	90.5	100	86.3	92.4	96.2	90.2
SC-2004	12 (11)	53 (19)	U, H, T	98.5	100	98.1	93.3	81.8	100	96.9	100	96.2

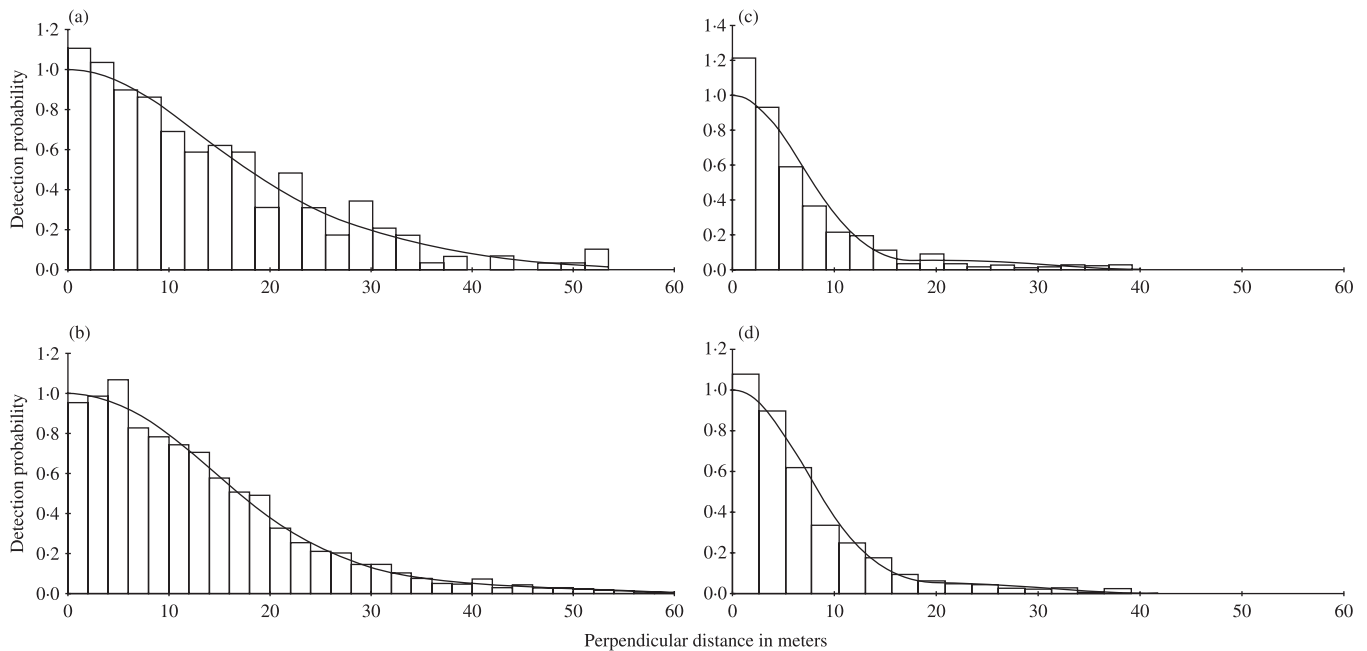
\*Seventy per cent of the original sample that was used to construct discriminant function analysis model; †remaining 30% of original sample used to validate model; ‡in cross-validation, each case is classified by the function derived from all cases other than that case; U, understorey; N, nest type; H, nest height; T, tree species.

studies of focal groups in this region have reported that gorillas frequently sleep on the ground with no nest construction (Mehlman & Doran 2002). There is considerable variation in the ground nesting behavior of gorillas (Yamagiwa 2001).

The tendency for western lowland gorillas to nest arboreally intersects with the nesting behaviour of sympatric chimpanzees in this region. Twenty-six per cent of gorilla nests in this study were arboreal. Similar results have been reported from other sites in central Africa: 41% of gorilla nests at Bai Hokou in Central African Republic and 35% of nests at Lopé Reserve in Gabon were arboreal (Remis 1993; Tutin *et al.* 1995). Tree nests without verifying signs are difficult to attribute

to either chimpanzees or gorillas with certainty, but differences in arboreal nesting behaviours between species have been cited in past literature (Furuichi, Inagaki & Angoue-Ovono 1997). For example, chimpanzee nests in the Goualougo tend to be higher off the ground than gorilla nests.

More than 90% of all gorilla nests were found in mixed species forest, which is similar to reports from Mondika in the Central African Republic, where 96% of gorilla nests were located in this forest type (Mehlman & Doran 2002). Gorillas in the Goualougo Triangle rarely nested in *Gilbertiodendron* forest, which comprises more than 20% of the study area. This forest type is also abundant at other sites in this region but rarely used by



**Fig. 6.** Observed perpendicular distances (bars) and fitted detection function (line) for nests attributed to (a) chimpanzees with certainty ( $n = 253$ ), (b) chimpanzees by discriminant function analysis ( $n = 2201$ ), (c) gorillas with certainty ( $n = 706$ ) and (d) gorillas by discriminant function analysis ( $n = 1199$ ).

gorillas for nesting (2% of nests at Mondika, 1% of nest sites at Bai Hokou; Remis 1993; Mehlman & Doran 2002). In contrast, chimpanzees utilized mixed species and monodominant *Gilbertiodendron* forest almost equally. Morgan *et al.* (2006) reported that chimpanzees showed a preference for nesting in *Gilbertiodendron* forest relative to its abundance. Chimpanzees and gorillas in the Goulougo Triangle were rarely observed in swamp forest, which is frequently used by gorillas in the nearby Likouala region of northern Congo (Blake *et al.* 1995; Poulsen & Clark 2004).

Gorillas showed an overwhelming preference for nesting in closed understorey habitats, whereas chimpanzees most often nested in open understorey habitats. Gorillas at several sites have shown a similar preference for closed understorey habitat, which often characterizes secondary forests (Tutin *et al.* 1995; Furuichi, Inagaki & Angoue-Ovono 1997; Basabose & Yamagiwa 2002). In contrast, chimpanzees have shown inclinations to feed and nest in primary forest (Plumptre & Reynolds 1994; Furuichi, Inagaki & Angoue-Ovono 1997; Basabose & Yamagiwa 2002). Chimpanzees in Uganda preferred nesting in trees that were most commonly found in primary forests (Hashimoto 1995; Brownlow *et al.* 2001). This observation is relevant to this region, where several tree species used by chimpanzees for nesting are specific to certain habitat types, found at low densities and exploited for timber.

We have demonstrated that predictive models to distinguish between the nests of sympatric chimpanzee and gorilla provide a promising approach to improving the quality of ape survey data. Attributing nests to either species increases the precision of resulting density estimates, which enhances the statistical power to

detect trends in population fluctuation. As would be expected with the use of qualitative variables, some assumptions of the discriminant function analysis were violated so we conducted a parallel analysis using logistic regression with fewer underlying assumptions to compare the classification efficacy of the two models (Press & Wilson 1978). Logistic regression was more than 90% accurate in its classification of validation subsets and used a similar suite of variables to discriminate between chimpanzee and gorilla nests for all three data sets. The strong similarity in results produced by these two approaches further supports our conclusion that carefully selected variables can effectively distinguish between chimpanzee and gorilla nests.

We recommend the extended application of classification models in nest discrimination to other sites with sympatric apes, but predict that specific variables will differ between sites with different habitat types, vegetative composition and faunal complement of large mammals. Data on nest characteristics of sympatric apes should be collected at each site and multivariate analysis used to identify site-specific variables with strong discriminating power. Our results suggest that candidate variables include nest height, nest type, habitat type, understorey closure and vegetation used to build the nest. We hope that the results of this study will encourage further refinement of existing survey methods and development of new techniques to monitor ape populations more effectively.

Estimating the size and status of sympatric chimpanzee and gorilla populations has proven a daunting charge for conservation managers and scientists working across western and central equatorial Africa. Scientific review of survey methods and enhancement of analytical tools

will increase our effectiveness in monitoring populations. There is urgency in the need for such improved approaches, as sudden and dramatic declines of chimpanzees and gorillas are occurring throughout the Congo Basin as a result of emerging diseases, poaching associated with the illegal bush meat trade and rapidly expanding human development (Huijbregts *et al.* 2003; Walsh *et al.* 2003). Increasing the accuracy and precision of survey methods will have an immense impact on preserving chimpanzee and gorilla populations, as development of effective conservation strategies and government policies are dependent upon reliable monitoring of these apes.

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